

**“Diversity and evolution of pteridophytes,  
with emphasis on the Neotropics”**

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## DISCLAIMER

The chapters of this thesis are designed as manuscripts suitable for direct submission. If a decision has already been made, formatting follows the guidelines of the respective journal in which the publication is planned.

All new species names and combinations in this thesis are considered as provisional. They will be validly published later in peer-reviewed journals.

Contribution of the doctorate candidate **Marcus Lehnert** to the chapters presented in this thesis:

### **I.1. Novelties of Cyatheaceae from the Neotropics.**

Concept: 100%

Gathering of data: 100%

Evaluation: 100%

Writing: 100%

### **I.2. On the identification of *Cyathea pallescens* (Sodirol) Domin (Cyatheaceae): the truth and its consequences.**

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## Summary

Pteridophytes, understood as taxonomic group containing ferns, horsetails, and clubmosses, are especially diverse and abundant in the tropical mountain ranges of South America. My work aims to understand better the diversity of these plants, how they have evolved, and how they function in the ecosystems.

Tree ferns are conspicuous elements of tropical montane rainforest. About 200 species of scaly tree ferns of the family Cyatheaceae occur in the Neotropics, ranging from small trunkless ferns of rocky outcrops to almost 20 m tall giants in dense forests. My work on these plants led to the recognition of 19 new and several formerly synonymized species in the genera *Alsophila* and *Cyathea*. The confusing nomenclature of the family was partially clarified by the correction of the typification of *Cyathea pallescens* (Sodirol) Domin. A checklist with keys to the Bolivian tree ferns was also accomplished during these studies.

The revision of the genus *Melpomene* revealed 27 species with 10 varieties, most of them small ferns with deeply pinnatifid fronds, which are mostly epiphytes in upper montane forests or characteristic terrestrial elements of treeless páramo vegetation. The phylogenetic analysis based on morphology and chloroplast DNA shows that this genus as currently morphologically circumscribed is monophyletic and originated in South America. The radiation of the core group is apparently directly connected with the uplift of the northern Andes, which is the center of diversity of this genus.

My ecologically orientated field studies of fern communities in southern Ecuador initiated several projects that aimed on different aspects. I found 248 different species of pteridophytes in our main study area, the Reserva Biológica San Francisco (RBSF), Prov. Zamora-Chinchipe, but this number is likely to increase in the future. The study area is part of the Amotape-Huancabamba zone, a stretch of low elevation in the Andes located at the overlap of several biogeographic subunits and thus rich in endemic and widespread species alike. I found that the upper limit in the elevational distribution of most of the widespread ferns follows this dent in the mountain range, indicating that probably a downward shift of all vegetation belts may be found.

The mountain ridges in the RBSF support a unique heath forest dominated by the otherwise rare tree *Purdiaea nutans* Planch., but these peculiarities are not reflected in the fern composition. Ridge habitats in the study area, including two comparative sites close to the RBSF, are less diverse than adjacent slopes, and there was no higher representation of localized species on ridges. Overall, widespread species were weakly but significantly more

abundant than localized species, and terrestrial – but not epiphytic – species were more abundant on ridges compared to slopes.

The observed influence of soils on the distribution of ferns in the Ecuadorian study area, where terrestrial and phylogenetically more derived taxa increase in diversity along a nutrient gradient caused by a downhill flux from the ridges to the gorges, encouraged me to look at the soil preferences of pteridophytes worldwide and see if it contains a phylogenetic signal. It seems that more derived lineages are better represented on rich soils, but have also a higher percentage of epiphytes. Looking at the mediator between soils and plant roots, the mycorrhizal fungi, I found that the published reports cover only a small fraction of the fern diversity and often give contradicting results. Focusing on neglected taxa, like the epiphytic Hymenophyllaceae, grammitid ferns (Polypodiaceae), and the genus *Elaphoglossum* (Dryopteridaceae), the investigation of root samples gathered in the Ecuadorian study area increased the known number of fern species with ascomycete infection considerably. The finding of this more derived type of mycorrhiza is in concordance with the phylogenetic position and life form of the host plants. Terrestrial and especially phylogenetically basal groups of pteridophytes have predominantly vesicular-arbuscular mycorrhiza, which is a very common and supposedly old form symbiosis.

### **Zusammenfassung**

Pteridophyten, zu denen hier Farne, Schachtelhalme und Bärlappgewächse gerechnet werden, sind besonders divers und üppig in den tropischen Gebirgen Südamerikas. Meine hier vorliegende Arbeit zielt darauf ab, die Diversität dieser Pflanzen besser zu verstehen, wie sie sich entwickelt hat und was ihre Funktion im Ökosystem ist.

Baumfarne sind auffällige Elemente des tropischen Bergregenwaldes. Ungefähr 200 Arten der schuppigen Baumfarne aus der Familie Cyatheaceae kommen in den Neotropen vor, vom kleinen stammlosen Farnen auf Blockhalden bis zum 20 m hohen Giganten in dichten Wäldern. Meine Arbeit an dieser Gruppe führte zur Erkennung 19 neuer und ehemals als Synonym geführter Arten aus den Gattungen *Alsophila* und *Cyathea*. Die verwirrende Nomenklatur wurde durch die korrekte Typisierung der *Cyathea pallescens* (Sodirol) Domin teilweise bereinigt. Ferner wurde eine aktuelle Checkliste der Baumfarne Boliviens im Rahmen dieser Dissertation erstellt.

Die Revision der Gattung *Melpomene* zeigte, dass sie 27 Arten mit 10 Varietäten umfasst, welche vornehmlich kleine Farne mit fiederschnittigen Wedeln sind und häufig als

Epiphyten oder charakteristische Elemente in Paramovegetation wachsen. Eine phylogenetische Analyse, die auf Morphologie und Chloroplasten-DNA basierte, zeigt, dass die Gattung so, wie sie morphologisch umschrieben wurde, monophyletisch ist und höchstwahrscheinlich in Südamerika entstanden ist. Die Evolution der Kerngruppe ist anscheinend direkt mit der Anhebung der Anden, die heute das Diversitätszentrum der Gattung sind, verbunden.

Die ökologisch orientierten Feldstudien an Farngemeinschaften im Süden Ecuadors waren Ausgangspunkt für verschieden gestaltete Analysen. Insgesamt wurden 248 Arten im Hauptuntersuchungsgebiet, der Reserva Biológica San Francisco (RBSF), Prov. Zamora-Chinchipec, gefunden, aber diese Zahl wird sich wahrscheinlich in Zukunft noch nach oben bewegen. Dieses Areal befindet sich in der Amotape-Huancabamba-Region, einem sehr niedrigem Abschnitt der Anden, der das Überlappungsgebiet vieler biogeografischer Einheiten darstellt und daher sehr artenreich ist. Ein Vergleich der oberen Verbreitungsgrenzen weit verbreiteter Farne zeigt, dass diese dem allgemein niedrigeren Verlauf der Gebirgszüge unten in der Amotape-Huancabamba-Region folgen. Dies kann man als Indiz für eine Verschiebung der Vegetationszonen nach sehen.

Die Grate in der RBSF weisen einen einzigartigen Heidewald auf, der vom sonst seltenen Baum *Purdiaea nutans* Planch. dominiert wird. Diese Besonderheiten spiegeln sich allerdings nicht in der Farnkomposition wider. Grathabitats in den untersuchten Gebieten, zu denen auch zwei Vergleichsstandorte nahe der RBSF zählen, sind generell weniger divers als die angrenzenden Hänge und beherbergen nicht sonderlich viele endemische Arten. Generell sind weit verbreitete Arten wenig aber signifikant zahlreicher als Arten mit kleinem Verbreitungsareal, und terrestrische, jedoch nicht epiphytische Arten waren auf den Graten individuenreicher als auf den Hängen.

Der beobachtete Einfluss des Bodens auf die Verbreitung der Farne innerhalb des Untersuchungsgebietes, in dem terrestrische und phylogenetisch abgeleitete Arten entlang eines bergab gerichteten Flusses von Nährstoffen zunehmen, ermunterte mich, dies bei den Farnen weltweit zu studieren und nach einem phylogenetischen Signal zu suchen. Abgeleitete Farngruppen haben eine höhere Zahl an Arten, die auf nährstoffreichen Böden wachsen, aber auch an Arten, die epiphytisch wachsen. Bei den „Mittelsmännern“ zwischen Böden und Wurzel, den Mykorrhizapilzen, fand ich, dass diese in bisherigen Studien nur bei einem geringen Bruchteil der Farndiversität untersucht wurden, oft mit widersprüchlichen Ergebnissen. Meine eigenen Untersuchungen an im Süden Ecuadors gesammelter Wurzelproben bisher vernachlässigter Gruppen wie den epiphytischen Hyemnophyllaceen,

den grammitoiden Farnen (Polypodiaceae) und der Gattung *Elaphoglossum* (Dryopteridaceae) führte zu einer beträchtlichen Zunahme der bekannten Ascomyceteninfektionen bei den Farnen. Das Vorkommen dieser abgeleiteten Mykorrhizatyps stimmt mit der phylogenetischen Position und Lebensweise der Wirtspflanzen überein, denn bei terrestrischen und phylogenetisch basalen Gruppen herrscht die vesikulär-arbuskuläre Mykorrhiza vor, die eine weit verbreitete und anscheinend sehr alte Form der Symbiose ist.





## GENERAL INTRODUCTION & OUTLINE

A fern frond is one of nature's most elegant creations. First, it is a bud of constant proportions that hides its beginning while unfolding; when fully extended it can be a green lace of elegant complexity in the shade, composed of recurring geometrical patterns; or it can be a simple leaf, undivided, tough, and withstanding the full sun.

Pteridologists are fortunate to have this variety in the fronds among the different species of ferns and fern allies because a frond is in most cases all they have to work with. Other useful characters like scaly petioles and rhizomes are often lacking or worn in the old collections. Today the importance of these parts is known and collecting them has become standard. With this new information and the possibility of molecular analysis, the taxonomy of the pteridophytes has been pushed forward to a more natural system in the last few decades.

There are some peculiarities one must consider when working with ferns. Reproductive organs, like blossoms, on which the systematics of Angiosperms heavily depends, are not present in the plants we know as ferns. Their sexual generation is a separate diminutive plant, the prothallium, characterized by a great uniformity within the larger taxonomic groups. The only traces of sexuality in a fern are the sporangia, arranged in differently shaped sori, which ultimately release the spores that develop into the prothallia. In many cases, these sori are born on unspecialized, green fronds that are kept for a longer time; in the cases where sori are born in special fronds or frond parts, these persist longer than the typical flower. Thus pteridologists are free of the obligation to wait for flowering time; they can usually acquire all taxonomically important characters whenever they collect their plants.

Moreover, ferns are independent from insects and other animals for reproduction and dispersal. The spores are distributed by wind; once they land on a suitable site, they need only water to fulfill the life cycle. Consequently, ferns do presumably reflect the abiotic conditions of the environment they inhabit more directly than do most seed plants, one should assume. Also, the fern distribution across a continent should be more uniform than that of seed plants because of their easy dispersal. Yet it is easily observed and long known that ferns follow principally the same patterns in distribution as do seed plants. Endemic ferns can be found not only on isolated islands, but also in continuous stretches of a given geographic unit, e.g., the Andes. Sometimes a species shows gaps in its distribution and is missing over wide distances although the conditions of the area appear suitable for its existence. Reasons may be historical

(extinction, long distance dispersal) or of ecological nature (competition, succession, human influence). For ferns, most explanations are less plausible than for other plant groups.

In the following three chapters I will try to address and explore these topics. My studies focused on the Andes, the largest continuous mountain range in the tropics, where fern diversity is high and evolutionally young. Because the major part of the Andes has experienced its final uplift in geologically recent history, and because most fern species are restricted to mountainous areas, the majority of the species must have evolved accordingly in a similar short period, including phylogenetically old lineages in the same manner as derived ones.

I chose the tree fern family Cyatheaceae and the genus *Melpomene* of the polygrammoid ferns as case studies for the taxonomic and phylogenetic topics discussed in chapter I. These groups also exemplify the biogeographic aspect of chapter II, which is then widened to encompass the fern assemblage in southern Ecuador. For the ferns of this area, not only is the spatial distribution considered but also the altitudinal zonation. In chapter III, I look at the ecology of ferns, with an emphasis on the different types of substrates and the important mediator between root and substrate, the mycorrhizal fungi.

## Chapter I

### **Ferns as species: systematics and phylogeny**

“Móhala maka’í ke oho o ke kupu kupu.”

*Unfolded well are the fronds of the ferns.*

Hawaiian proverb, from *Ólelo No’eau*.

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**W**hat is a species? - This is still a pressing question among taxonomists (Mayr, 1957a, b; Dade, 1995; Luckow, 1995; McDade, 1995). Species are not constant; there is seen (i.e., morphological) and unseen (i.e., genetic) variation among individuals, which is changing over time (e.g., aging, adaptation, evolution). Among the different species concepts that have been devised to cope with this situation, the morphological and the biological species concepts are the best known. The morphological concept unites all individuals that are matching in certain morphological and behavioral traits within specific limits. The advantage is that one does not necessarily need the whole population of the species in question. A morphological species may be identified by only one specimen, and may be characterized by the comparison with single representatives of other related species. The disadvantage is that one always draws a subjective line between the character states, which may not always be sharply set. The biological species concept unites all individuals that may potentially interbreed and produce fertile offspring (i.e., they form a gene pool) (Mayr, 1957a, b). This concept also separates taxa that are morphologically identical but are not genetically compatible (e.g., apomicts) and vice versa (e.g., dimorphic gender). However, testing this hypothesis unambiguously would mean to cross all individuals and check if their offspring are fertile. In the case of metazoans and seed plants, data of such expressiveness can be approximately gained by simple field observations. Successful mating and transfer of sperm or pollen can be seen as evidence for genetic compatibility (i.e., reticulation). In animals this is often achieved by innate behavior; among seed plants, there are many strategies aimed at avoiding cross-pollination between incompatible individuals, like different flowering times, flower anatomy, and pollinators.

If the behavioral or anatomical separation between species fails, the genetic barrier between them will become visible either by the failure of the development of the zygote (i.e., abortion) or by the sterility of the offspring (Rieseberg et al., 2005). The latter hybrids are troublesome because they are usually morphologically intermediate to their parents. If they occur regularly, they may be mistaken for a discrete species (hybrid swarms). Sometimes, especially among plants, they overcome their genetic constraints (i.e., uneven chromosome number, missing alleles), are stabilized (e.g., by polyploidy), and form a new species, which is then not crossable with its ancestors.

In ferns, there is not easy approach to test the biological species concept. The reproductive stages, the prothallia, are separate from the sporophyte. They are small, inconspicuous, have fewer morphological characters than the sporophyte, and may not be assigned unambiguously to a species. This means that even if prothallia are found in the wild,

they may not be useful for testing the compatibility between morphologically distinct sporophytes one may find nearby. Mendelian crossing experiments may be conducted in vitro, but fertilization paths are not as easily traceable as in seed plants with their pollen: the sperm cells of pteridophytes reach the egg cell by active motion in a water film and their direction can hardly be controlled (Kubitzki et al., 1997). Prior fixing of the gender in the prothallia by the antheridiogen method still leaves a greater chance of unwanted fertilization paths to occur (Kubitzki et al., 1997). Even if favoring the biological species concept, fern taxonomists (like most taxonomist do) have to rely on morphology as a first basis for the definition of species.

Many other species concepts have been conceived of and discussed in the past fifty years (Luckow, 1995), roughly falling into two categories, mechanical and historical species concepts. Mechanical concepts like the biological and ecological species concepts see species as active players in the evolutionary process, and are often criticized as being not testable (Luckow, 1995). Historical species concepts, on the other hand, regard species as preliminary endpoints of evolutionary lineages. Most of these concepts are based on the theories of Hennigian cladistics (Hennig, 1979), either allowing or denying monophyly to species (Luckow, 1995). One of them, the phylogenetic species concept (Luckow, 1995, and references therein) is favored here. It sees species as the smallest diagnosable units, united by the set of constant character states (Olmstead, 1995). It agrees with the biological species concept in allowing reticulation only within species but it does not necessarily connect this to genetic isolation (Luckow, 1995).

The two fern groups exemplify the needs for both morphological and phylogenetic analysis at the species level. The tree ferns of the family Cyatheaceae comprise about 200 neotropical species and have been collected frequently but fragmentarily in the past, omitting such important characters like the scaly petiole and descriptions of the trunks. Thus, the delimitation of many tree fern species had remained uncertain about for a long time. Despite a large-scale revision of the neotropical species of this group in the seventies and eighties of the last century, there are still new species to be discovered (chapter I.1.) and many nomenclatural changes to be made (I.2.), based solely on a new evaluation of known morphological characters. Opposed to the tree fern lineage is the phylogenetically young family Polypodiaceae (Pryer et al., 2004; Schneider et al., 2004). However, in both families, we can observe a high species number in the Andes, indicating an adaptive radiation subsequent to the final uplift of the geologically young mountain range. The fern genus *Melpomene* (Polypodiaceae) is well represented in the mountain regions of South America and comprises 27 species, which are mostly small epiphytes (chapter I.3.). The morphological differences

among the species are often weak and ambiguous, and even most genetic data give only an unsatisfactory resolution between the species (chapter I.4.), underlining active evolutionary processes occurring in this genus.

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## I.1. Novelties of Cyatheaceae from the Neotropics

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**Abstract:** Following species of Cyatheaceae are described for the Neotropics: **Alsophila conantiana** Lehnert, **Cyathea brucei** Lehnert, **C. moranii** Lehnert, **C. obnoxia** Lehnert, **C. plicata** Lehnert, **C. sylvatica** Lehnert, **C. aemula** Lehnert, **C. ars** Lehnert, **C. chontilla** Lehnert, **C. convergens** Lehnert, **C. diabolica** Lehnert, **C. guentheriana** Lehnert, **C. nephele** Lehnert, **C. oxapampana** Lehnert, **C. polliculi** Lehnert, and **C. praetermissa** Lehnert.

Keywords: Andes, *Alsophila*, *Cyathea*, Neotropics.

## Introduction

The pteridophyte flora of the Andes is one of the richest in the world (Tryon & Tryon, 1982). Even though frequently collected and studied (Tryon 1970, 1971, 1976, 1986; Tryon & Stolze 1989; Gastony 1973; Stolze 1974; Barrington 1978; Conant 1983), new discoveries are still being made in the scaly tree ferns (Cyatheaceae; Smith, 1990, 2006; Moran, 1991, 1995a; León & Moran, 1996; Moran & Øllgaard, 1998; Lehnert, 2002, 2003, 2004, 2005, 2006a, b; Murillo & Murillo, 2003). The complex taxonomy of the tree ferns, fragmentary collections, inadequate descriptions, and special descriptive vocabulary all contribute to our poor knowledge of this group. Hence, the list of published names is vast as many widespread species have been described several times, based mainly upon the distances between the collection sites and not because of convincing differences in morphology. Tryon (1976) and his students recognized this and synonymized many names for some widespread and rather variable species; yet they had only a relatively small number of specimens at hand. Character variability had been poorly understood, and distributions often showed large gaps. Today, with more extensive collection activity, specimens are sufficient to better display distribution and variability of most species. These advances enable us to resurrect some species that had been united with others; they also allow us to recognize new species.

Invaluable starting points for taxonomic studies are regional floras and checklists, which are like a roadmap for field trips. The authors often incorporate valuable additional information about consistency and regional or ecological variability in the morphology of the species. Good floral treatments covering tree ferns are available for Mesoamerica (Moran & Riba, 1998), especially Guatemala (Stolze, 1979), Costa Rica (Rojas, 1999; Rutherford, 2000), and Mexico (Mickel & Beitel, 1988; Mickel & Smith, 2004), the Chocó region (Lellinger, 1987), and the Caribbean (Proctor, 1985, 1989). The treatments for Ecuador (Tryon, 1986), Peru (Tryon & Stolze, 1989), and Bolivia (Killeen et al., 1993) are already outdated because species number has increased significantly (León-Yanez et al., 1993; Smith et al., 2005; Kessler & Smith, in prep.) and the concept of the used genera has changed since their publication.

There have been conflicting generic systems in the past (Holttum, 1963; Tryon, 1970; Lellinger, 1987) recognizing one to six genera, but recent phylogenetic studies of the tree fern alliance indicate that five natural groups of Cyatheaceae occur in South America that may be recognized as genera (Korall et al., 2006). Surprisingly, the monogeneric Hymenophyllopsiaceae, long suspected to be related to Cyatheaceae (Kramer & Green, 1995), nests within the neotropical clade of *Cyathea* in the strict sense (Lellinger, 1987;



Korall et al. 2006). The species of *Hymenophyllopsis* have yet not been transferred into *Cyathea*, but because all of them are restricted to the tepuis of the Guayana Highland, this has no impact on the present study, which focuses on the Andes. It is more important to point out here that the species of *Nephelea* (Gastony, 1973) are included in *Alsophila* (Conant, 1983), and those of *Trichipteris* (Barrington, 1978) as well as some of *Sphaeropteris* (Windisch, 1977, 1978) have been transferred to *Cyathea* (Lellinger, 1987). The phylogenetic studies, which support these measures, also strongly suggest the incorporation of *Cnemidaria* (Stolze, 1974) in *Cyathea*. The new species reported here would have been placed in *Nephelea*, *Trichipteris*, or *Cyathea* in Tryon's system (1970).

Following is a summary of unpublished and recently published new species in the genera *Alsophila* and *Cyathea*, which I have discovered in the course of the revision of the neotropical Cyatheaceae.

### Materials and Methods

Specimens studied included collections I made in Ecuador, Peru, and Bolivia deposited at UC and GOET; additional duplicates are deposited at the main herbaria of the respective countries (LPB, QCA, USM). I screened collections at NY and US personally for types and interesting specimens during visits in October 2006. Loans were made available by GH, F, MO, NY, and US, during my stay at the herbarium UC, University of California, Berkeley from August 2006 to May 2007. Several other herbaria have been visited or have provided loans over the past seven years, e.g., AAU, B, BM, COL, and P.

### Systematic treatment

***Alsophila conantiana*** Lehnert, Org. Divers. Evol. 6: 321; Electr. Suppl. 13: 1. 2006. Type: ECUADOR. Zamora-Chinchiipe: new road Loja - Zamora, ca. 4 km E of pass *El Tiro*, ridge from white cross on left road side (towards the valley), study plot C6, 03°59'S, 79°08'W, 2500-2600 m, 07 Oct 2004, *Lehnert 1415* (holotype: GOET, isotypes: LOJA, QCA, UC).

(Fig.1)

*Ab Alsophila erinacea* (H. Karst.) D. S. Conant *laminis valde tripinnatis indusiisque subsphaeropteroides* (vs. *bipinnato-pinnatifidis vel parce tripinnatis et indusiis cyatheoideis*

*urceolatisque vel subsphaeropteroideis cum orificio latiore), ab A. salvinii Hook., A. polystichoide H. Christ et A. tryoniana (Gastony) D. S. Conant in presentia indusiorum firmorum persitentiumque (vs. indusiis tenuis fragilibusque vel absentia indusiorum) absentiaque alarum in parte distale pinnarum differt.*

**Etymology:** This species is named for David S. Conant, Lyndon State College, Vermont, to honor his work on Cyatheaceae and especially *Alsophila*, from which my studies have greatly benefitted.

*Trunks* to 4 m high and 11 cm diam., densely covered with thin lanceolate scales to 15 mm long, with black squaminate spines 6-11 mm long, without old petiole bases, frond scars small, round, and hardly visible between the scales; trunk apices overtopping the youngest whorl of fronds. *Petioles* to 110 cm long, dark brown to atropurpureous, with persistent scales and scurf of erect, white, flattish squamules with several dark apical setae; aplebiae or aplebioid basal pinnae absent. *Petiole scales* to 17 x 1 mm, linear to long-lanceolate (Fig. 1H), with differentiated margins of differently orientated and coloured cells, with dark l setae to 0.7 mm long; larger scales usually with one apical seta (sometimes a second smaller apical seta present), no marginal setae, bicolorous with tan to brown centre and yellowish-white margins (Fig. 1H, right); smaller scales bicolorous with only a brown central stripe apically, or concolorous yellowish white (i.e., the colour of the margins of larger scales), some with small lateral setae (Fig. 1H, left). *Laminae* to 240 x 130 cm, tripinnate nearly throughout (except for distal fifth of pinnae and pinnules), opaque dark green adaxially, opaque pale green abaxially; broadly ovate, the apices abruptly reduced, pinna-like. Rhachises and costae dark-brown to atropurpureous, inermous, scabrous by the insertions of small acaroid (i.e., round with many setae and often indurated center; see Conant, 1983), stellate, and flattish squamules to 0.5 mm long, these present abaxially and adaxially, white pluricellular hairs only on distal parts abaxially, some larger scales, similar to those of the petiole, abaxially on costae; insertion of costae into rhachises slightly raised abaxially, bearing each a lunulate, flat to concave, brick-red pneumathode. *Pinnae* to 74 cm long, stalked to 2 cm, not green alate distally (Fig. 1A); basal pinnae reduced, more or less patent (Fig. 1B). Costules each with strongly raised adaxial ridge (Fig. 1D), stramineous to tan abaxially and adaxially, not green-alate between the distal segments (Fig. 1D, E); with white pluricellular hairs (0.5-0.7 mm, mainly medially and distally) and stellate, acaroid, and flattish setate scales (to 2 mm long, mainly basally) abaxially (Fig. 1G, left), no bullate scales present; pluricellular hairs adaxially

either wholly castaneous or with white base. *Pinnules* (Fig. 1C) to 13.0 x 2.8 cm, sessile, pinnate nearly throughout, truncate basally, attenuate apically; segments (= tertiary leaflets) to 14 x 4 mm, free, sessile to petiolulate to 1 mm, oblong, distal segments weakly falcate (Fig. 1C, D, E); margins subentire (to weakly crenate basally in the proximal segments), weakly convolute in fertile segments; midvein flat to weakly concave adaxially, glabrous or with 1-3 white, pluricellular hairs (Fig. 1D), weakly to strongly convex abaxially, with acaroid to ovate-lanceolate setate scales (Fig. 1E); sterile and fertile veins mostly once-forked, basal ones sometimes 2-forked, distal ones often simple, yellowish to stramineous adaxially (Fig. 1D), blackish dark green abaxially, with white stellate hairs adaxially (in young leaves) (Fig. 1D), glabrous or with some acaroid squamules abaxially. *Sori* 1-8 per segment, costal, vein forks (Fig. 1E); indusia subsphaeropteroid, almost closed (rupturing at maturity into 3-4 parts and appearing urceolate to cyatheoid), firm, castaneous, with persistent small stellate squamules (Fig. 1F). Spores not examined.

**Distribution.** - Known only from the type locality in SE Ecuador, Prov. Loja. In moist montane forest at 2500-2600 m; found near a stream at the bottom of a ravine.

**Additional specimen examined. ECUADOR. Zamora-Chinchipe:** New road Loja - Zamora, ca. 4 km E of pass "El Tiro", ridge from white cross on left road side (towards the valley), study plot C6, 03°59'S, 79°08'W, 2500-2600 m, 07 Oct 2004, *Lehnert 1414* (GOET, QCA, UC).

At first, I mistook this species for *Alsophila erinacea* (H. Karst.) D. S. Conant; indeed both species share the same diagnostic features that distinguish them from other species of spiny neotropical *Alsophila*. Their pinnae are not green-alate distally, the larger petiole scales of the abaxial side have only one apical and no lateral setae, and the indusia are firm, persistent, and lack hairs. *Alsophila conantiana* differs from *A. erinacea* in having wholly tripinnate laminae (vs. only sometimes tripinnate at the pinna-bases), free tertiary segments (vs. always adnate), and subsphaeropteroid indusia (vs. predominantly cyatheoid to urceolate, only rarely some indusia subsphaeropteroid). Other, subtler differences lie in the fine indument of the lamina; e.g., the small flattish squamules of *A. erinacea* have longer and thinner hyaline processes and fewer setae (vs. many setae and rather short white cilia in *A. conantiana*). However, with just two specimens of *A. conantiana* at hand, I cannot assess the whole variability of the indument of the species.

*Alsophila cuspidata* (Kunze) D. S. Conant has subsphaeropteroid to sphaeropteroid indusia with stellate hairs that resemble those of *A. conantiana*. It can be distinguished by the distally alate pinnae (vs. non-alate in *A. conantiana*), petiole scales with several lateral setae (vs. none or irregularly single setae), acute segments (vs. obtuse), and occurrence at lower elevations (200-1500 m vs. 2500-2600 m).

Other tripinnate *Alsophila* species include *A. salvinii* Hook., *A. polystichoides* H. Christ, and *A. tryoniana* (Gastony) D. S. Conant from Central America. All three can be distinguished by their distally green-alate pinnae and their fugacious or absent indusia (vs. non-alate pinnae and persistent indusia). Conant and Cooper-Driver (1980) hypothesized that *A. polystichoides* and *A. tryoniana* are stabilized recombinants of a cross breeding between *A. salvinii* and *A. firma* (Baker) D. S. Conant. This is supported by their co-occurrence: the presumed parents occur from southern Mexico to Costa Rica, *A. firma* also extending along the western slope of the Andes through the Colombian Chocó to southern Ecuador. The putative hybridogenic species are restricted to Central America; both share the tripinnate fronds and bullate scales from their common ancestor *A. salvinii*. The recent discovery of *A. salvinii* in the Andes of northern Peru (van der Werff *et al.* 15666, MO, UC) gives rise to the question of whether *A. conantiana* could be another hybrid, this time with *A. erinacea*, given the similarity to that species. *Alsophila salvinii* may occur in southern Ecuador as well, as the region still is scantily explored and close to the Peruvian site. However, apart from the free tertiary segments, there are only a few features that support this assumption. Aborted spores in sporangia that often do not open are usually a sign of hybrid origin in ferns. The fertile type specimen of *A. conantiana* has already shed most sporangia. The few remaining sporangia are open or were aborted at an early stage, which is not unusual to find in tree ferns. So we can conclude that at least most sporangia were well developed, but we cannot say anything about the spores with certainty. Even if they were well developed and viable, this does not rule out a hybrid origin of *A. conantiana*. Furthermore, *Alsophila conantiana* has hairs on the costae abaxially; the costae of *A. erinacea* usually have some hairs at least distally, those of *A. salvinii* are glabrous. Distinct laminar squamules (Fig. 1G, center) occur in *A. salvinii* and *A. conantiana* (also in *A. polystichoides* and *A. tryoniana*), but are lacking in *A. erinacea*. Such scales are also present in *A. firma*, making this character ambiguous and rendering it worthless for analysis. The nearly closed subsphaeropteroid indusia of *A. conantiana* are not present in either presumed parent (*A. salvinii* is exindusiate, *A. erinacea* has cyatheoid to urceolate or subsphaeropteroid indusia that are never as closed as in *A. conantiana*). Thus *A. conantiana* appears to merit species status.

**Cyathea brucei** Lehnert, Org. Divers. Evol. 6: 321; Electr. Suppl. 13: 3. 2006. Type. ECUADOR. Zamora-Chinchipec: Campamento Miazic, in forest and cliffs along Río Nangaritzac, ca. 04°18'S, ca. 78°40'W, 900 m, 19 Feb 1994, *van der Werff et al.* 13287 (holotype, QCNE; isotypes, MO, UC).

(Fig. 2)

*A Cyathea haughtii* Maxon *indusiis nullis pinnisque petiolulatis differt.*

**Etymology:** This species is named for Bruce Gray, co-collector of the type specimen.

Small trunkless fern. *Rhizomes* ascending, ca. 6 cm long, 1.5 cm diam. (Fig. 2A), hidden in a dense mass of old petiole bases and adventitious roots. *Fronde*s to 32 cm long (Fig. 2A). Petioles inermous, brown to dark brown, scurf absent. *Petiole scales* 7-10 x 2-3 mm, lanceolate or ovate-lanceolate, concordantly whitish to stramineous (Fig. 2A), or sometimes with an irregular brown dot at the insertion point, or with larger, more basal scales strongly bicolorous with irregular blackish streaks or central regions; scale margins differentiated, without marginal seta or teeth. *Laminae* widest at the middle, to 5 cm (Fig. 2A), dark green adaxially, pale gray-green abaxially, pinnate, abruptly to usually gradually reduced, ending in a small non-articulate pinna or pinnatifid apex. *Rhachises* inermous, non-alate, brown, with many red-brown, curved, pluricellular hairs to 1 mm adaxially and some small flattish scales adaxially towards the base. *Pinnae* sessile to petiolulate with stalks to 2 mm long (Fig. 2B), oblong, obtuse, shallowly lobed, bases rounded to cuneate, equilateral to subequilateral; the acroscopic basal lobe weakly pronounced in larger pinnae; the margins subentire to crenate. *Costae* (= midveins) glabrous (Fig. 2B). Veins glabrous, forked to pinnate, only the distalmost simple. *Sori* medial to supramedial, medial on vein (Fig. 2B), exindusiate; receptacles small, globose, paraphyses red-brown, ca. 0.2 mm long; spores not examined.

**Distribution and habitat.** - Known only from the type locality in SE Ecuador, Prov. Zamora-Chinchipec; grows on sandstone rocks.

*Cyathea brucei* is very similar to *C. haughtii* Maxon from northern Colombia (Fig. 2C), but *C. brucei* is exindusiate; *Cyathea haughtii* has small, appressed semicircular indusia. This indusial difference between evident sister species points out the untenability of generic

delimitation between *Cyathea* (indusiate) and *Trichipteris* (exindusiate), as advocated by Tryon (1970). The differences in the pinnules (sessile and with rounded bases in *C. haughtii* vs. petiolulate and cuneate to rounded in *C. brucei*) may not be significant. Because presence of indusia is normally regarded as crucial difference between species of tree ferns, I propose the recognition of *C. brucei*. Nevertheless, both species must be closely related because they are identical in their ecology; both have been found only on vertical sandstone cliffs, a habitat that supports many narrowly ranging, specialized species. *Cyathea brucei* and related species, such as *C. falcata* (Kuhn) Domin, form a group restricted to the Guayana Highlands and the northern Andes (Barrington 1978).

**Cyathea moranii** Lehnert, Org. Divers. Evol. 6: 322; Electr. Suppl. 13: 4. 2006. Type: Ecuador. Zamora-Chinchipe: New road Loja - Zamora, ca. 4 km E of pass El Tiro, ridge from white cross on left road side (towards the valley), 03°59'S, 79°08'W, 2500-2600 m, 03 Oct 2004, *Lehnert 1380* (holotype, GOET; isotypes, LOJA, QCA, UC).

(Fig. 3)

*Species ex grege Cyathea platylepis* (Hook.) Domin *statura media, truncis nudis, petiolis patentibus, segmentis angustis longisque; a Cyathea holdridgeana* Nisman & L. D. Gómez *atque C. arnecornelii* Lehnert *indusiis sphaeropteroideis differt.*

**Etymology:** This species is named for Robbin C. Moran, New York Botanical Garden, renowned pteridologist, prolific writer and collector, to honor his contributions to our knowledge of the Ecuadorian fern flora.

*Trunks* to 4.5(-6.0) m high, 8-10 cm diam., inermous, without old petiole bases (Fig. 3A), petioles falling off cleanly, scars round to ovate, well spaced, slightly raised at their base; trunks densely covered with broad ovate scales; scales to 22 x 8 mm, bicolorous, dark brown to tan with grayish to white margins, to almost concolorous grayish light brown, their apices obtuse to long-acute, differentiated margins fragile, without setae or teeth (Fig. 1B); trunk apices hemispherical, raised above the last whorl of green fronds, the young crosiers clearly visible (Fig. 3A), densely covered with scales like those of the trunks. *Fronds* to 270 cm long, arching. *Petioles* 30-110 cm long, inermous to sparsely scabrous, grayish brown to blackish, scurf abundant, consisting of appressed light brown, gray or whitish hair-like, easily abraded

squamules; petiole scales identical with trunk scales, present only at the very base of the petioles, caducous (Fig. 3B). *Laminae* 80-160 x 60-110 cm, bipinnate-pinnatifid to tripinnate at pinnule bases (Fig. 3E, F); light green to olivaceous adaxially, paler abaxially, opaque; apices gradually reduced (Fig. 3D). *Rhachises* inermous, brown to stramineous, with scattered brown pluricellular hairs adaxially and appressed scurf like that of the petioles abaxially and adaxially. *Pinnae* to 36 cm long, sessile or stalked to 12 mm (Fig. 3C), each with a darkened callus bearing a whitish planar pneumathode at the insertion to the rhachis. *Costae* inermous, brown to stramineous, adaxially with many tan to brown pluricellular hairs, abaxially appressed scurf of lacerate squamules to 0.5 mm and larger flattish squamules, these papery, concolorous brown, margins entire; costae distally weakly green-alate. *Pinnules* to 75-135 x 12-30 mm, sessile to subsessile, rarely short-stalked to 3 mm, linear (Fig. 3F) to long-triangular (Fig. 3E), truncate basally, attenuate apically, ending in deeply crenate tips (Fig. 3C, E, F); costules densely hairy adaxially with whitish to tan pluricellular hairs, sparsely hairy distally on the abaxial side, with relatively few to many squamules and scales (Fig. 3G); mainly brown to tan, flattish (Fig. 3H) and bullate squamules (Fig. 3J) with whitish elongated tips (Fig. 3J), also some larger (1-5 mm) concolorous brown, papyraceous, weakly clathrate scales (Fig. 3G). *Segments* to 15 x 4 mm, sessile (Fig. 3G), adnate or free acroscopically and decurrent basiscopically (Fig. 3F), rarely truly free, and then with deeply crenate margins (Fig. 3E); sinuses quadrangular, wide (Fig. 3G), reaching segment width at pinnule bases (Fig. 3E, F); margins subentire to weakly crenate, tips obtuse; midveins with relatively few to many pluricellular hairs (0.4-0.7 mm) adaxially and abaxially, hairs sparser or lacking on lateral veins (Fig. 3G); bullate scales like those on costules abaxially; fertile and sterile veins simple or forked, sometimes 2-forked in free segments. *Sori* costal (Fig. 3G), in the fork of the midvein and a lateral vein; indusia sphaeropteroid, without or with a weak apical umbo, glabrous, tan, translucent, fragile, irregularly rupturing at maturity, persisting as cups or discs with irregular margins (Fig. 3G); paraphyses shorter than or equalling the sporangia, receptacles globose. *Spores* pale yellow, tetrahedral-globose, exospore deeply verrucate, often irregularly shaped (Fig. 3K).

**Distribution and habitat.** – Known from Prov. Zamora-Chinchipe in SE Ecuador, in moist montane forests at 2400-2600 m, mainly in sheltered side valleys and ravines.

**Additional specimens examined. ECUADOR. Zamora-Chinchipe:** Reserva Tapichalaca, sector Ventanillas, trail to study plots B2 and B3, 04°29'S, 79°07'W, 2550-2600

m, 02 Nov 2003, *Lehnert 1076* (GOET, QCA, UC); Reserva Tapichalaca, sector Ventanillas, 04°29'S, 79°07'W, 2520-2600 m, *Lehnert & Kessler 1270* (GOET, LOJA, QCA, UC); Estación Científica San Francisco, study plot A 9, along trail T1 above refuge, 03°59'30"S, 79°04'15"W, 2400 m, 11 Nov 2004, *Lehnert 1548* (GOET, LOJA, QCA, UC).

The diagnostic characters of *Cyathea moranii*, e.g., petiole scales, petiole scurf and indusial shape, are regrettably easily lost by collecting and drying. The scales are persistent only on the trunks and crosiers; on petioles they are easily shed. The scurf is only loosely attached to the petioles, but the scurf squamules are intertwined to form a papery tissue; once this closed cover is ruptured, the scurf falls off in flakes. In dried specimens, the indusia are never observed in their original form; they are either cyatheoid or even hemitelioid when ruptured. This is important to know because the most closely related and similar species, *C. holdridgeana* Nisman & L. D. Gómez (including *C. albomarginata* R. C. Moran) from Costa Rica and Panama, and *C. arnecornelii* Lehnert from Bolivia, have true hemitelioid indusia. All three species are similar in morphology and have the same habit (Fig. 3A). Their petioles are inermous, abscise cleanly, and are well-spaced, allowing free sight of the apex and the crosiers (Fig. 3A). The frond scars on the trunk are markedly raised. The pinnules vary in dissection and width characteristically, ranging from rather narrow pinnatisect pinnules to basally pinnate pinnules with the costules narrowly green-alate between the segments (the stronger dissection prevails in shaded sterile plants). Vegetative reproduction by adventitious buds has not been observed or reported for any of the three species. Apparently all have the same spore type with a strongly verrucate exospore and without perispore (Fig. 3K).

The trunks are densely and persistently scaly in *Cyathea holdridgeana* (Rojas 1999) and *C. moranii* (Fig. 3A). In the latter species, I observed a regular growth of green algae and mosses between the scales below the last whorl of fronds; in Reserva Tapichalaca, Prov. Zamora-Chinchipec, Ecuador, undetermined filamentous cyanobacteria grow as a turquoise cover on the apical trunk scales of this species. In *C. arnecornelii*, the trunks are glabrous below the last whorl of fronds, or only sparsely scaly. This species, however, is closer to *C. moranii* in laminar indument. Both species have concolorous brown, flattish and bullate scales on lamina axes and veins abaxially. *Cyathea holdridgeana* evidently lacks bullate scales, and the larger flattish scales on the costules can be bicolorous (Moran 1991, as *Cyathea albomarginata*).

Mature spores of *Cyathea moranii* under the light microscope show exospore with irregular bumps, and there is no obvious perispore. Spores of *C. arnecornelii* have been



examined with SEM (*Lehnert 003*, GOET), but the irregular shape and the lack of perine had been interpreted to be due to their immaturity (Fig. 3K). The spores of *C. holdridgeana* have been described by Tryon (1976); the irregularity of the exospore was one criterion by which he considered the species to be a hybrid between *Cyathea divergens* Kunze var. *divergens* and *Trichipteris* (= *Cyathea*) *bicrenata* (Liebmann) R. M. Tryon. With *Cyathea moranii*, there are now three habitually nearly identical species with similar spore morphology. Evidently, the irregular spores (Fig. 3K) are a feature shared by the three species, and not due to immaturity or abortion.

Other similar species are *Cyathea heliophila* R. M. Tryon, from Ecuador and Colombia, and *C. xenoxyla* Lehnert, from Colombia to Bolivia. *Cyathea heliophila* has persistently scaly trunks with elongate apices and without old petiole bases like *C. moranii*; it also shares the dissection pattern of the lamina (pinnatisect to pinnate pinnules with often long-tapering tip) and the scale shape. It differs in the white scales (rarely with a brown basal spot), which are persistent on the petioles and trunks, in the firmer, darker laminae that are sparsely scaly, and in the longer, drooping fronds. The trunk apices of *C. heliophila* are characteristic because the scales are moderately to strongly spreading (appressed in *C. moranii*, *C. arnecornelii*, and *C. holdridgeana*).

The widespread *Cyathea xenoxyla* Lehnert also sheds the petioles completely and has distantly placed petioles that do not hide the trunk apices and the crosiers, just as in *C. moranii* (Fig. 3A). Both species have the same indusial shape and variability (sphaeropteroid, fragmenting to cyatheoid, or even to hemitelioid). It differs in its spiny petioles and the vegetative reproduction by adventitious buds on the trunk (not present in *C. moranii*); scales are lacking on the trunks (scales present and persistent in *C. moranii*, *C. holdridgeana*, and *C. heliophila*, caducous in *C. arnecornelii*) and present only on the young crosiers.

***Cyathea obnoxia*** Lehnert, *Brittonia* 58: 4. 2006. Type: ECUADOR. Zamora-Chinchipec: Estación Científica San Francisco, above refuge, along trail T1, study plot A 4, 03°59'39.4"S, 79°04'18.5"W, 2530 m, 30 Sep 2003, *Lehnert 943* (holotype, GOET; isotypes, LOJA, QCA, UC).

(Fig. 4).

*Cyathea media trunco nudo, lamina pilosa ad apicem gradatim contracta, pinnis planis oppositis vel alternis, pinnulis in margine duplicato-serratis vel bicrenatis, indusio firmo sphaeropteroideo cum umbone praestans.*

Etymology: This species is named for the combination of small size and lack of spines which makes it easily collectible (Latin, *obnoxius* = submissive, defenseless; *not* obnoxious).

*Trunks* to 2-4 m high, to 7-8(-12) cm diam., erect, dull dark brown to blackish; trunks over 1 m high without persistent old petiole bases (Fig. 4D), a skirt of last year's fronds or petioles may be present; scars not protruding, inconspicuous, similar to trunk cortex in color; trunk scales concolorous dull brown, present around the scars near the apex. *Petioles* to 60 cm long, inermous (Fig. 4D), smooth to scabrous, livid light green when young, dull brown when mature, with a tomentum of stiff, translucent white pluricellular hairs (0.5-1.0 mm) and scattered dark brown glandular hairs (0.1-0.2 mm) (Fig. 4F, arrow), scaly scurf lacking or sparsely among the hairs; rarely petioles almost glabrous. *Petiole scales* with differentiated margin without marginal teeth or setae, lanceolate, to 22 x 3-5 mm, broad at petiole bases, narrow distally (Fig. 4E), concolorous dull to golden brown, or weakly bicolorous with the margins lighter than the center. *Laminae* to 140 x 80 cm, bipinnate-pinnatifid, broadly ovate, dull green to dark green adaxially, pale grayish green abaxially, apices gradually reduced. *Pinnae* to 40 cm long, sessile (Fig. 4A), either opposite throughout in fronds with a rather short apices or laminae distally with alternate pinnae/segments, and then the apical rhachis prolonged and bent in a zigzag pattern; lowermost pinna pair not or only weakly deflexed. *Leaf axes* inermous, green to dull brown, with white to tan pluricellular hairs 1-2 mm long, often catenate at base. *Pinnules* to 75 x 15 mm, oblong-linear to oblong-obovate, sessile, cuspidate to short attenuate at tip (Fig. 4A, B); segments patent to curved, with deeply double-serrate margins along the sides, at tip weakly serrate to crenate (Fig. 4C), basal segments with pronounced basispic lobules that partly cover the costa (Fig. 4B); densely hairy on and between veins on both sides, the hairs white, erect, to 1 mm long abaxially (Fig. 4C), appressed, to 0.5 mm long adaxially; with some small scales to 3 mm long, opaque whitish to tan, plane or wrinkled, not bullate (Fig. 4C). Sterile veins forked or simple, fertile veins forked (Fig. 4B, C). *Sori* costal to subcostal, in forks of veins (Fig. 4C). *Indusia* sphaeropteroid, firm, with umbo, rupturing irregularly at maturity, one part normally bearing the umbo (Fig. 1C); paraphyses as long as the sporangia. *Spores* trilete, exospore smooth, perispore baculate.

**Distribution and habitat.** – Wide spread but local from northern Colombia to southern Ecuador and western Bolivia at 2000-2700 m. Usually found in shaded ravines that are moister and richer in nutrients than the surrounding forest.

**Additional specimens examined. COLOMBIA. Antioquia:** Alto de Sapa, NW of Vega del Ingles, Paramillo PN, 07°10'N, 75°54'W, 2700 m, 3 Jun 1993, *Gentry & Cuadros 79105* (UC).

**ECUADOR. Zamora-Chinchipec:** Cuesta Carrizal, heading down from Cerro Cruz Grande opposite the refuge of Quebrada Honda, along the road Yangana-Valladolid, 04°28'59"S, 79°07'31"W, 2470 m, *Garmenda & Paredes 638* (QCNE); Estación Científica San Francisco, 30 km E of Loja on road to Zamora, Quebrada "El Milagro," 03°58'35"S, 79°04'14"W, 2100 m, 20 Apr 2000, *Neill et al. 12693, 12694, 12695* (MO, QCNE); Parque Nacional Podocarpus, trail into quebrada San Francisco, Km 9.4 E of pass on Loja - Zamora road, 03°59'S, 79°06'W, 2000-2300 m, 25 Mar 1998, *Øllgaard & Lozano 2985* (AAU, QCA); Zamora, Parque Nacional Podocarpus, road Loja-Zamora, San Francisco, 03°59'S, 79°06'W, 2250 m, Jan 1995, *Palacios & Tirado 13445* (MO, QCNE).

**PERU. Amazonas:** Prov. Bagua, Cordillera Colán SE of La Peca, third camp, 2300-2400 m, 30 Sep 1978, *Barbour 3723* (F). **Cajamarca:** Prov. San Ignacio, Tabaconas, National Sanctuary Tabaconas-Namballe, 05°15'S, 79°19'W, 2300-2400 m, 14 Nov 1998, *Campos J. et al. 5688* (MO, UC); San José de Lourdes, slopes of Cerro Picorana, 04°58'S, 78°53'W, 2500-2540 m, 05 Dec 1998, *Campos J. et al. 5953* (UC). **San Martín:** Prov. Rioja, Buenos Aires, along road Pedro Ruiz-Rioja, 05°42'09"S, 77°53'06"W, 21 Mar 1998, *van der Werff et al. 15337* (MO, UC).

**BOLIVIA. La Paz:** Prov. Muñecas, Madidi, Camata-Cuibaja, Monte Puncu (Machayani), 15.18.35S, 68.46.00W, 2680 m, *Fuentes A. et al. 10883* (LPB, MO).

*Cyathea obnoxia* belongs to a group of species allied to *Cyathea suprastrigosa* (H. Christ) Maxon, which is characterized by abundant hairs on the veins adaxially or on both surfaces, absent or poorly developed, evanescent petiole scurf, and concolorous (rarely weakly bicolorous) brown petiole scales. The Mesoamerican *Cyathea suprastrigosa* matches *C. obnoxia* in the auriculate basal pinnule segments, but it is less hairy, has more squamules on the lamina abaxially, spiny petioles, and often small aphlebioid pinnae at the base of the petiole (both absent in *C. obnoxia*). *Cyathea herzogii* Rosenst. from Bolivia and Peru

resembles *C. obnoxia* in being as hairy on the laminae and in lacking aphlebioid pinnae, but it lacks auriculate pinnule segments, and has scabrous to spiny petioles that normally show remnants of a brown scaly scurf but largely lack hairs. All three species can be distinguished from *C. delgadii* Sternb. by their dull brown petiole and abundant hairs on and often between the veins adaxially. *Cyathea delgadii* has shiny dark brown to black petioles (at least basally) and only few hairs adaxially on the veins. Its hairs between the veins (if present) are restricted to the abaxial lamina surface.

Only recently I discovered several specimens from outside of Ecuador. These collections extend the distribution of *C. obnoxia* through the northern and central Andes. Plants from northern Colombia are conspicuously long-hairy but match otherwise in pinnule shape and indument the type population in southern Ecuador. Peruvian material displays a greater variation in the abundance of hairs on the petioles, with one specimen having almost glabrous petioles. The Bolivian material has abundant hairs but also few erect brown squamules on the petioles, which reminds of the sympatric *C. herzogii*. Hybridization is not excluded here as an explanation. The similarity between the two species suggests a recent phylogenetic divergence; maybe the reproductive boundaries are not well developed between the *C. herzogii* and *C. obnoxia*.

**Cyathea plicata** Lehnert, Brittonia 58: 6. 2006. Type: ECUADOR. Zamora-Chinchi: Estación Científica San Francisco, areas intervenidas (pastizales, campos y remnantes del bosque) arriba de la estación, 03°57'48"S, 79°04'12"W, 2290 m, 14 Sep 2003, *Lehnert 844* (holotype, GOET; isotypes, LOJA, QCA, UC).

(Fig. 5, 6).

*Cyathea media trunco nudo, lamina glabra ad apicem gradatim contracta, pinnis alternis per pinnulis erectis plicatis, pinnulis in margine crenulatis vel crenatis, indusio sphaeropteroideo fragili praestans.*

Etymology: The name refers to the upward pointing pinnules, which make the pinnae furrowed and give the whole frond a plicate look (Latin, *plicatus* = folded).

*Trunks* to 4 m high, to 12-16 cm diam., erect and straight, not covered by old petiole bases, frond scars pale brown to grey, arranged in horizontal whorls, few oval vermilion

pneumathodes below them (Fig. 5C, arrow), to 10 x 5 mm, immersed 1-2 mm into the cortex; the cortex dark brown to blackish, densely scaly towards apex (Fig. 5C); the scales long-lanceolate, dull orange-brown, concolorous or bicolorous with the centre darker brown, or the narrow margins lighter orange to whitish. *Petioles* to 25 cm long, scabrous to finely muricate at base, rarely inermous or with some longer spines; bright green when young, dull light brown when old, with caducous scurf of brown squamellae with strongly crispate margins (Fig. 5E). *Petiole scales* long lanceolate with elongated tips, to 50.0 x 3.6 mm, narrow at petiole bases, broader in upper parts, nearly concolorous orange brown to bicolorous with orange brown to castaneous centre and orange to whitish narrow margins (Fig. 5D). *Laminae* bipinnate-pinnatifid, 105-165 x 60-70 cm, apices gradually reduced (Fig. 5C), firm-chartaceous to subcoriaceous, often glossy adaxially (especially when young), opaque abaxially. *Lamina axes* inermous, glabrescent except for the adaxial side; rhachises and costae brown adaxially, otherwise bright green to stramineous when dried, densely hairy adaxially; costa base conspicuously swollen and ring-like where it joins the rachis; *costules* of the same color as laminae, moderately hairy adaxially, glabrous or glabrescent abaxially. *Pinnae* alternate, to 40 cm long, sessile to short stalked to 2 cm (Fig. 6), acute to short attenuate at tip, green-alate between distal pinnules and segments. *Pinnules* linear-lanceolate, 3.0-7.0(-8.0) x 1.0-1.5 cm, sessile or rarely short-stalked (to 3 mm), base truncate to subcordate, tip short-acute (Fig. 5A); pinnules turned upwards with respect to the costae and often twisted towards the rhachis, especially in proximal half of the pinnae; glabrous adaxially except for hairs on costae, abaxially glabrous or with few short hairs to 0.5 mm long on costae and veins, rarely between them, sometimes also small tan flattish squamules: indumenta development increasing with size, fertility, and sun exposure, but always inconspicuous; segments patent with subentire to crenulate or rarely crenate margins; sterile veins forked or simple, fertile veins forked. *Sori* inframedial to costal, in forks of veins. *Indusia* sphaeropteroid, without umbo, tan, opaque, transparent, fragile, remaining as brown discs at maturity. *Paraphyses* as long as sporangia. *Spores* trilete, bright yellow.

**Distribution and habitat.** - Frequent in elfin forests and scrubs along the passes leading from Loja to Saraguro and Zamora, also in more open sites of the upper montane forest, such as ridges and clearings, from 2000-2800 m.

The restricted distribution of *Cyathea plicata* in southern Ecuador coincides with a special geological area where nutrient-poor Precambrian rocks prevail (Litherland et al., 1994). The only collection from Prov. Sucumbios (*Løjtnant et al. 12330*) is sterile and has all

the pinnules in one plane; it is placed here tentatively because it comes from an area with a similar geology, and matches in general appearance.

**Additional specimens examined. ECUADOR. Loja:** Loja-Saraguro road, 3-5 km N of San Lucas, 2700-2800 m, 22 Apr 1980, *Harling & Anderson 18508* (AAU); Road Loja-Zamora, km 10.5, 04°00'S, 79°10'W, 2600 m, 17 Apr 1973, *Holm-Nielsen et al. 3653* (AAU, B); Loja-Zamora road, 2-7 km W of the pass, 03°59'S, 79°10'W, 2400–2700 m, 17 Jun 1979, *Lojtnant et al. 15030* (AAU); road between Loja and Zamora ca. Km 9, 2500-2750 m, 31 Dec 1978, *Luteyn et al. 6543* (AAU, NY); Parque Nacional Podocarpus, E of Nudo de Cajanuma, just N of "Centro de Información", 04°05'S, 79°10'W, 2900 m, 16 Sep 1989, *Madsen 86174* (AAU, QCA); new road Loja-Saraguro, Km 17, 03°55'S, 79°15'W, 2600-2650 m, 19 Mar 1989, *Øllgaard & Pena-Feil 91118* (AAU, QCA). **Sucumbios:** Cartagena, Km 25 from El Carmelo on road towards La Bonita, 00°37'N, 77°30'W, 2800 m, 13 Apr 1979, *Lojtnant et al. 12330* (AAU). **Zamora-Chinchipe:** Estación Científica San Francisco, along transect T2, 03°58'S, 79°04'W, 2200 m, 8 Nov 2003, *Lehnert 1089* (GOET, QCA, UC).

This distinctive species is readily recognized by the furrowed pinnae of the relatively short fronds. The upward-pointing pinnules can be detected in herbarium specimens: As the pinnae are impossible to flatten without breaking off the pinnules, they are normally pressed folded, with the abaxial sides of the acroscopic pinnules lying on those of the basiscopic pinnules. This new species seems to be most closely related to *Cyathea carolihenrici* Lehnert from Bolivia, which has similar scurf, lamina texture, and trunk morphology. However, its scurf consists of even finer dissected castaneous squamules than in *C. plicata*, and the pinnules are held perfectly horizontally. Both species share a circularly swollen juncture between rhachis and costa with some other sphaeropteroid indusiate *Cyathea* species, such as *C. chimborazensis* (Hook.) Hieron. and *C. divergens* Kunze, but the significance of this character considering relationships still is uncertain. The long-lanceolate, concolorous to weakly bicolorous petiole scales that characterize *C. plicata* also occur in *C. patens* H. Karst. and *C. parvifolia* Sodiro (= *C. brevistipes* R. C. Moran). Both species differ from *C. plicata* in a generally stronger lamina indument of scales and hairs, more triangular basal pinnules and stronger crenate to serrate segment margins. *Cyathea patens* has a moderate to large amount of small to relatively large (3 mm long) flattish, brown to orange-brown, wrinkled scales (sometimes with fimbriate margins) on costules and veins abaxially (in *C. plicata* only very few tan small squamules). *Cyathea parvifolia* has few dark-brown to brown flattish scales on

costules and veins, and either a pair of remote pinnae at the petiole bases, or basally gradually tapering laminae and only very short petioles, or long petioles and triangular laminae (*C. plicata* always with oval-elliptic laminae and distinct petioles without basal pinnae).

**Cyathea sylvatica** Lehnert, Org. Divers. Evol. 6: 322; Electr. Suppl. 13: 5. 2006. Type. ECUADOR. Loja: Reserva Protegida Privada “El Bosque,” near San Pedro de Vilcabamba, ca. 04°13'S, ca. 79°02'W, 2600 m, 07 Oct 1997, *Bussmann 1803* (holotype, QCA, isotypes, ECSF, LOJA).

(Fig. 7)

*Cyathea pygmaea truncum deficiens frondibus bipinnatis vel bipinnato-pinnatifidis, non plus ultra 20 cm longis, indusiis sphaeropteroideis praestans.*

Etymology: The name refers to the type locality, the private nature reserve “El Bosque” (= the forest) near San Pedro de Vilcabamba, Ecuador, Prov. Loja (lat. *sylvaticus* = belonging to the forest).

*Trunks* absent; rhizomes to 4 cm long, 15 mm diam. (Fig. 7A), with many adventitious roots. *Petioles* to 12 cm long, inermous, atropurpureous, with small gray pneumathodes to 2.0 x 0.4 mm, scurf lacking or rarely of scattered tan trichomidia. Petiole scales to 10.0 x 2.5 mm (Fig. 7D), concolorous orange-brown, lustrous, ovate-lanceolate, acute, with differentiated margins without setae or teeth. *Laminae* to 16 x 7 cm, bipinnate with the pinnules strongly crenate to pinnatifid, apices gradually reduced (Fig. 7A). *Rhachises* inermous, atropurpureous to brown basally, dark brown to stramineous apically, with many tan to whitish, antrorsely curved, pluricellular hairs to 0.7 mm long adaxially, with scattered white hairs to 1.0 mm long and few entire flattish brown scales abaxially. *Pinnae* to 42 x 18 mm (Fig. 7A), broadly lanceolate, short acute to obtuse at tips, sessile with stalks to 2 mm, pinnate basally, pinnatifid apically. *Costae* inermous (Fig. 7B), brown to stramineous, densely hairy abaxially (Fig. 7C), scarcely so abaxially, with scattered trichomidia and flattish scales, narrowly green-alate between the pinnules; distal segments adnate and decurrent into costae. *Pinnules* to 9 x 5 mm, sessile (Fig. 7B, C), oblong, truncate to rounded basally, obtuse apically, margins deeply crenate to pinnatifid, strongly hairy adaxially with whitish, pluricellular hairs 0.6-0.8 mm long (Fig. 7C), only few appressed brown trichomidia and flattish scales abaxially on costulae and

veins (Fig. 7B). Fertile and sterile veins forked to pinnate (Fig. 7B, C). *Sori* costal, borne in forks of veins (Fig. 7B). *Indusia* opaque brown, sphaeropteroid, without umbo (Fig. 7B), gradually fragmenting at maturity, paraphyses few, much shorter than sporangia. *Spores* not examined.

**Distribution and habitat.** - Endemic; known only from the type locality in Ecuador, Prov. Loja, at 2600 m, growing in elfin forest.

This small species appears to be most closely related to *Cyathea patens* H. Karst., a large species with trunks to 10 m. The two species are similar in indusial type, hairiness, and laminar texture. Even the dissection pattern of the lamina is similar but modified according to the difference in size: medial and distal pinnae of *C. sylvatica* look like small pinnules of *C. patens*. However, the petiole scales of *C. sylvatica* seem to be constant in colour and shape (concolorous lustrous orange-brown, ovate-lanceolate) while in *C. patens* they vary from broadly to narrowly lanceolate and are generally duller in colour than in *C. sylvatica* (brown to dark brown, or if some orange-brown then not lustrous; also some of the longer scales are bicolorous with narrow, whitish margins).

Juvenile plants of *Cyathea delgadii* Sternb. are similar to *C. sylvatica*, especially in the dark petioles and the lustrous scales, but they are generally less hairy and not known to be precociously fertile. The elevational distribution is also different: *C. delgadii* does not occur above 1200 m in Ecuador, whereas *C. sylvatica* grows only at 2600 m.

***Cyathea aemula*** Lehnert, sp. nov. ined. Type: ECUADOR. Pastaza: Mera Cantón, 2 km NW of Mera, Campamento Vacacional Evangelico Mangayacu, up the ridge behind the Campamento, 01°26'00"S, 78°07'30"W, 1350-1500 m, 29 Jul 1992, *Fay & Fay 3781* (holotype, UC; isotype, MO).

(Fig. 8)

*Cyathea pulchra incertae affinitatis exindusiata apicibus frondorum abrupte terminantibus, furfure petiolorum albicante, squamis discordanter bicoloratis, paraphysibusque longibus praestans; in pinnulis longe petiolatis similis ad C. kalbreyeri* (Baker) Domin vel *C. divergentem* Kunze, sed ab hac in paraphyibus longis squamisque



*bicoloratis* (vs. *paraphysibus cortis squamisque concoloratis Cyatheae kalbreyeri*), *ab illa in absentia indusiorum* (vs. *C. divergens cum indusiis sphaeropteroidis instructis*) *differt*.

Etymology: Refers to the similarity to several, apparently not closely related *Cyathea* species (Latin, *aemulus* = mimicking).

*Trunks* slender, to 7 m tall, otherwise unknown. *Petioles* to 85-95 cm long, verrucate to muricate, stramineous to pale brown; lenticels not seen in dried material; without adventitious (aphlebioid) pinnae at the petiole bases; petiole scurf a matted tomentum of small branched hairs and dissected squamules 0.2-0.4 mm long, yellowish white with brown parts, grayish white in general aspect; long persistent. *Petiole scales* broadly lanceolate to long-ovate, 14.0-20.0 x 4.5-5.0 mm, their tips straight; shiny auburn to dark brown, concordantly bicolorous with broad, pale to golden brown margins; colors transient, not sharply contrasted. *Fronds* to 235 cm long, presumably arching to weakly drooping. *Laminae* to 90-140 x 80-90 cm, bipinnate-pinnatifid, chartaceous; dark olive green adaxially, not blackish when dried, olive green abaxially; apices abruptly reduced, conform, or gradually reduced. *Pinnae* to 40-45 cm long, 4-5 pairs per frond, long-stalked to 5.0-6.0 cm, distally very narrowly green alate, the distal segments decurrently adnate. *Leaf axes* brown on both sides; completely glabrous abaxially except for scurf remnants, hairy only adaxially on costules, costae and distal parts of rhachises, hairs 1.0-1.5 mm long, tan to brown; costae smooth, 2-3 mm wide; insertions of costae into rhachises swollen, each abaxially with one inconspicuous pneumathode acroscopically, orange brown, elliptic, to 1.0 x 0.4 mm, and with a diffuse black spot basiscopically, at least when dried. *Pinnules* 12.0-14.0 x 2.8-3.2 cm, the largest ones stalked to 10-14 mm, alternate, (0.6-)1.5-2.6 cm between the stalks, linearly oblong to lanceolate, incised to 1/2 or more of their width, sterile pinnules truncate to cuneate at their bases, fertile pinnules truncate to weakly cordate, tapering from beyond the middle to long-acuminate to short-attenuate tips; the brown stalks inarticulate, their bases with an orange brown, elliptic pneumathode to 1.0 x 0.4 mm, and a diffuse black spot in dried specimens; the segments patent to ascending, with entire margins; tips falcate, obtuse to acute; basal segments usually opposite, the lowest ones not remote from each other, sinuses acute and narrow (1.0-1.5 mm) in sterile pinnules, wide (2.0-3.0 mm) and obtuse to acute in fertile pinnules. *Veins* prominent abaxially and adaxially, ending at segment margins; midveins brown abaxially and adaxially, lateral veins not different from the lamina in color abaxially, yellow adaxially; glabrous adaxially, abaxially glabrous except for scurfy gray-brown to brown trichomoidia and

catenate hairs, these on and between the veins, also along the segment margins; sterile veins simple or forked, fertile veins forked. *Sori* 1.2-1.6 mm diam., inframedial to subcostal (triangle pattern), indusia absent, receptacles globose to ellipsoid, 0.4-0.5 mm diam.; paraphyses numerous, hyaline, white, longer than sporangia (0.8-1.0 mm). *Spores* not examined.

**Distribution and habitat.** – Moist tropical montane forests at 1350-1500 m on the eastern Andean slopes of southern Colombia and northern Ecuador.

**Additional specimen examined: COLOMBIA. Putumayo:** Mocoa, Corregimiento de San Antonio, Vereda Alto Campucana, finca La Mariposa, 1400 m, *Mocoa Fernández et al. 11120* (COL).

The pinnule shape and the petiole characters (i.e., scurf, scales) of *Cyathea aemula* are similar to *Cyathea divergens* Kunze, which can be distinguished by the presence of indusium (vs. *C. aemula* is exindusiate) and the short paraphyses (vs. long paraphyses). *Cyathea aemula* has conspicuous prominent veins and a tendency towards leaf dimorphism, which is characteristic of the genus *Gymnopshaera* but unusual in *Cyathea*.

The indument characteristics with the white, hairlike dissected squamules and the long paraphyses is shared by *C. gibbosa* (Klotzsch) Domin from Venezuela, which has more shortly stalked and generally narrower pinnules than *C. aemula* as well as concolorous shiny auburn petiole scales.

***Cyathea ars*** Lehnert, sp. nov. ined. Type: ECUADOR. Zamora-Chinchipec: Nangaritza, Cordillera de Naguipa, Cerro Colorado, ridge 8 km SSE of Nambija, 20 km ESE of Zamora, 04°07'51"S, 78°46'36"W, 2630 m, 20 Feb 2002, *Coyle, Delinks & Neill 258* (holotype, UC; isotype, MO).

(Fig. 9)

*Cyathea ex grege C. platylepis* (Hook.) Domin *squamis valde bicoloribus atrobrunneis vel castaneis cum marginibus albis latis praestans; a Cyathea heliophila* R. M. Tryon et *C. vilhelmii* Domin *in squamis petiolorum valde bicoloribus (vs. squamis concoloribus), a C. platylepe* (Hook.) Domin et *C. oxapampana* Lehnert *paraphysibus brevioribus differt.*

Etymology: The name refers to the artful pattern the scales create on trunks and petioles; it also honors Alan R. Smith, American pteridologist, whose initials happen to form the word. The name is a noun in apposition.

*Trunks* to 1.5 m tall, otherwise unknown, presumably without old petiole bases, with dense cover of scales, and apices not hidden between petioles. *Fronde*s to ca. 1 m long, presumably arching. *Petioles* to 20 cm long, probably more, dull brown to orange-brown, inermous, scurf white to tan, consisting of many tortuous white hairs to 2 mm, grading into brown, subbullate squamules with few white, long, apical ciliae, persistent; pneumathodes absent or not evident; persistently densely scaly throughout. *Petiole scales* to 9.0-16.0 x 4.0-5.0 mm, lanceolate-ovate, shiny, strongly bicolorous, discordantly so in lower parts, concordantly in upper parts of the petiole, dark castaneous with yellowish to cream-white margins; differentiated margins to 1 mm wide, fragile, lacerate to erose, with cells strongly exerted, without setae or ciliae. *Laminae* to ca. 80 x 100 cm, bipinnate-pinnatifid to tripinnate, opaque, dark green adaxially, blackish when dried, pale grey-green abaxially, apices gradually reduced. *Rhachises* inermous, with many spreading ovate scales similar to petiole scales but with narrower margins; adaxially with many appressed, brown, pluricellular, uniseriate hairs to 1.0(-1.5) mm long, abaxially glabrescent with white scurf like on the petioles, but with more squamules, whitish to brown, with more white marginal ciliae than those on the petioles; junctures of rhachises and costae not swollen, abaxially each with one planar, brown, elliptic pneumathode to 2 x 1 mm. *Pinnae* to 45-50 cm long, stalked to 2.5 cm, inarticulate, patent to ascending, basal pinnules only 1/2 the size of medial pinnae, weakly to strongly reflexed. *Costae* inermous, to 1.5-2.0 mm wide, dull dark brown to carnose, short-hairy adaxially, hairs to 1 mm long, pluricellular, tan to brown, antrorsely curved, abaxially glabrescent with scurf and few dark-brown, flattish scales with undulate margins. *Pinnules* to 5.0-6.5 x 1.1-1.7 cm, lanceolate to long-triangular, pinnatifid to pinnatisect, sessile to stalked; stalks to 5 mm, decurrently green-alate; 1.0-1.5 cm between the stalks; pinnule bases truncate to weakly cordate at base, basal segments sometimes remote, not free, tips long-acute to attenuate; costules dark brown to dark carnose, strongly prominent and ridged adaxially, with tan to brown, antrorsely curved hairs to 1 mm long, abaxially weakly prominent, with tortuous hairs to 2 mm long, tan to brown squamules with white marginal ciliae, and some ovate to almost round, pseudopeltately attached, shiny brown scales to 4 x 3 mm; costules basally without pneumathodes; segments to 9 x 3 mm, patent to weakly ascending, straight or distally falcate,

the tips obtuse to rounded, segment margins crenulate to inciso-crenate, in proximal segments usually basiscopically more strongly dissected, sinuses acute to obtuse, to 1 mm wide; margins often still planar when dried; midveins adaxially ridged, lateral veins planar; veins adaxially glabrous or with few erect, pluricellular, uniseriate hairs and ephemeral tortuous hairs, none between the veins, abaxially with tortuous white hairs, midveins also with few bullate brown squamules to 3 mm long with white apical ciliae; sterile veins forked or simple, fertile veins forked. *Sori* to 1.0 mm diam., subcostal, in fork of vein; indusia hemitelioid, dark brown, shiny, firm, ascending, with lacerate margins, reaching 1/3 to 1/2 around the receptacles, covered entirely by intact sori; receptacles globose, 3-4 mm diam., paraphyses thin, hyaline, tan, shorter than sporangia (0.2-0.3 mm). *Spores* not examined.

*Cyathea ars* is superficially similar to *C. heliophila* R. M Tryon, from which it differs in distinctly bicolorous petiole scales (vs. mainly concolorous in *C. heliophila*) and many concolorous brown, ovate to round scales on the leaf axes (vs. white to bicolorous, ovate-lanceolate scales). *Cyathea ars* is characterized by tortuous white hairs and brown scales on the leaf axes, which are also found in *C. frigida* (H. Karst.) Domin; that species is exindusiate and has dark brown, only weakly bicolorous petiole scales (vs. hemitelioid indusiate and strongly bicolorous petiole scales with white margins in *C. ars*).

There are several specimens of putative hybrids between *C. heliophila* and *C. frigida*, all of them from trunkless plants. The main indicator for hybrid origin is, apart from intermediate morphology, the irregularly developed sporangia. The single collection of *C. ars* has immature sporangia, so an investigation of aborted or malformed spores as indicator of hybrid origin is not possible. Still, it is highly likely that this species and *C. oxapampana* Lehnert represent recurring hybrids with different parental character recombinations. Until their status is cleared, they should be recognized as separate species, which will help further studies.

***Cyathea chontilla*** Lehnert, sp. nov. ined. Type: PERU. Cajamarca: San Ignacio, Hurango, localidad Romerillo, Cordillera entre Romerillo y Nuevo Mundo, 05°14'S, 78°46'W, 2300 m, 29 Jul 1992, *Campos et al.* 4294 (holotype, UC; isotype, MO). Fig. 10.

*Cyathea pygmaea squamis anguste lanceolatis cupreis, laminis triangularibus gradatim reductis, rachidibus sparse vel abundante squamatis, indusiisque sphaeropteroideis. A C. patente* H. Karst. *statura minore, a C. sylvatica* Lehnert *laminis subcoriaceis (vs. herbaceis), squamis petiolorum majoribus (usque 10.0 x 2.5 mm vs. 12.0-20.0 x 2.0-3.5 mm) differt.*

Etymology: The name is a diminutive of „chonta,“ a vernacular name for tree ferns in northern Peru, referring to the small size of the plant.

*Trunks* absent, rhizomes short-ascending; apices hidden in fascicles of petioles; adventitious buds lacking. *Fronde*s 45-110 cm long, erect. *Petioles* 15-36 cm long, dark-brown to blackish, weakly shiny, inermous; scurf brown, dense, consisting of variously sized, erect to appressed, ovate to lanceolate squamules with fimbriate margins and brown tortuous hairs to 1 mm long; without pneumathodes; densely scaly proximally, moderately to sparsely so in distal parts. *Petiole scales* to 12.0-20.0 x 2.0-3.5 mm, narrowly lanceolate, shiny, concolorous or weakly bicolorous, deep brown with margins yellowish to cream white, the tips elongate, undulate, not twisted, differentiated margins narrow with cells strongly exerted, shortly dentate, without setae or ciliae. *Laminae* to 30-85 x 25-35 cm, bipinnate to bipinnate-pinnatifid, long-triangular to lanceolate, coriaceous, dark green adaxially, black when dried, grey-green abaxially, apices gradually reduced, tapering. *Rhachises* inermous, dark brown to castaneous, densely hairy on both sides with brown, twisted, pluricellular hairs to 1.0 mm long, also with scattered, lanceolate to linear scales to 4 mm long. *Pinnae* to 17 cm long, weakly ascending, stalked to 5 mm, mostly alternate, fully pinnate only in proximal halves, narrowly green alate distally; basal pinnae about the size of the medial pinnae, not reflexed, sometimes opposite. *Costae* dark-brown to castaneous, inermous, adaxially densely hairy with whitish to tan, antrorsely curved, pluricellular, uniseriate hairs to 1.0 mm long, abaxially glabrescent with sparser twisted hairs and few concolorous brown, lanceolate scales with whitish shortly fimbriate margins, most frequently in the axils; junctures of rhachises and costules not swollen, each abaxially with a circular, prominent pneumathode to 1 mm diam., dark gray to black in dried specimens. *Pinnules/segments* to 20.0-40.0 x (6.0-)8.0-14.0 mm, oblong to oblanceolate, sessile, ca. 0.7 cm between the midveins, cuneate to weakly cordate at base, tips obtuse to rounded, patent, weakly ascending, straight to distally falcate, margins shallowly to deeply crenate with entire lobes, often revolute when dried; segments with few whitish to tan, erect hairs 0.5-0.8(-1.0) mm long on the veins abaxially, restricted to the

midveins/costules adaxially, none between the veins; with few to many dark-brown scales on the midveins/costules abaxially, ovate-lanceolate, flat or bullate, to 2.0 x 0.8 mm with weakly dentate-lacerate margins; veins weakly protruding abaxially, planar or sunken adaxially, sterile veins forked or simple, fertile veins forked. *Sori* to 1.0-1.2 mm diam., subcostal to inframedial, on the back of vein; indusia sphaeropteroid, with prominent umbo, shiny dark brown, translucent; receptacles globose, 0.3-0.4 mm diam, paraphyses thin, hyaline, tan to brown, as long as sporangia (0.4 mm). *Spores* not examined.

**Distribution and habitat.** – Known only from Peru, growing in ridge-top vegetation at 2300-2850 m.

**Additional specimen examined. PERU. Pasco:** Prov. Oxapampa, Dist. Oxapampa, Chacos (antena telefonica), 10°37'S, 75°17'S, 2850 m, 21 Sep 2003, *Rojas R. et al. 1487* (MO, UC).

*Cyathea chontilla* is superficially similar to *C. polliculi* Lehnert but can be distinguished by the more strongly dissected pinnules (vs. entire in *C. polliculi*), the more concolorous petiole scales, and the firm sphaeropteroid indusia (vs. hemitelioid). *Cyathea chontilla* probably belongs to the *C. patens* group, which is characterized by fimbriate laminar scales and scurf of tortuous hairs. This group of sphaeropteroid-indusiate tree ferns is typical of the upper mountain rain forests from Costa Rica through the Andes, and constitutes several small species like *C. parvifolia* Sodiro (syn. *C. brevistipes* R. C. Moran). The latter species can be distinguished from *C. chontilla* by longer petiole scales, stronger dissected pinnules, and the regular presence of aplebioid pinnae at the petiole bases. *Cyathea sylvatica* Lehnert is another diminutive species from this group, which can be distinguished from *C. chontilla* by less indument abaxially on the laminae and smaller, concolorous petiole scales. *Cyathea chontilla* has also more hairs abaxially on the veins than adaxially (vice versa in *C. sylvestris*) and fringed margins on the laminar squamules (vs. margins mostly entire).

***Cyathea convergens*** Lehnert, sp. nov. ined. Type: VENEZUELA. Amazonas: Prov. Atabapo, slope of Cerro de Marahuaca, Río Yameduaka Arriba, 03°38'N, 65°28'W, 1225 m, 21 Feb 1985, *Liesner 17814* (holotype, UC; isotype, MO).

(Fig. 11)

*A Cyathea divergente* Kunze var. *divergente pubescentia breve laminarum squamellisque petiolorum brunneis bicoloratis cum marginibus pallidioribus dentibus obfuscatis instructis* (vs. *pubescentia carens squamellisque petiolorum albidis, dentibus carens vel sparse nigrescentibus instructis*) differt.

Etymology: The epithet alludes to the similarity with *Cyathea divergens* Kunze.

*Trunks* to 0.5-2.0 m tall, to 5 cm diam., with old petiole bases, presumably without them if larger; upper parts invested in concolorous dark brown scales, similar to petiole scales; trunk apices hidden in fascicles of the youngest petioles; adventitious buds lacking. *Petioles* 30-55 cm long, sparsely muricate, dark brown to atropurpureus, basally often black; without adventitious (aphlebioid) pinnae at the petiole bases; petiole scurf well developed, whitish to pale brown, consisting of multiple types of squamules; squamules mainly erect to appressed, ovate, 0.5-1.0 mm long, with brown to tan center, whitish to yellowish margins, and irregularly set, small pale brown marginal teeth. *Petiole scales* ovate-lanceolate to lanceolate, 12-20(-25) x 3-4 mm, their tips straight, concordantly bicolorous or nearly concolorous, brown to dark brown center sharply set against the white to yellowish margins, usually shiny. *Fronde*s to 150-200 cm long, arching. *Laminae* to 150 x 50-150 cm, bipinnate-pinnatifid, chartaceous, apices gradually reduced; dark green adaxially, usually blackish when dried, pale olive green abaxially. *Pinnae* to 30-75 cm long, ca. 12-15(-20) pairs per frond, stalked (1.5-)1.7-4.0(-5.0) cm, distally narrowly green alate, the distal segments decurrently adnate. *Leaf axes* brown to dark brown, hairy only adaxially on costules and distal parts of costae and rhachises, hairs 0.5-1.0 mm long, whitish to tan, without hairs abaxially, but with tan to brown scurf consisting of small squamules 0.2-1.0 mm long, like those of the petiole, usually strongly dissected to fimbriate, persisting in junctures of costae with costules and rhachises; costae smooth, rarely more than 2-3 mm wide. *Pinnules* (6.0-)9.0-11.5 x (1.2-)2.0-2.7 cm, largest stalked to 2-6 mm, alternate, 0.5-2.0 cm between the stalks, lanceolate to oblong, truncate to weakly cordate at bases, tapering from above the middle (rarely in large pinnules from the base) to short attenuate tips, the segments patent to weakly falcate with finely crenate margins and rounded to obtuse tips; basal segments alternately placed, sometimes remote from each other, sinuses narrow to wide (0.2-2.0 mm), rectangular to acute; sterile segments usually broader than fertile ones. *Veins* adaxially glabrous, abaxially glabrous or with few white, erect, multicellular, uniseriate hairs to 0.5 mm long mostly on the veins, some also between them; with small flattish, brown, ovate squamules with elongated tips and

finely dissected dark brown squamules, sometimes single subbullate brown squamules distally on the midribs of segments; sterile veins forked or simple, fertile veins forked. *Sori* 1.0(-1.5) mm diam., costal to subcostal, indusium sphaeropteroid, with umbo, tan, translucent, fragile, persisting as a cup; paraphyses as long as or shorter than sporangia. *Spores* not examined.

**Distribution and habitat.** – In the southern tepuis of Venezuela, Edo. Amazonas, in cloud forests, gallery forests, and bromeliad thickets at 1225-2560 m; to be expected in N Brazil (Neblina range).

**Additional specimens examined: VENEZUELA. Amazonas:** Dpto. Atabapo, Cerro Marahuaca, 03°40'30"N, 65°26'20"W, 2560 m, 10-12 Oct 1983, *Steyermark 12940* (MO, UC); Dpto. Río Negro, Camp VII, Cerro de la Neblina, 5.1 mi NE Pico Phelps (= Neblina) (21.5 km E Neblina Base Camp), up new trail from heliport (1850 m) to steep, E facing escarpment of W wall of valley, 00°50'40"N, 65°58'10"W, 1875 m, 02 Feb 1985, *Beitel 85122* (NY, UC).

*Cyathea convergens* has been determined as *C. divergens* var. *divergens* in the past but can be easily distinguished from that species by the tan (whitish in general aspect) scurf consisting of ovate squamules with lacerate margins 0.5-1.0 mm long (vs. white scurf with larger lanceolate squamules 0.5-2.0 mm long in *C. divergens*) and the narrower petiole scale margins; it also has some hairs to 0.5 mm on and between the veins, a characteristic that *C. divergens* lacks. Two varieties of *C. divergens* occur together with *C. convergens* on the slopes of the Venezuelan tepuis, var. *divergens* and var. *sipaliwini*. The var. *divergens* is quite distinct with purely white scurf squamules that lack blackish marginal teeth; it is wide spread in the Andes and Central America and has been found on the slopes of the Neblina massif, but is otherwise absent in the Guayana Highland. The var. *sipaliwini* has whitish to partially tan or light brown scurf squamules, coming close to the condition in *C. convergens*, but the latter has usually darker petiole scales with narrower margins than *C. divergens* var. *sipaliwini*. *Cyathea convergens* also has smaller and thinner trunks than *C. divergens* (5 cm vs. 12 cm diam.), which apparently includes a sheath of persistent petiole bases (vs. old petioles soon shed in *C. divergens*).

*Cyathea meridensis* is very similar to *C. convergens* in the generally dark brown coloration of axes and scales, the short-stalked pinnules, and the thin trunks. Both can be distinguished by the color of scurf (whitish to tan in *C. convergens* vs. dark brown to castaneous in *C.*



*meridensis*) and petiole scales (bicolorous dark brown to castaneous with whitish margins and brown teeth vs. bicolorous to concolorous castaneous to blackish with brown to orangish margins without differently colored teeth). Both species may have inconspicuous short uniseriate hairs abaxially on the veins, but these are appressed in *C. meridensis* and erect in *C. convergens*. *Cyathea convergens* may represent a hybrid between *C. divergens* var. *sipaliwini* and *C. meridensis*.

**Cyathea diabolica** Lehnert, sp. nov. ined. Type: ECUADOR. Zamora-Chinchipec: new road Loja-Zamora, trail to *Podocarpus* patch at Quebrada del Diablo, 2000-2400 m, 01 May 1987, *van der Werff & W. Palacios* 9252 (holotype, UC; isotype, MO).

(Fig. 12)

*Cyathea ex grege C. venezuelensis* A. R. Sm. *pinnulis oblongis basim cordatis petiolulatis*; a *C. sagittifolia* (Hook.) Domin et *C. barringtonii* A. R. Sm. ex *Lellinger paraphysibus longioribus*, a *C. ulei* (H. Christ) Domin *pinnulis minoribus (usque 3.8 cm vs. 10.5 cm longis) differt*.

Etymology: The name refers to the type locality “Quebrada del Diablo”.

*Trunks* to 3 m tall, slender, otherwise unknown. *Petioles* to 20 cm long, inermous or verrucate, dark castaneous; lenticels not observed in dried material; without adventitious (aphlebioid) pinnae at the petiole bases; petiole scurf ephemeral, consisting of brown to reddish trichomidia and branched multicellular hairs 0.2-0.4 mm long. *Petiole scales* lanceolate, 5.0-6.0 x 1.5(-2.0) mm, their tips straight, shiny auburn to dark reddish brown, concolorous or with narrow paler to golden brown margins; colors transient, not sharply contrasted. *Fronde*s to 110 cm long, presumably straight and ascending. *Laminae* to 80 x 45 cm, lanceolate, bipinnate to bipinnate-pinnatifid, chartaceous, apices abruptly to gradually reduced, i.e., a conform apical pinna is followed by two to three transitional pinnae; dark green adaxially, black when dried, dark olive-green abaxially. *Pinnae* to 25 cm long, ca. 10 pairs per frond, basal pairs not greatly reduced (ca. 1/3 the size of medial pinnae), long stalked to 1.0-1.5 cm, distally not or very narrowly green-alate, the distal segments free. *Leaf axes* (i.e., rhachises, costae, and costules) brown to pale castaneous adaxially and abaxially; completely glabrous abaxially except for some remnants of scurf; hairy adaxially on costules,

costae and rhachises, hairs 1.0-1.5 mm long, brown atropurpureous; costae inermous, 1.5-2.0 mm wide; insertions of costae into rhachises swollen, each with one brown pneumathode, elliptic to 1 mm long, and a black lunular spot to 3 x 1 mm. *Pinnules* 2.8-3.4 x 0.5-0.8 cm, the largest ones short-stalked to 1.0-2.0 mm, alternate, ca. 1 cm between the stalks; the stalks articulate, with a dark ring basally, each with an inconspicuous, elliptic pneumathode 1.0 mm long at their base; pinnules linear-oblong, pinnatifid, lobed less than halfway to the costules, sometimes with revolute margins, with truncate to cordate bases, tapering from beyond the middle to acute tips; basal segments/lobes opposite, the lowest pair as small auricles, not covering the costae; costules abaxially with reddish brown, flat lanceolate squamules to 2 mm long. *Veins* dark brown and weakly prominent adaxially and abaxially; glabrous adaxially, abaxially with appressed, tan to reddish brown trichomidia and branched pluricellular hairs; sterile veins simple, fertile veins forked. *Sori* 1.0-1.2 mm diam., medial, sitting on the back of lateral veins, either in or below vein's fork; receptacles globose, 0.2-0.3 mm diam., without subtending squamules, indusia absent; paraphyses as long as or a bit longer than sporangia (0.5-0.6 mm). *Spores* not examined.

**Distribution and habitat.** – Known only from the type locality in southern Ecuador; growing in the shade in montane rainforests at 2000-2400 m.

The overall dark aspect of the type specimen may be due to alcohol conservation, although it is not explicitly labelled as conserved-in-alcohol. Another remarkable thing is that the fronds are fertile from base to tip, indicating good growth conditions. Maybe this species has considerably wider pinnules in shaded, sterile plants. Similar trends are observed in the related *C. barringtonii* and *C. sagittifolia*. The latter species, which have generally the same pinnule outline, have much shorter paraphyses than *C. diabolica*. None of the habitually similar species occur in the known range of *C. diabolica*; using existing keys, the species will come out as *C. ulei*. That species is generally larger and has much longer and wider pinnules than *C. diabolica* (to 10.5 x 2.4 cm vs. 3.8 x 0.8 cm).

**Cyathea guentheriana** Lehnert, sp. nov. ined. Type: ECUADOR. Napo: Quijos Cantón, Reserva Ecológica Antisana, Río Aliso, 8 km SW of Cosanga, 00°35'S, 77°57'W, 2530 m, 12 Nov 1998, *Vargas H. et al. 2949* (holotype, UC; isotype, MO).

(Fig. 13)

*Cyathea incertae affinitatis dissectione laminarum simile Cyathea xenoxyla* Lehnert, *sed ab ea soris majoribus (1.0-1.2 mm vs. 0.8-1.0 mm in C. xenoxyla), squamis persistentioribus nigribus (vs. squamis brunneis deciduis), petiolis purpureis parce nitentibus (vs. petiolis viridis vel stramineis usque brunneis opacis) differt.*

Etymology: Named after Rebecca Guenther, UC Berkeley, in acknowledgement of her support of tree fern studies.

*Trunks* to 2-6 m tall, to 12 diam., otherwise unknown; presumably adventitious buds lacking. *Frond* dimensions unknown (here estimated to be to 200 cm long, erect and stiffly planar). *Petioles* 35 cm or more long, weakly to strongly spiny, with spines to 3-5 mm long, dark brown to atropurpureous, weakly shiny; without adventitious (aphlebioid) pinnae at the petiole bases; with a discontinuous row of narrowly elliptic lenticels to 9 x 1-2 mm, dark orange-brown in dried material; petiole scurf dense, long lasting, concolorous whitish to tan or pale brown, consisting of small, erect to appressed, ovate to round squamules 0.2-0.5(-1.0) mm long, with strongly crested to fimbriate margins, without dark marginal teeth, only abraded in inermous petiole parts. *Petiole scales* lanceolate, 20.0-32.0 x (3.0-)4.5-5.5 mm, their tips straight to falcate, undulate, concordantly bicolorous, the bases cordate, pseudopeltately attached, the black (deeply atropurpureous in backlight) center sharply set against the golden brown margins, very shiny. *Laminae* to ca. 150 x 100 cm, bipinnate-pinnatifid, firm herbaceous, widest at the middle, apices gradually reduced; dark green adaxially, blackish to plumbeous when dried, dull grayish green abaxially. *Rhachises* dark purpureous to brown, usually darker adaxially, glabrous or weakly hairy in distal parts; sometimes with remnants of tan to brown scurf, especially in the axils to the costae, consisting of squamules similar to those on the petiole. *Pinnae* to 55 cm long, presumably 12-15 pairs per frond, inarticulate, ascending, sessile or short stalked to 0.5 cm, distally not green alate, the distal segments simply adnate. *Costae* dark stramineous to purpureous, adaxially often darker, adaxially densely hairy, hairs 0.5-1.0 mm long, tan to brown, antrorsely curved to appressed; abaxially glabrous, inermous to muricate, 3-4 mm wide; junctures of costae and rhachises abaxially weakly swollen, each with a planar pneumathode to 4 x 1-2 mm, brown, inconspicuous. *Pinnules* to 8.0-9.5 x 1.7-2.0 cm, largest ones sessile to stalked to 1.0 mm, alternate, inarticulate, 2.0-2.2 cm between the stalks, linear-oblong, cuneate to rounded at bases, tapering from beyond the middle to attenuate tips with serrate to crenulate margins;

costules dark stramineous to dark-brown, adaxially moderately hairy with appressed tan to brown hairs to 0.5-1.0 mm long, abaxially glabrous, rarely with remnants of whitish to tan scurf or with some single erect white hairs to 1 mm long in distal parts; costules basally without pneumathode; segments ascending, distally straight to weakly falcate, tips rounded to obtuse, margins deeply crenate-dentate; basal segments alternate, not remote from each other, or if so then connected by laminar tissue, sinuses 1-2 mm wide, obtuse; sterile and fertile pinnules not different. *Veins* glabrous adaxially except for some white to tan, erect pluricellular hairs to 1 mm long on the midveins; abaxially glabrous except for single hairs to 1 mm long sometimes on the midveins; sterile veins forked or simple, fertile veins forked. *Sori* 1.0-1.2 mm diam., costal, indusia subsphaeropteroid to sphaeropteroid, without umbo, tan, translucent, fragmenting to a shallow cup or disc; receptacles globose, 0.3-0.5 mm diam, paraphyses many, hyaline, tan, shorter than sporangia (0.3-0.4 mm). *Spores* tetrahedral-globose, pale yellow, hyaline.

**Distribution and habitat.** – Known only from eastern Ecuador, Prov. Napo, growing at 2000-2530 m in perhumid montane rainforest.

**Selected specimens examined. ECUADOR. Napo:** Quijos Canton, Reserva Ecologica Antisana, Cordillera de Guacamayos, proposed ARCO oil pipeline route, 00°38'N, 77°51'W, 2000 m, 1 Oct 1997, *Neill et al.* 10790 (MO, UC); Tena Cantón, P.N. Llanganates, trail Salcedo-Tena, Km 74, shore of Río Mulatos, 01°01'S, 78°12'W, 2020 m, 10 Sep 1998, *Vargas H. et al.* 2179 (MO, UC)

*Cyathea guentheriana* resembles in the dark coloration other species of *Cyathea* with sphaeropteroid indusia, like the common *C. squamipes* H. Karst. and *C. meridensis* H. Karst. These differ from *C. guentheriana* in the shape of the pinnules and segment margins: In *C. squamipes* and *C. meridensis*, they are lanceolate to long-triangular with truncate to weakly cordate bases and crenulate margins; they are linear-oblong with cuneate to rounded bases and deeply crenate inciso-serrate margins in *C. guentheriana*. The pinnae and pinnules of *C. guentheriana* are usually sessile or very short-stalked; in *C. squamipes*, the largest pinnules may be stalked to 5 mm, in *C. meridensis* even more than 1 cm. The whole fronds of *C. guentheriana* seem to be planar and held stiffly erect due to the stout leaf axes, with markedly straight, ascending costae. In *C. squamipes* and *C. meridensis*, the fronds are arching to drooping with mostly patent pinnae.

No field observations of the habit of *C. guentheriana* are available; the similarity with *C. xenoxyla* in characters of the frond suggests that it may share the distinct trunk morphology of that species. The petioles, however, have relatively large insertions and a characteristic bend near the bases, which is typical of species that form a tight fascicle of petioles around the trunk apex, hiding and protecting the young crosciers. In *C. xenoxyla*, the insertions are small and the bases are straight because the petioles do not form a fascicle but go off directly from the trunk, giving full sight to the young crosciers on the hemispherically shaped trunk apex.

Regarding the fronds, *C. guentheriana* is best described as *C. xenoxyla* dyed in a darker hue. The petiole scales are very shiny, almost concolorous black (vs. weakly shiny dark brown to castaneous with usually paler margins in *C. xenoxyla*) and the leaf axes are dark brown to purpureous and weakly shiny (vs. green in fresh material, stramineous to brown dried material).

Despite the clear bipolar connection of *C. guentheriana* with the habit of one species and the coloration of the other, there are no indications of a hybrid origin of this species. Sporangia and spores are well formed and of equal size, indicating a regular development involving matching chromosome pairs.

**Cyathea nephele** Lehnert, sp. nov. ined. Type: PERU. Pasco: Prov. Oxapampa, Distrito Huancabamba, Parque Nacional Yanachaga-Chemillén, 10°22'S, 75°28'W, 3110 m, 05 Dec 2003, *Monteagudo A et al. 6430* (holotype, UC; isotype, MO).

(Fig. 14)

*A Cyathea frigida* (H. Karst.) Domin *squamis petiolorum longioribus lanceolatis brunneis pallidioribus sive concoloribus* (vs. *squamis ovato-leanceolatis atro-brunneis usque castaneis cum marginibus pallidis vel albidis*), *a C. patente* H. Karst. *absentia indusiis* (vs. *indusiis sphaeropteroideis*) *differt*.

Eytymology: Named after the Greek goddess of the clouds (Greek, *nepfos* = cloud) in reference to the cloud forests this species inhabits.

*Trunks* to 6-8 m tall, 8-10 cm diam., otherwise unknown, presumably without old petiole bases; apices hidden in fascicles of petioles; adventitious buds lacking. *Fronds* to 2-4 m long, presumably arching. *Petioles* to 40 cm long, probably longer, dull brown to orange-

brown, basally blackish, aculeate to muricate, spines with scales on their tips in young petioles; scurf white to tan, flakey, consisting of spaced, appressed, round squamules to 0.5 mm diam. with tortuous marginal ciliae, persistent; with long elliptic brown pneumathodes to 18 x 1 mm on the sides basally. *Petiole scales* to 25.0-35.0(-40.0) x 2.5-4.0(-5.0) mm, long-lanceolate, shiny, plain deep brown, concolorous or concordantly bicolorous, with margins paler brown, sometimes yellowish or cream white; scales persistent only on the sides of the petioles. *Laminae* to 160 x 70-80, bipinnate-pinnatifid, green to dark green adaxially, often blackish when dried, pale grey-green abaxially, apices gradually reduced. *Rhachises* inermous or weakly muricate basally, dark yellowish brown to orange-brown, adaxially with whitish to yellowish, antrorsely curved hairs to 0.8 mm long, abaxially glabrous or glabrescent with white to tan squamellae like in the petiole scurf. *Pinnae* to 45 cm long, patent to ascending, basal pinnules only half the size of the medial pinnae, weakly to strongly reflexed. *Costae* and costules tan, stramineous or dull orange-brown, inermous, short-hairy adaxially, hairs to 1 mm, white, antrorsely curved; abaxially glabrescent with white to tan arachnoid scurf and few bright orange-brown flattish scales with undulated, fimbriate margins, most frequently in the axils. *Pinnules* to 5.0-6.5 x 1.1-1.7 cm, linear-oblong to lanceolate, sessile to subsessile (stalked to 1 mm), 1.0-1.5 cm between the stalks, truncate to weakly cuneate, rarely weakly cordate at base, tips long-acute to attenuate, pinnatifid to pinnatisect, basal segments sometimes remote but not free; segments to 11 x 3 mm, weakly ascending, falcate, the tips obtuse to rounded, segment margins crenulate to crenate, often remaining planar when dried; segments with few to many whitish to tan, erect hairs 0.5-0.8(-1.0) mm long on and between the veins abaxially; veins adaxially glabrous or with few short hairs, none between the veins; with relatively few to many small scales abaxially, ranging from broadly ovate, flat ones (to 3.0 x 2.5 mm) to bullate ones with broadly flaring or twisted, elongated tips (to 2.5 x 1.0 mm), tan to orange-brown, often with the thin margins paler brown to whitish, fimbriate to lacerate with considerably long processes; sterile veins forked or simple, fertile veins forked. *Sori* to 1.0 mm diam., subcostal, in forks of veins; indusia absent; receptacles globose to ellipsoid, 3-4 mm diam, paraphyses thin, hyaline, white to tan, as long as or shorter than sporangia (0.3-0.4 mm). *Spores* not examined.

**Distribution and habitat.** – Frequent in central Peru, Dept. Pasco, rare in the north, Prov. Amazonas and San Martin, in upper montane forest and ridge top dwarf forests at 2800-3400 m.

**Selected specimens examined. PERU. Amazonas:** Prov. Chachapoyas, Distrito Leymebamba, road to Celendín, between Ishpingo and Pomacocha, 2800-3000 m, 20 Aug 1998, *Quipuscoa et al. 1390* (UC). **Pasco:** Prov. Oxapampa, Dist. Huancabamba, sector Santa Barbara-Milpo, 10°22'58"S, 75°37'23"W, 2900 m, 01 Feb 2005, *Mellado L. F. et al. 2779* (UC, MO); P.N. Yanachaga-Chemillén, 10°22'S, 75°28'W, 3110 m, 05 Dec 2003, *Monteagudo et al. 6430* (UC). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo National Park, 3000-3100 m, 13 Jul 1988, *León B. 2141* (UC, USM)

Most specimens of *Cyathea nephele* were previously mistaken for *C. frigida* (H. Karst.) Domin, but both species are supposedly not closely related. The most striking difference is the overall appearance of the specimens, which is summed up from relatively minor differences. The petiole scales of *C. nephele* are narrower and paler in color than in *C. frigida* (concolorous brown or bicolorous with paler brown to whitish margins vs. dark brown to castaneous with white margins); the paraphyses in *C. nephele* are not longer than the sporangia while they may be much longer than the sporangia in *C. frigida*; the segments of *C. frigida* are gibbose with revolute margins whereas they are flat in *C. nephele*, which makes the crenulate margins of the latter species more notable in dried specimens. *Cyathea frigida* is very variable in the frond size, with smaller fronds having stiffly straight pinnae while they are characteristically curved and flexuous in larger plants. In *C. nephele*, the pinnae have always straight, distally weakly curved costae. Furthermore, the fronds of *C. frigida* often have few long persisting ovate scales with weakly dentate margins, remaining from the crozier stage on rhachises and costae; if larger scales are present in *C. nephele*, they vary from ovate to long lanceolate or linear and have fimbriate and ciliate margins. Generally, *C. nephele* matches *C. patens* H. Karst. and allies in the fine indument of tortuous hairs and ciliate squamules on axes and laminae; also the petiole scales clearly align it to *C. patens*, which is easily distinguished by sphaeropteroid indusia (vs. lack of indusia in *C. nephele*).

***Cyathea oxapampana*** Lehnert, sp. nov. ined. Type: PERU. Pasco: Prov. Oxapampa, near antenna past Chacos, 10°38'S, 75°15'W, 2450 m, 19 Jul 2003, *van der Werff et al. 18647* (holotype, UC; isotype, MO). Fig. 15.

*A Cyathea heliophila* R. M. Tryon et *C. wilhelmii* Domin in *statura minore (truncum deficiens vs. trunco usque 7 m alto) paraphysibusque longioribus, a C. platylepe* (Hook.) Domin *squamis petiolorum bicoloribus (vs. squamis concoloribus) differt.*

Etymology: Named after the type locality, the Prov. Oxapampa, Peru.

*Trunkless*; rhizome apices hidden in fascicles of petioles; adventitious buds presumably lacking. *Fronde*s to 3 m long, pendent from banks or trailing over adjacent vegetation. *Petioles* to 70-150 cm long, probably longer, shiny, castaneous to atropurpleous, basally blackish, inermous, with dense, matted, white scurf consisting of appressed, strongly dissected squamules and tortuous marginal hairs, often abraded in older material; without pneumathodes, only scatteredly scaly in lower half. *Petiole scales* to 11.0-15.0 x 3.5-4.0(-5.0) mm, lanceolate, discordantly bicolorous, brown to dark brown or blackish with white margins; differentiated margins to 0.6 mm wide, cell rows strongly exerted, without ciliae or setae. *Laminae* to 150 x 60-70, long-triangular to lanceolate, bipinnate-pinnatifid to partly tripinnate, green to dark green adaxially, often becoming blackish when dried, pale grey-green abaxially, apices gradually reduced. *Rhachises* inermous, dark castaneous to atropurpleous, densely pubescent with whitish to tan, cobwebby hairs to 2.0 mm long, abaxially often glabrescent. *Pinnae* to 35 cm long, patent, alternate to subopposite, stalked to 2.5-3.0 cm, distally green alate, the distal segments before the pinnatifid apical section simply adnate; basal pinnules of the size of the medial pinnae, weakly reflexed. *Costae* and costules dark castaneous to atropurpleous, inermous, to 2.0 mm wide, adaxially with tan to brown, antrorsely curved, pluricellular, uniseriate hairs to 1.5 mm long, abaxially glabrescent with white to tan scurf and few bright orange-brown flattish scales with undulated, fimbriate margins, most frequently in the axils. *Pinnules* to 5.5-6.5 x 1.5-2.2 cm, long triangular to lanceolate, stalked to 4 mm, 1.5-2.0 cm between the stalks, bases truncate to weakly cordate, tips long-acute to attenuate, pinnatifid to pinnatisect, basal segments sometimes remote, connected by thin strands of laminar tissue; segments to 9.0-12.0 x 2.5-5.0 mm, weakly ascending, straight, the sinuses acute to obtuse, to 1.0 (-2.0) mm wide, the tips obtuse to rounded, segment margins crenulate to inciso-dentate, the basiscopical margins of the lowest segments often stronger incised; costules planar to weakly protruding abaxially, ridged adaxially, yellowish to dark carnose, with many curved brown hairs to 1.2 mm long adaxially, glabrous abaxially, with broadly ovate, flat squamules to 3.0 x 2.5 mm, and bullate squamules to 2.5 x 1.0 mm, with fimbriate tips, tan to orange-brown, often with the thin margins paler



brown to whitish, fimbriate to lacerate with long processes; segments with few to many deciduous, whitish, contorted, catenate hairs to 2.0 mm long, mainly abaxially and along the margins; veins planar to weakly immersed, yellowish to carnose, adaxially with few brown, erect hairs to 1.2 mm long, not between the veins; abaxially glabrous or with few trichomidia; sterile veins forked or simple, fertile veins forked. *Sori* to 1.2 mm diam., subcostal to costal, in fork of veins, yellowish brown to dark orange brown at maturity; indusia hemitelioid, small, appressed, tan to opaque brown, with entire margins or with one or two marginal ciliae, fragile and evanescent; receptacles globose, 0.4-0.5 mm diam, paraphyses thin, hyaline, white to tan, longer than sporangia (0.4-0.5 mm). *Spores* tetrahedral-globose, dark orange-brown.

**Distribution and habitat.** – In open forests and pajonal-vegetation in central Peru at 2450-2800 m.

**Additional specimens examined. PERU. Pasco:** Prov. Oxapampa, San Gotardo, 36 km W of Oxapampa, 10°37'S, 75°09'W, 2710-2800 m 26 Jan 1984, *Smith D. N. & Canne*, 5902 (MO, UC); Dist. Oxapampa, sector Chacos, 10°37'25"S, 75°17'43"W, 2750 m, 03 Feb 2004, *Mellado et al.* 1664 (MO, UC); Dist. Huancabamba, sector Quebrada Yanachaga (P. N. Yanachaga-Chemillén), 10°22'46"S, 75°27'43"W, 2910 m, 14 Feb 2004, *Mellado & Monteagudo* 464 (MO, UC).

*Cyathea oxapampana* is very similar to *C. heliophila* R. M. Tryon regarding the overall appearance of the fronds; it can be distinguished by the lack of a trunk (vs. *C. heliophila* usually with trunks to 7 m tall), bicolorous brown-white petiole scales (vs. predominantly concolorous whitish), the contorted hairs on the laminae (vs. contorted hairs absent), and the long paraphyses (vs. paraphyses as long as sporangia or shorter than those). The indusia of *C. oxapampana* are very thin, appressed to the lamina, and often caduceous, which may lead to the assumption that the species is exindusiate. *Cyathea heliophila* has always clearly recognizable, persistent indusia. The irregular shape and evanescence of the indusia of *C. oxapampana* may be indicators of a hybrid origin of this species, with the sympatric *C. heliophila* and *C. frigida* (H. Karst.) Domin as putative parents. Traits of *C. frigida* would be the long paraphyses, the brown color in the petiole scales, and the tendency to form real trunks only rarely. A similar parentage is hypothesized for *C. ars* Lehnert.

**Cyathea polliculi** Lehnert, sp. nov. ined. Type: ECUADOR. Zamora-Chinchipe: El Pangui, Cordillera del Condor, 2 km S of Condor Mirador Military post (observatorio #1), deep gorge of Río Tumdayme, 03°37'26"S, 78°23'35"W, 2010 m, 16 Dec 2000, *Pabón G. et al.* 359 (holotype, UC; isotype, MO). Fig. 16.

*Cyathea pygmaea squamis anguste lanceolatis brunneis bicoloribus cum margine albidis, laminis bipinnatis lanceolatis, indusiisque hemitelioideis. A C. bipinnata* (R. M. Tryon) R. C. Moran *statura minore squamisque petiolorum atrocioribus (bicoloribus brunneis cum marginibus albicantibus vs. squamis usque concoloribus albidis in C. bipinnata), apicibus laminarum gradatim reductis (vs. abrupte reductis) differt.*

Etymology: Refers to the relatively small stature of the species, which is a “Tom Thumb“ in its genus (Latin *polliculus* = small thumb or finger).

*Trunks* absent; apices hidden in fascicles of petioles; adventitious buds lacking. *Fronde*s to 0.7 m long, erect. *Petioles* to 20 cm long, dull dark-brown to blackish, opaque, sparsely muricate; scurf absent; with elliptic, brown pneumathodes to 5 x 1 mm on the sides basally; scaly only in lower third. *Petiole scales* to 10.0 x 2.5-3.5 mm, lanceolate, weakly shiny, discordantly bicolorous, deep brown with margins yellowish to cream white; scales persistent only on the sides of the petioles. *Laminae* to 50 x 20, pinnate-pinnatifid to bipinnate, long triangular to lanceolate, dark green adaxially, black when dried, gray-green abaxially, apices gradually reduced, long-tapering. *Rhachises* inermous or sparsely verrucate, dark purpleous to castaneous, with whitish to tan, antrorsely curved or appressed, uniseriate hairs, adaxially to 1.5 mm long, abaxially 0.5-0.8(-1.0) mm long. *Pinnae* to 12 cm long, weakly ascending, fully pinnate only in proximal third, narrowly green alate throughout; basal pinnae about the size of the medial pinnae, not reflexed. *Costae* dark purpleous to castaneous, inermous, adaxially densely pubescent with whitish to tan, antrorsely curved, uniseriate hairs to 1.0-1.5 mm long, abaxially glabrescent with shorter hairs and few brown flattish scales with whitish, shortly fimbriate margins, most frequently in the axils; junctures of rhachises and costules not swollen, each abaxially with a circular, prominent pneumathode to 1 mm diam., dark gray to black in dried specimens. *Pinnules/segments* to 17.0 x 3.5-4.0 mm, linear-oblong to hastate, sessile to subsessile (stalked to 0.5 mm), ca. 0.7 cm between the midveins, cuneate to weakly cordate at base, tips obtuse to rounded, patent, weakly ascending, straight to distally falcate,

segment margins crenulate, often revolute when dried; segments with few to many whitish to tan, erect hairs 0.5-0.8(-1.0) mm long on the veins abaxially and adaxially, none between the veins; with few brown scales on the midveins abaxially, ovate-lanceolate, flat, to 2.0 x 0.8 mm with weakly dentate-lacerate margins; sterile veins forked or simple, fertile veins forked. *Sori* to 1.0-1.2 mm diam., subcostal, in forks of veins; indusia hemitelioid, reaching half way around the receptacles, brown, translucent, appressed, covered completely by sori; receptacles globose to ellipsoid, 3-4 mm diam, paraphyses thin, hyaline, tan to brown, as long as sporangia (0.4 mm). *Spores* not examined.

**Distribution and habitat.** – Known only from the type locality in southern Ecuador, where it grows on poor sandstone derived soils in ridge top forest at 2010 m. To be expected at similar sites in northern Peru.

*Cyathea polliculi* may be confused with *C. palaciosii* R. C. Moran, which grows at the same locality. It can be distinguished by the pinnate-pinnatifid fronds without free segments (vs. at least partially bipinnate with free segments in *C. polliculi*) and the lack of indusia (vs. with small hemitelioid indusia). A true relationship between these two species may exist. Similar stronger dissected forms of have been found in the usually pinnate-pinnatifid, exindusiate *C. bipinnatifida* (Baker) Domin. The larger, bipinnate plants also sport irregular indusia and have been regarded as possible hybrids with stronger dissected, indusiate species (Lehnert, 2006c). Whether hybrids or not, such intermediate plants may be clearly distinguished and should be named in order to facilitate future studies. The regular shape of the indusia supports *Cyathea polliculi* as a non-hybridogenic species.

The only other species in Ecuador with a similar pinnule shape is *C. bipinnata* (R. M. Tryon) R. C. Moran, which has abruptly reduced frond apices (vs. gradually reduced in *C. polliculi*) and is restricted to the western slopes of the Andes in the north of the country (vs. known only in the southeast). Further distinguishing characters are the narrowly lanceolate, dark brown, bicolorous petiole scales, with narrow whitish margins and often with brown marginal teeth (vs. with broad white margins or almost concolorous white, without marginal teeth), and abundant short hairs on the veins (vs. glabrous).

**Cyathea praetermissa** Lehnert, sp. nov. ined. Type: PERU. Amazonas: A few Km from Molinopampa, [ca. 10°38'S, 75°15'W, 2450 m,] 14 Mar 1998, *van der Werff et al. 14935* (holotype, UC; isotype, MO). Fig. 17.

*Cyathea acaulescens laminis triangularibus vel anguste lanceolatis gradatim reductis rhachidibusque etiam costis indumento cinereo obtectis; a Cyathea oxapampana* Lehnert, *C. heliophila* R. M. Tryon et *C. frigida* (H. Karst.) Domin *indusiis sphaeropteroideis differt.*

Etymology: This species may often be overlooked and not recognized as a tree fern due its small stature (Latin, *praetermissus* = overlooked, excluded).

*Trunks* absent; rhizome apices hidden in fascicles of petioles; adventitious buds presumably lacking. *Fronde*s to 150 m long, presumably arching or pendent from banks. *Petioles* 40 cm long, probably more, weakly shiny, castaneous to atropurpureous, basally blackish, inermous, with sparse scurf consisting of appressed, strongly dissected squamules and tortuous hairs, apparently ephemeral; without pneumathodes, only sparsely scaly in lower half. *Petiole scales* to 18.0 x 2.5-3.0 mm, lanceolate, almost concolorous, dark auburn to brown with paler brown to yellowish margins, long attenuate, bases round to cordate, pseudopeltately attached; differentiated margins narrow, with cells strongly exerted, with teeth or short ciliae to 0.5 mm long, without setae. *Laminae* to 150 x 60-70, ovate-lanceolate, bipinnate-pinnatifid, green to dark green adaxially, blackish when dried, pale grey-green abaxially, apices gradually reduced, tapering. *Rhachises* inermous, dark castaneous to purpureous, densely hairy with tan to brown, antrorsely curved, uniseriate hairs to 1.5 mm long adaxially, with white, cobwebby, tortuous hairs to 2.0 mm long abaxially, glabrescent. *Pinnae* to 14 cm long, patent, alternate to subopposite, stalked to 1.2 cm, distally not or very narrowly green alate, the distal segments before the pinnatifid apical section simply adnate; basal pinnules nearly the size of the medial pinnae, not reflexed. *Costae* dark brown, inermous, to 1.0(-1.5) mm wide, adaxially with tan to brown, antrorsely curved, uniseriate hairs to 1.5 mm long, abaxially glabrescent with white scurf of tortuous hairs and few tan to brown, flattish scales with undulate, fimbriate to short-ciliate margins, most frequently in the axils; insertions of costae and rhachises not or only abaxially weakly swollen, each with a planar, elliptic pneumathode to 2.3 x 1.5 mm, blackened in dried material. *Pinnules* to 3.8 x 1.0 cm, lanceolate, sessile, 1.0-1.5 cm between the costules, bases truncate to weakly rounded, tips long acute to attenuate, pinnatifid to pinnatisect, basal segments never remote; costules

adaxially prominent, ridged, with antrorsely curved, white, pluricellular, uniseriate hairs to 1.0 mm, abaxially densely covered with white, tortuous hairs to 2 mm long and some tan to brown, subclathrate, ovate-lanceolate scales to 2.0-3.0 x 1.5-2.0 mm with fimbriate to ciliate margins; segments to 9.0-12.0 x 2.5-5.0 mm, weakly ascending, straight, the sinuses acute, to 0.5(-1.0) mm wide, segment tips obtuse to rounded, segment margins crenulate, revolute, the basiscopical margins of the lowest segments not differently incised; segments with few to many deciduous, whitish, contorted, catenate hairs to 2.0 mm long, mainly abaxially and along the margins; lateral veins planar on both sides or weakly raised adaxially, blackish to carnose, with few persistent, brown, erect hairs to 1.2 mm long, not between the veins; sterile veins forked or simple, fertile veins forked. *Sori* to 1.0 mm diam., subcostal to costal, in fork of veins, yellowish brown at maturity; indusia sphaeropteroid, tan to opaque brown, fragile, often fragmented to a cup or disc; receptacles globose, 0.3-0.4 mm diam, paraphyses thin, hyaline, white to tan, as long as the sporangia (0.4 mm). *Spores* not examined.

**Distribution and habitat.** – In scrub with *Sphagnum* on sandy soil with rock outcrops in northern Peru at ca. 2400 m. Known only from the type.

*Cyathea praetermissa* may be confused with small plants of *C. frigida* (H. Karst.) Domin, a species with similar dense indument of tortuous hairs and a comparable petiole scale color, but it *C. frigida* differs in lacking indusia (vs. *C. praetermissa* with closed sphaeropteroid indusia) and having larger and broader scales. Like many other species of *Cyathea* from similar localities, they have both a reduced trunk. *Cyathea frigida*, however, may develop a massive trunk to 4 m tall under more favorable conditions. *Cyathea nephele* is sympatric with *C. praetermissa* and matches in most indument characters, but it is generally much larger and lacks indusia.

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## Figure Captions

**Fig. 1.** *Alsophila conantiana*. **A.** medial pinna; **B.** basal pinna; **C.** basal pinnule of medial pinna, abaxially; **D.** distal segment of pinnule, adaxially; **E.** medial segment of pinnules, abaxially; **F.** indusia, left one entire, right one split open, showing receptacle with short paraphyses; **G.** squamules from pinnules, clockwise from right: large squamule from costule base, medium squamule from costules and midveins, small squamules found on all veins and axes abaxially; **H.** petiole scales (all *Lehnert 1415*, GOET).

**Fig. 2.** *Cyathea brucei*. **A.** whole plant, arrow indicates apical segment; **B.** medial pinnule, abaxially (*van der Werff et al. 13287*, QCNE). *Cyathea haughtii*. **C.** Whole plant, arrow indicates pinnatifid apex (*Haught 1957*, COL).

**Fig. 3.** *Cyathea moranii*. **A.** trunk; **B.** petiole scale; **C.** medial pinna, **D.** lamina apex, **E.** large pinnule abaxially, basal segments crenate, **F.** medium pinnule adaxially, basal segments entire; **G.** pinnule segment, abaxially; **H.** peltately attached squamule from costule; **J.** subbullate squamule from midvein, dotted line indicates corresponding parts at rupture; **K.** spores (all *Lehnert 1380*, GOET).

**Fig. 4.** *Cyathea obnoxia*. **A.** Medial pinna; **B.** Pinnule, adaxially; **C.** Segment showing hairs and two sori (arrow); **D.** Trunk apex, with remnants of old petiole (arrow); **E.** Scales from basal and upper petiole; **F.** Detail of petiole, abaxially: pluricellular trichomes and small glandular hairs (arrow). (All from *Lehnert 943*, GOET).

**Fig. 5.** *Cyathea plicata*. **A.** Pinnule from medial pinna, abaxially; **B.** Lamina apex; **C.** Trunk apex; showing pneumathodes (arrow); **D.** Petiole scales from upper and lower petiole; **E.** Squamules of petiole scurf. (All from *Lehnert 844*, GOET).

**Fig. 6.** Strongly ascending pinnules are characteristic of *Cyathea plicata* (Photo M. Lehnert of *Lehnert 1089*).

**Fig. 7.** *Cyathea sylvatica*. **A.** whole plant; **B.** pinnule abaxially, showing sphaeropteroid indusia; **C.** pinnule adaxially, showing hairs; **D.** petiole scale (all *Bussmann 1803*, QCA).

**Fig. 8.** *Cyathea aemula*. Type specimen, (*Fay & Fay 3781*, UC).

**Fig. 9.** *Cyathea ars*. Type specimen, (*Coyle et al. 258*, UC).

**Fig. 10.** *Cyathea chontilla*. Type specimen, (*Campos et al. 4294*, UC);

**Fig. 11.** *Cyathea convergens*. Type specimen, (*Liesner 17814*, UC).

**Fig. 12.** *Cyathea diabolica*. Type specimen, (*van der Werff & W. Palacios 9252*, UC).

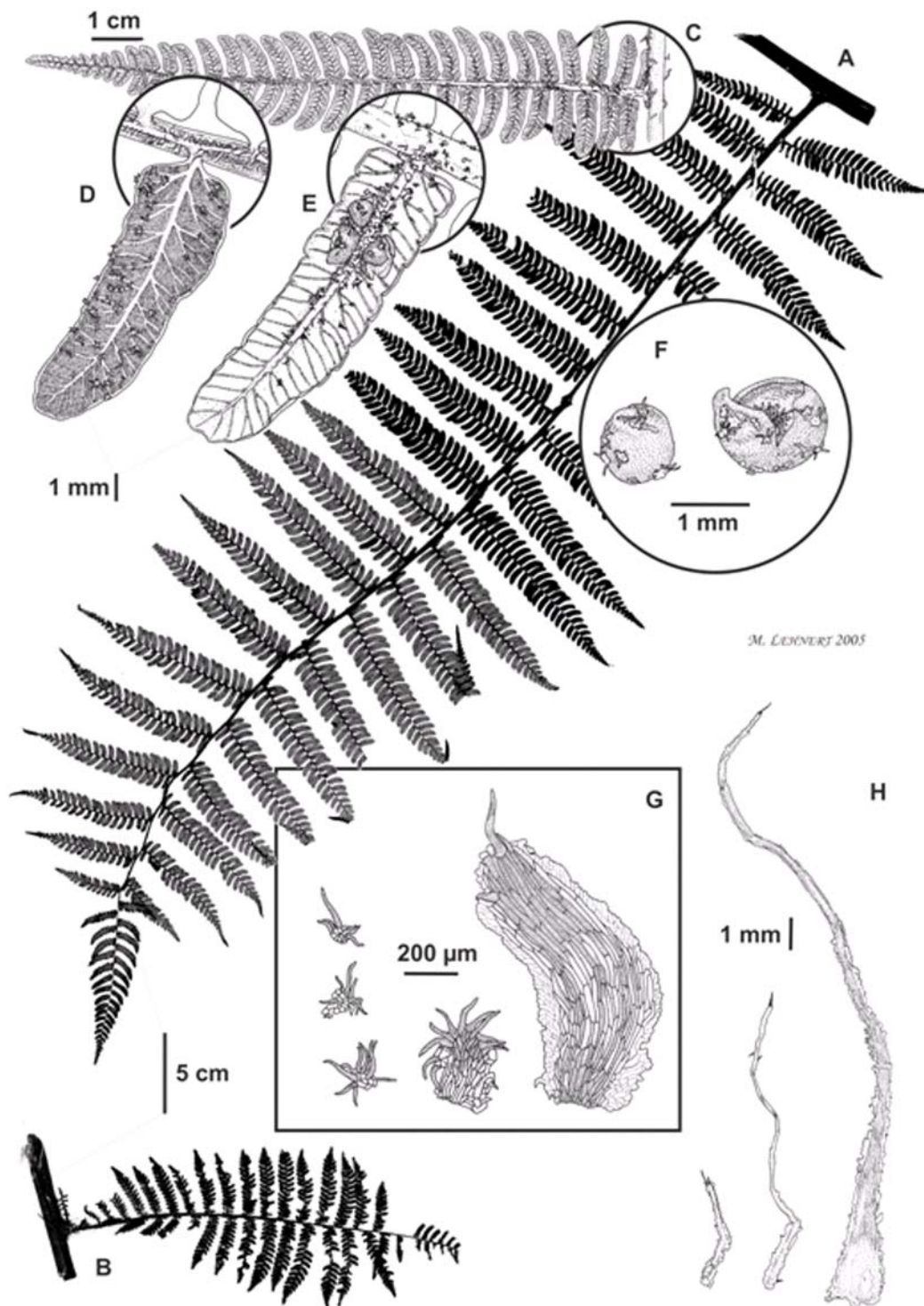
**Fig. 13.** *Cyathea guentheriana*. Type specimen, (*Vargas H. et al. 2949*, UC).

**Fig. 14.** *Cyathea nephele*. Type specimen, (*Monteagudo A. et al. 6430*, UC).

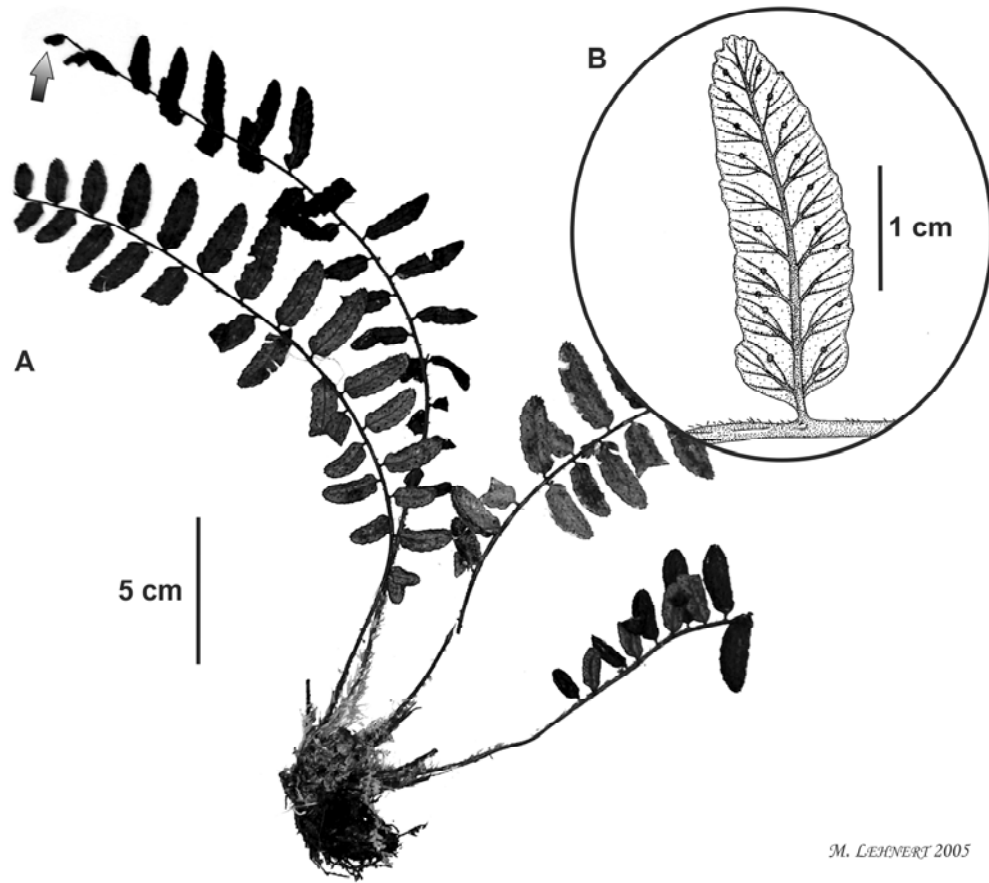
**Fig. 15.** *Cyathea oxapampana*. Type specimen, (*van der Werff et al. 18647*, UC).

**Fig. 16.** *Cyathea polliculi*. Type specimen, whole frond, (*Pabón et al. 359*, UC).

**Fig. 17.** *Cyathea pratermissa*. Type specimen, whole frond, (*van der Werff et al. 14935*, UC).



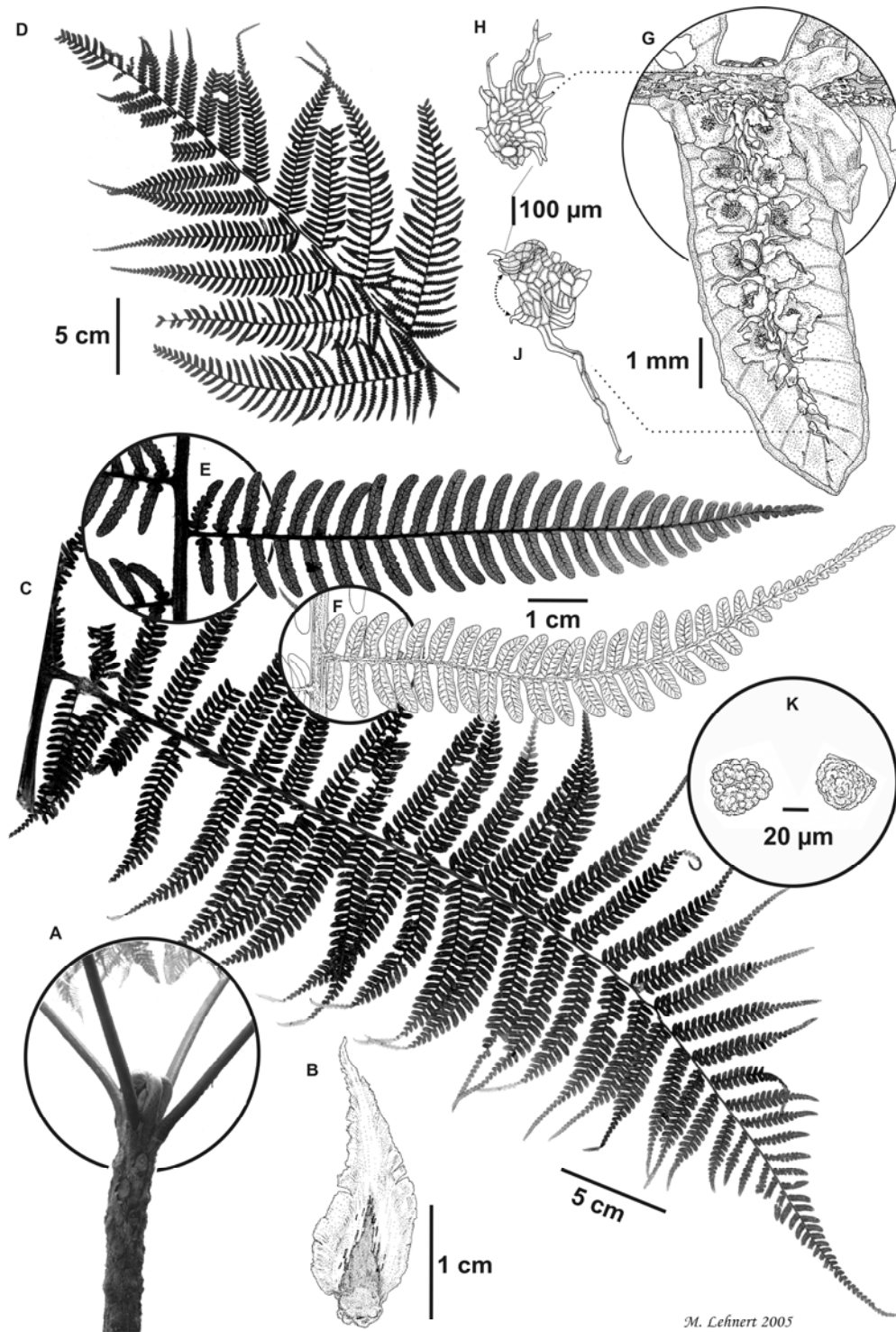
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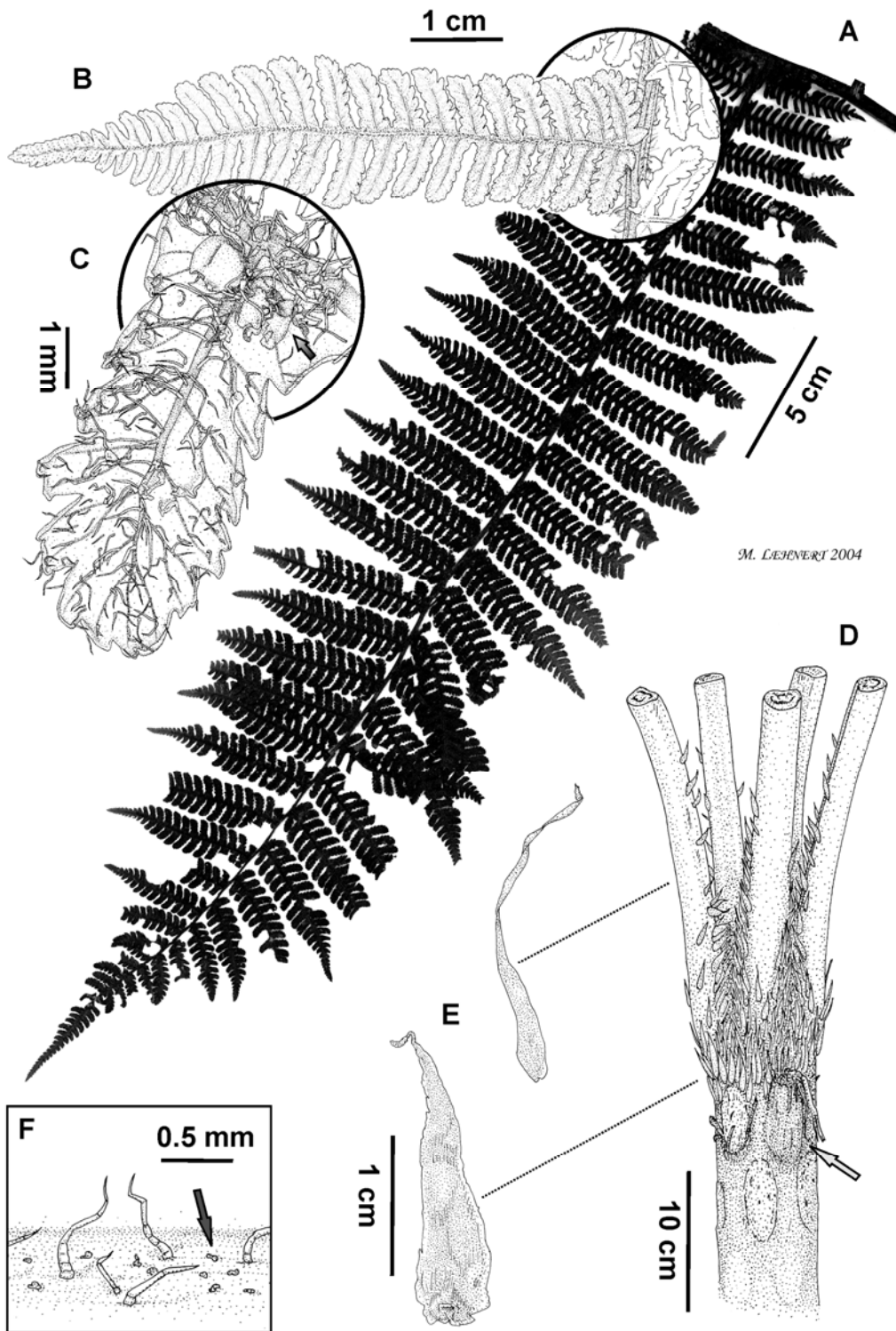
M. LEHNERT 2005



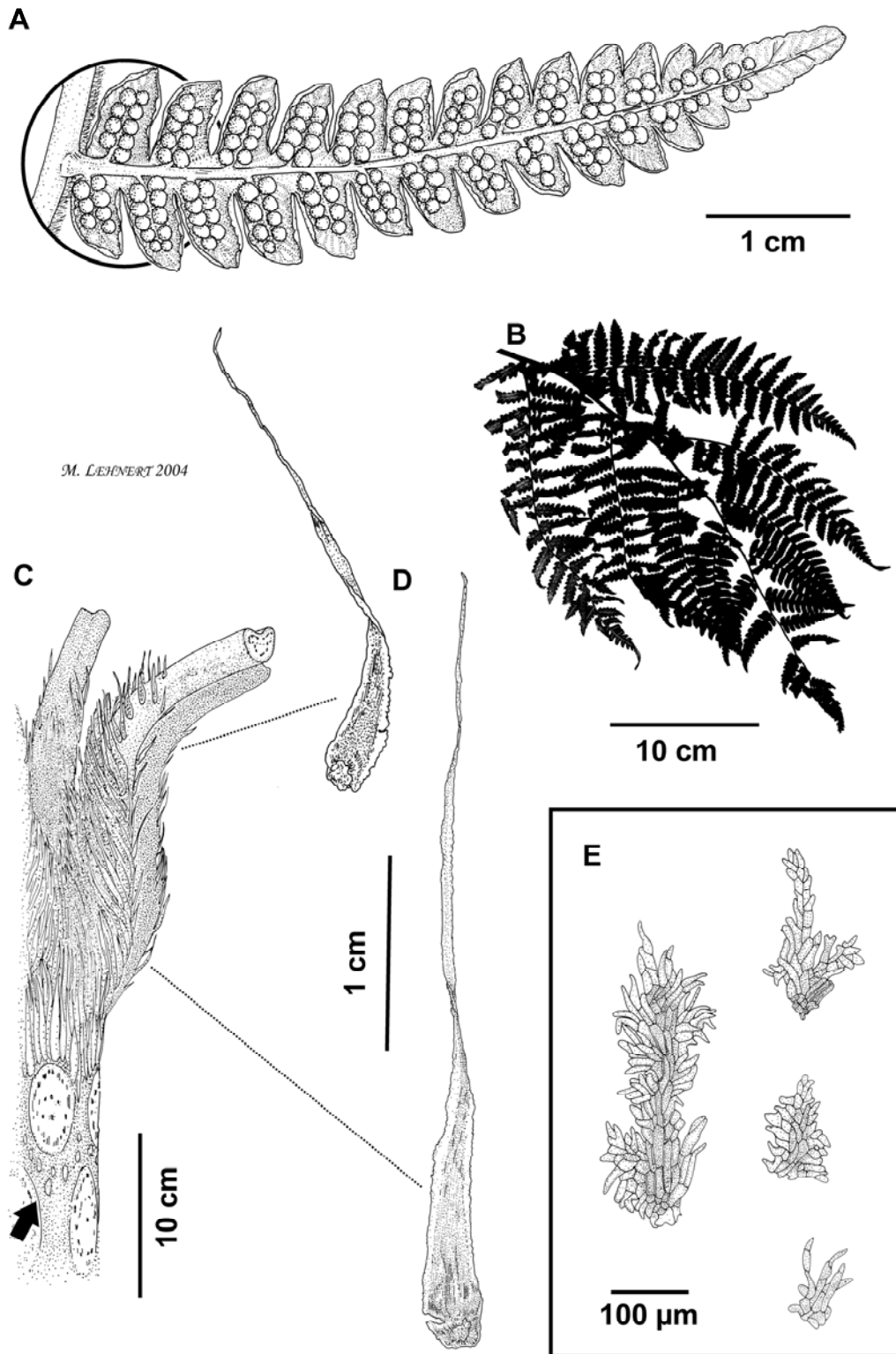
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**Fig. 3.** *Cyathea moranii*. **A.** trunk; **B.** petiole scale; **C.** medial pinna, **D.** lamina apex, **E.** large pinnule abaxially, basal segments crenate, **F.** medium pinnule adaxially, basal segments entire; **G.** pinnule segment, abaxially; **H.** peltately attached squamule from costule; **J.** subbullate squamule from midvein, dotted line indicates corresponding parts at rupture; **K.** spores (all *Lehnert 1380*, GOET).

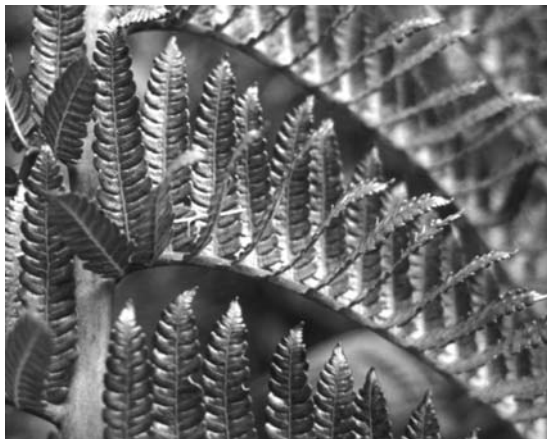


**Fig. 4.** *Cyathea obnoxia*. **A.** Medial pinna; **B.** Pinnule, adaxially; **C.** Segment showing hairs and two sori (arrow); **D.** Trunk apex, with remnants of old petiole (arrow); **E.** Scales from basal and upper petiole; **F.** Detail of petiole, abaxially: pluricellular trichomes and small glandular hairs (arrow). (All from *Lehnert 943*, GOET).

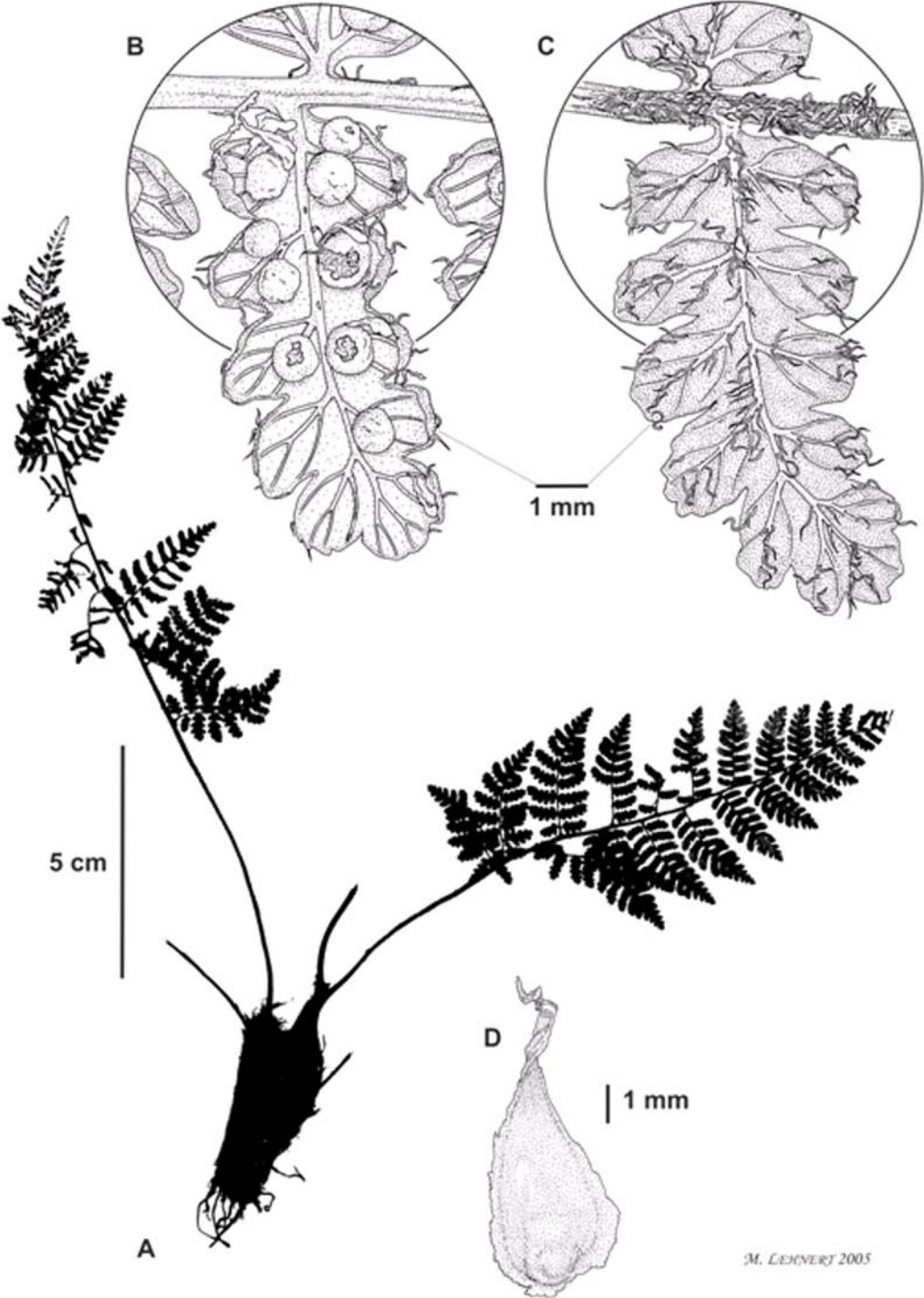


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**Fig. 6.** Strongly ascending pinnules are characteristic of *Cyathea plicata* (Photo M. Lehnert of *Lehnert 1089*).



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Fig. 8. *Cyathea aemula*. Type specimen, (Fay & Fay 3781, UC).

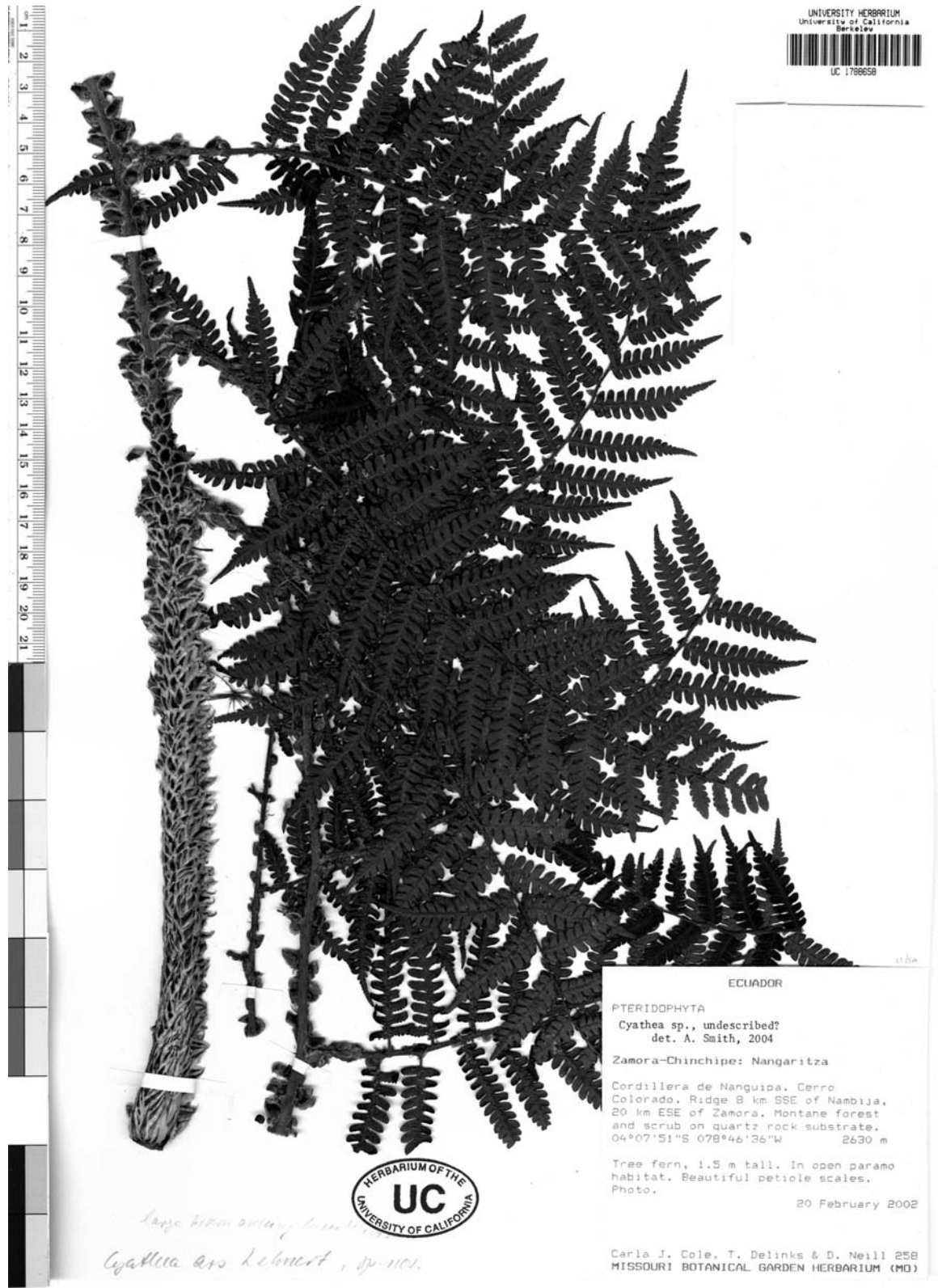


Fig. 9. *Cyathea ars*. Type specimen, (Coyle et al. 258, UC).

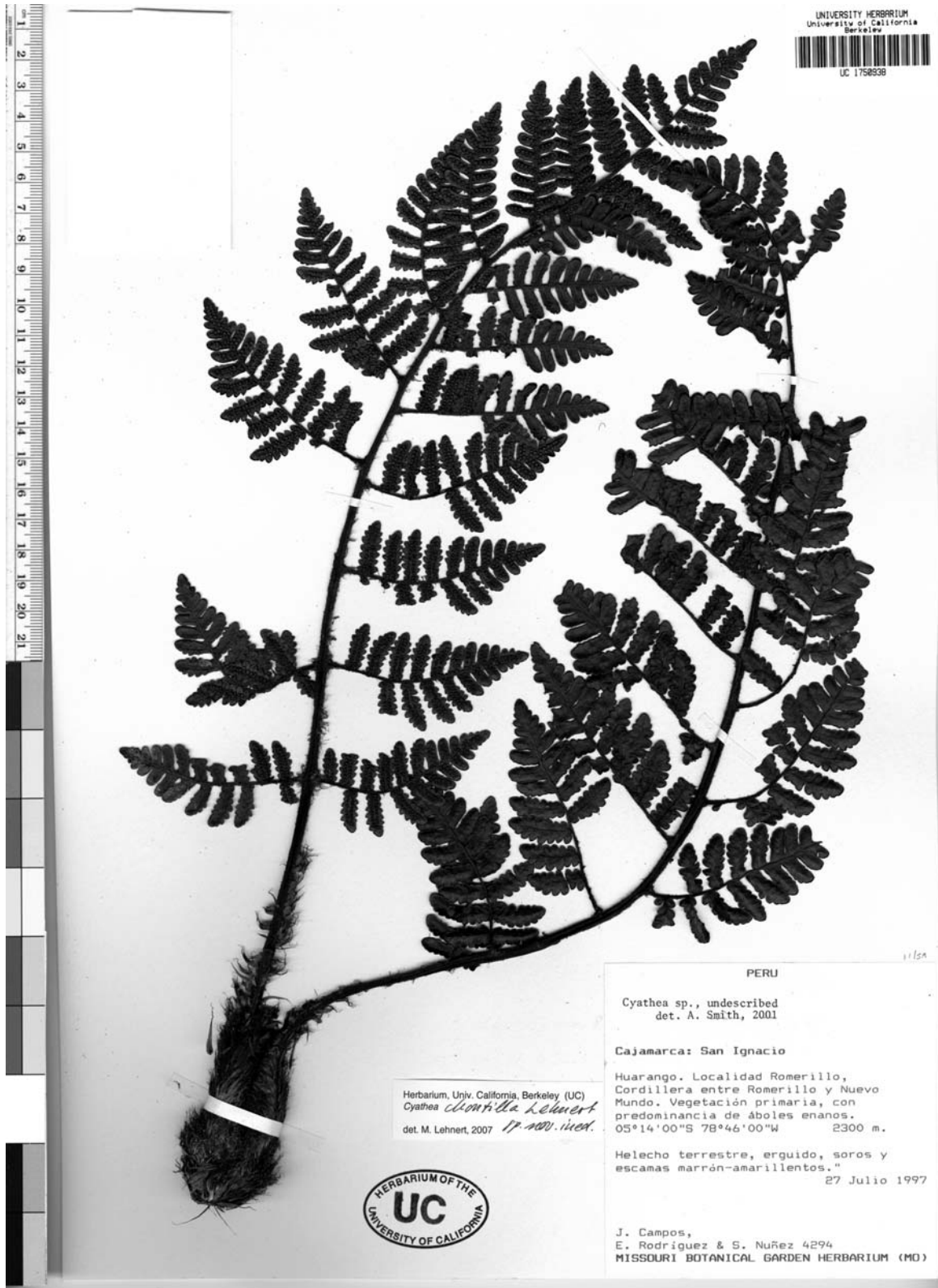


Fig. 10. *Cyathea chontilla*. Type specimen, (Campos et al. 4294, UC);.



Fig. 11. *Cyathea convergens*. Type specimen, (Liesner 17814, UC).



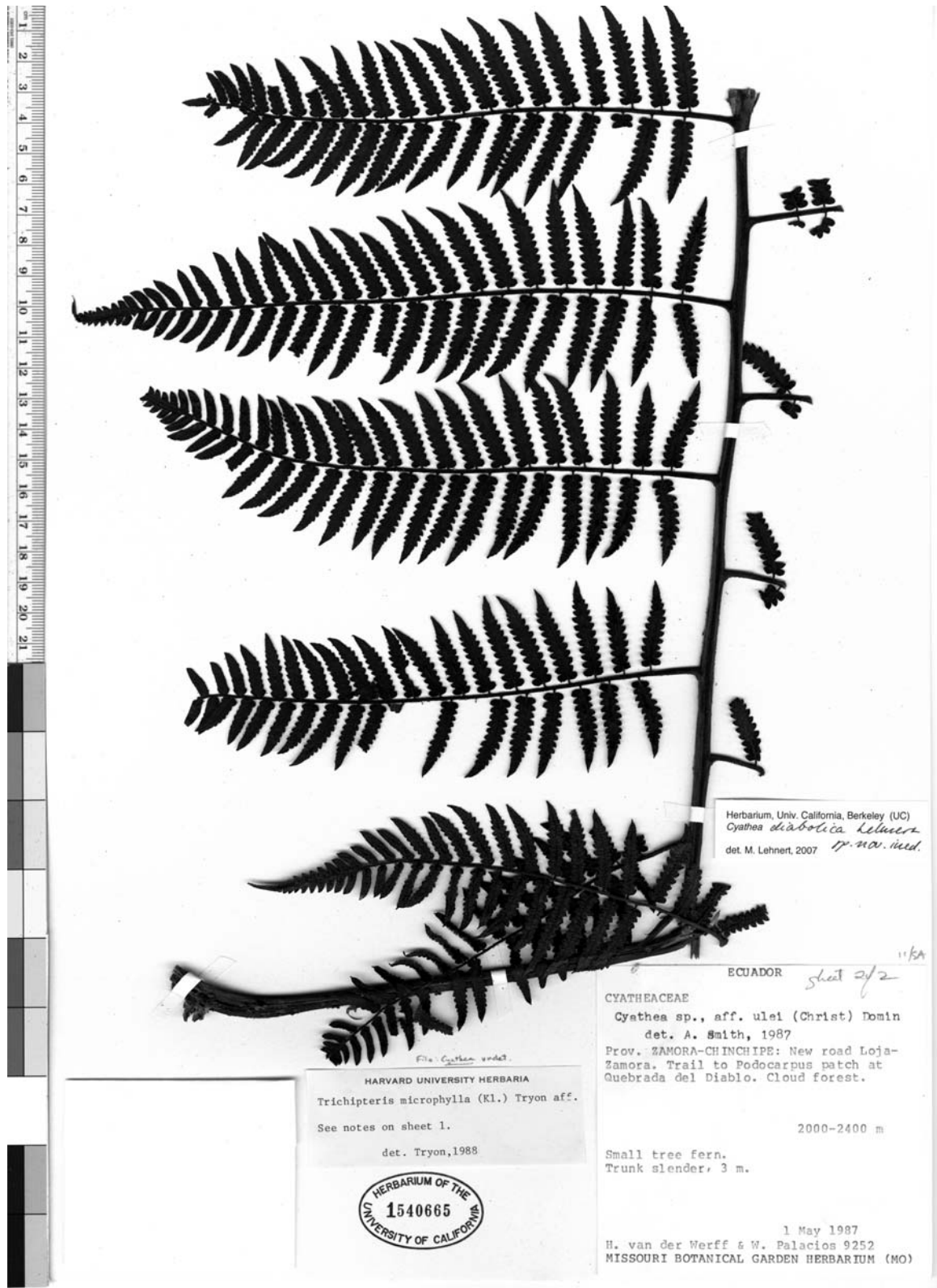


Fig. 12. *Cyathea diabolica*. Type specimen, (van der Werff & W. Palacios 9252, UC).

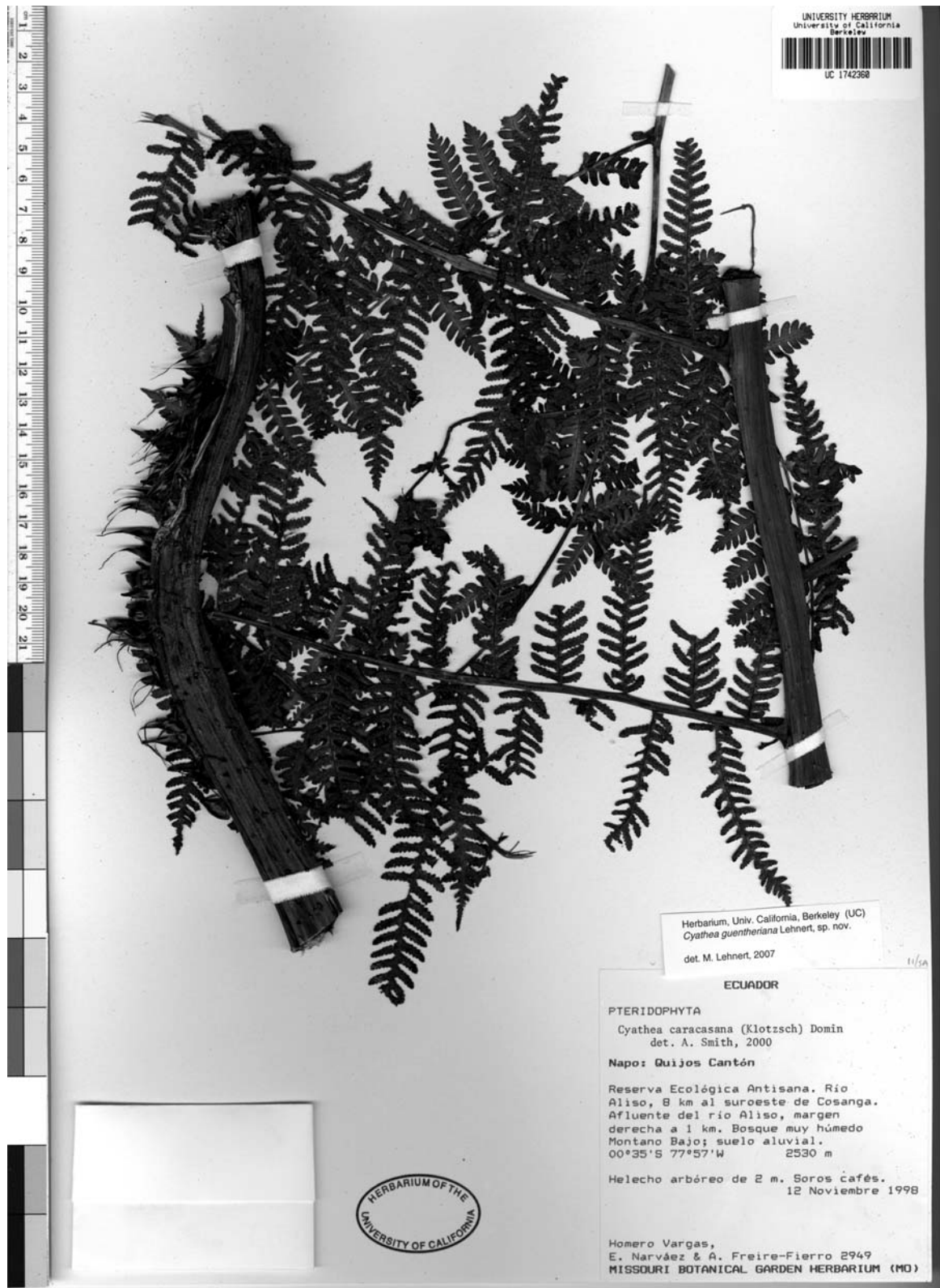


Fig. 13. *Cyathea guentheriana*. Type specimen, (Vargas H. et al. 2949, UC).





Fig. 14. *Cyathea nephela*. Type specimen, (León 2141, UC).

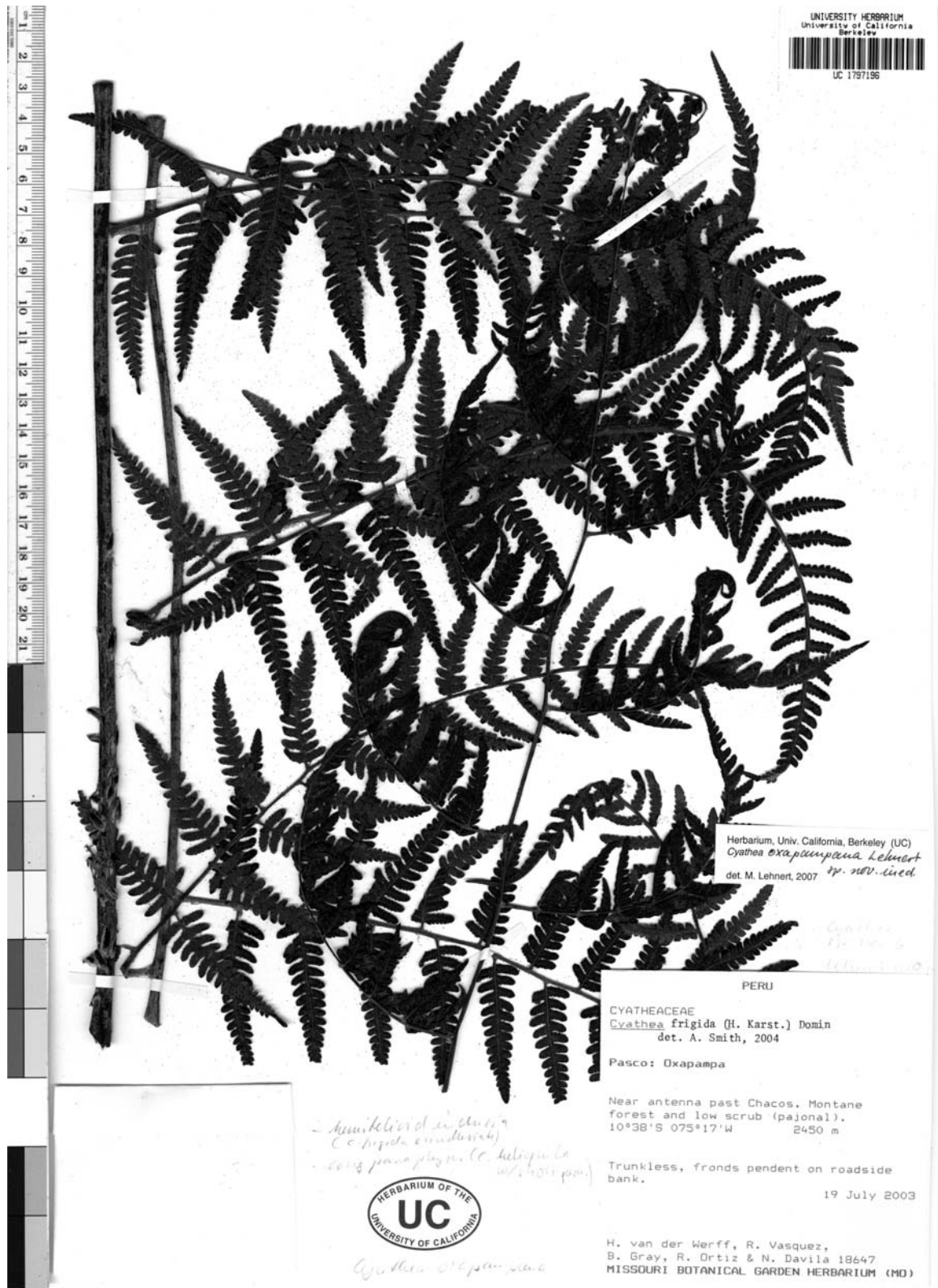


Fig. 15. *Cyathea oxapampana*. Type specimen, (van der Werff et al. 18647, UC).

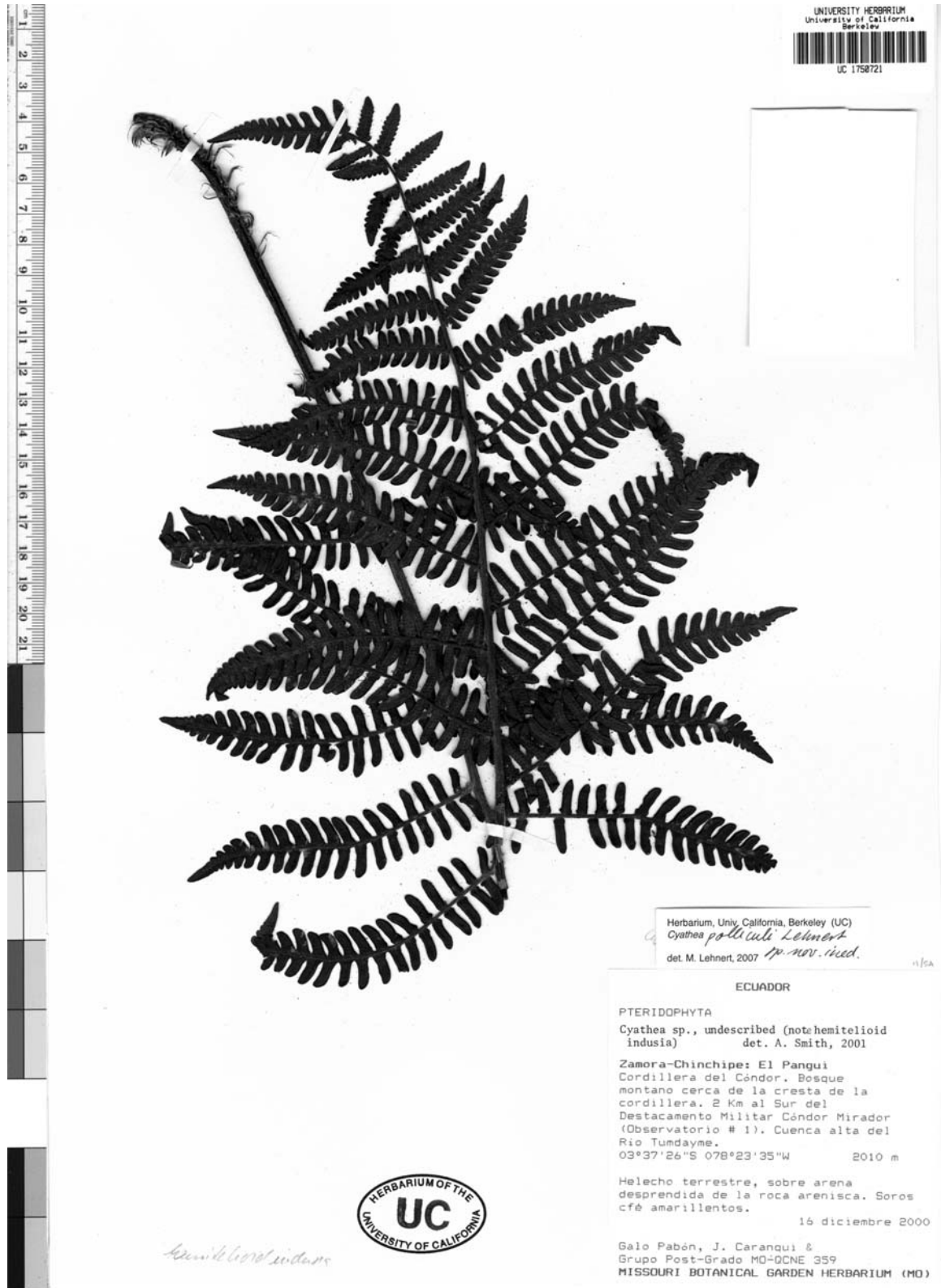


Fig. 16. *Cyathea polliculi*. Type specimen, whole frond, (Pabón et al. 359, UC).

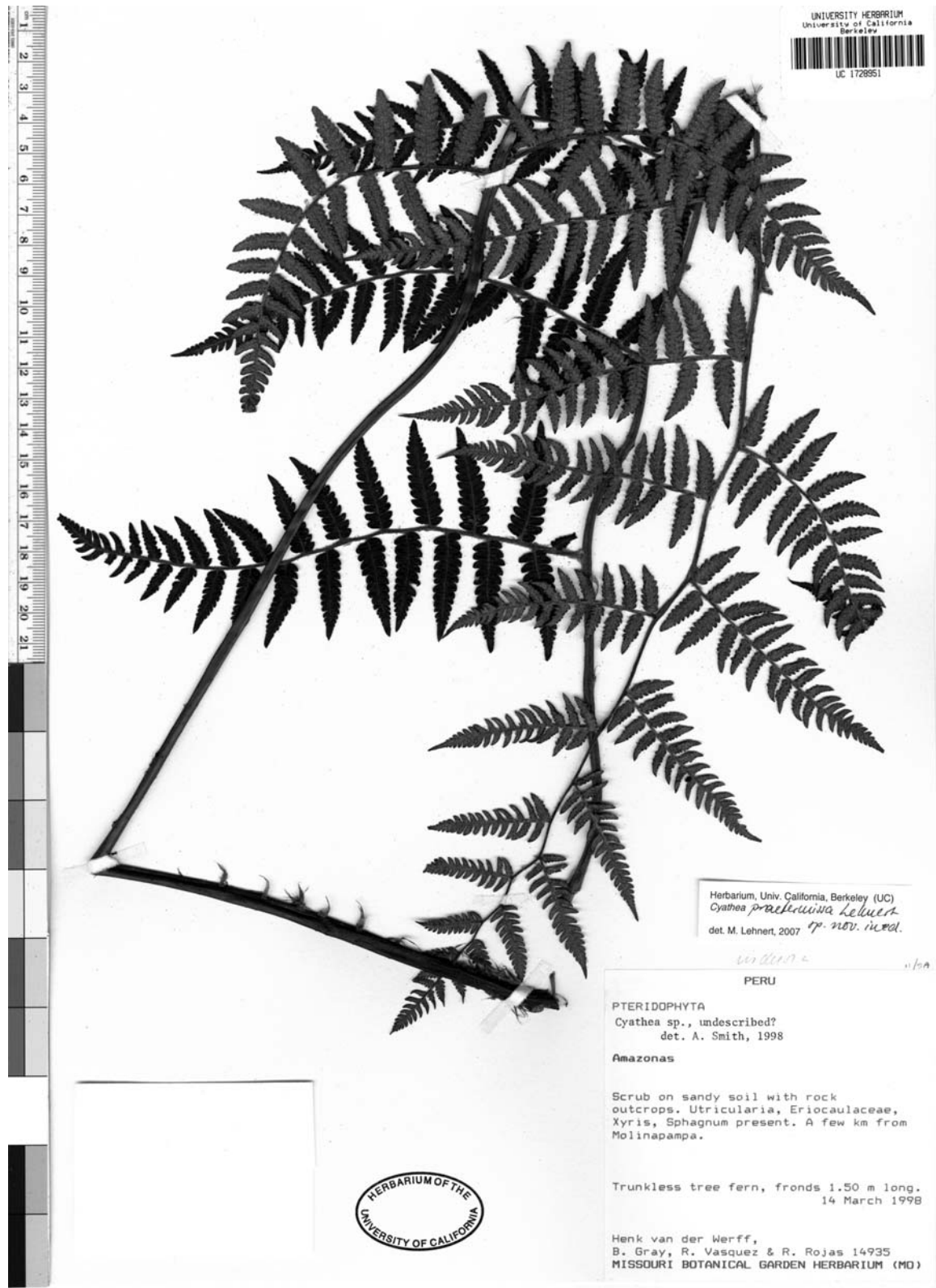


Fig. 17. *Cyathea pratermissa*. Type specimen, whole frond. (van der Werff et al. 14935, UC).

## **I.2. On the identification of *Cyathea pallescens* (Sodirol) Domin (Cyatheaceae): the truth and its consequences**

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**Abstract:** Based on studies of type material collected by L. Sodirol, several Andean tree fern species formerly united in *Cyathea pallescens* (Sodirol) Domin are hereby distinguished: *Cyathea pallescens* s.s. is an exindusiate species synonymous with *C. halonata* R.C. Moran & B. Øllg., and is restricted to the western slopes of the Cordillera Occidental in southern Colombia and northern Ecuador. Reinstated species are *C. tungurahuae* Sodirol, *C. brachypoda* Sodirol, and *C. chimborazensis* (Hook.) Domin with var. *chimborazensis*, var. *boreopallescens* M. Lehnert, and var. *leonis* M. Lehnert from the northern Andes; *Cyathea austropallescens* M. Lehnert is newly described from the central Andes. New descriptions of all species and illustrations of important characters are given. Added in shorter descriptions for comparison are *C. atahuallpa* (R.M. Tryon) D.B. Lellinger, , *C. corallifera* Sodirol, *C. divergens* (Baker) Domin, *C. simplex* R.M. Tryon, *C. straminea* H. Karst., and *C. ruiziana* Klotzsch (= *C. boliviana* R.M. Tryon).

**Key words:** Andes, *Cyathea austropallescens*, *C. brachypoda*, *C. chimborazensis*, *C. halonata*, *C. pallescens*, *C. tungurahuae*, exindusiate.

## Introduction

Among the most important Neotropical pteridophytes specimens are those collected by the Ecuadorian Padre Luis (Aloysio) Sodiro (1836–1909). He was the first native botanists who took a special interest in cryptogams; numerous diligent descriptions are based on his extensive collections. A drawback of his work is the maintenance of his collection. He did not use collection numbers, so the alignment of description and corresponding specimen has to rely on the citation of the locality in his descriptions of the Ecuadorian cryptogams (Sodiro 1883, 1893, 1908). This information has not necessarily been transferred literally when a label was copied; a perfect match of book and label is rare.

Also, the Sodiro collection is dispersed around the world today, from Berkeley to Budapest. Major parts were sold after Sodiro's death to the Instituto Darwinion, Argentina (SI). The rest is split up onto several herbaria in Quito, namely in the Herbario Universidad Central (Q), Herbario Padre Luis Sodiro (QPLS), and Herbario Nacional del Ecuador (QCNE), as well as in the Muséum National d'Histoire Naturelle in Paris (P) and other European herbaria. Because of the easier access to European and North American researchers, the Parisian samples have often been chosen as type material or as authentic material for reference.

In the following I will correct the typification of *Cyathea pallescens* (Sodiro) Domin based on the results of my studies of Sodiro's collections from the abovementioned herbaria.

In the course of this investigation, it became clear that many of the sphaeropteroid indusiate *Cyathea* species treated by Tryon (1976, 1986, 1989) need to be circumscribed newly in order to separate the sometimes very similar species properly. This is especially the case between the groups of *Cyathea pallescens*, *C. divergens*, *C. caracasana*, and *C. fulva* sensu Tryon (Tryon 1976). As it seems impractical to treat all species at one time, the number has been restricted to the synonyms of *C. pallescens* as given by Tryon (1976) as well as the true allies of what has previously been recognized as that species, i.e., all sphaeropteroid indusiate *Cyathea* with whitish petiole scurf and broadly white marginate to completely white petiole scales.

## Materials and Methods

The herbaria of AAU, B, BP, LPB, P, Q, QCNE, QPLS, SI and UC were searched for types of Cyatheaceae and matching specimens. Many collections were made personally in Ecuador during field work for the DFG (German Research Foundation) project “Cryptogamic plant diversity of the *Purdiaea nutans* forest in southern Ecuador and its relationship to soil,

climate, and vegetation structure” in the vicinity of the Podocarpus National Park in the Prov. Loja and Zamora-Chinchipec; specimens have been deposited mainly in the herbaria GOET, LOJA, QCA, and UC. The original works of Sodiro were kindly provided by Hugo Navarrete (QCA), Dave Barrington (VT), and David S. Conant (LSC).

The generic system used here is that of Lellinger (1987); the morphological terms follow Tryon (1970, 1976). Herbarium acronyms follow Holmgren et al. (1989).

### Results

*Cyathea pallescens* (Sodiro) Domin is an exindusiata species not closely related to what has formerly been supposed to be that species (Tryon 1976). One synonym, *C. borjae* Sodiro, is excluded; it belongs to *Alsophila cuspidata* (Kunze) D. S. Conant. Two of the synonyms can be reinstated as valid species, *C. brachypoda* Sodiro and *C. tungurahuae* Sodiro; *C. chimborazensis* (Hook.) Baker, which has formerly been treated as a variety of *C. caracasana* (Klotzsch) Domin (Tryon 1976), is reinstated, too; it has priority over *C. cystolepis* Sodiro, another synonym of *C. pallescens* sensu Tryon (1976). Two varieties of *C. chimborazensis* are newly described, var. *leonis* M. Lehnert and var. *boreopallescens* M. Lehnert, as well as the species *C. austropallescens* M. Lehnert. Except for *C. pallescens*, *C. brachypoda*, and, of course, *C. borjae*, all species and varieties were covered by Tryon’s species concept of *C. pallescens* (Tryon 1976) and are indeed closely related. All taxa are described and illustrated. Added in shorter descriptions are *C. atahuallpa* (R.M. Tryon) D.B. Lellinger, *C. boliviana* R.M. Tryon, *C. corallifera* Sodiro, *C. divergens* (Baker) Domin, *C. simplex* R.M. Tryon, *C. straminea* H. Karst., and *C. ruiziana* Klotzsch; these are species with which the species formerly regarded as *C. pallescens* (*C. austropallescens*, *C. chimborazensis* and varieties, *C. tungurahuae*) may be confused.

### Systematic Treatment

***Cyathea pallescens*** (Sodiro) Domin, Pterid. 263. 1929. *Alsophila pallescens* Sodiro, Rec. Crypt. Vasc. Quit. 20. 1883. Type. ECUADOR. Pichincha: “Bosques de Nanegal”, Sodiro s.n. (Holotype, Q [designated herewith]; isotypes, P, photo GH n.v., UC).

*Cyathea halonata* R.C. Moran & B. Øllgaard, Nord. J. Bot. 18: 431-434. 1998. Type: ECUADOR. Pichincha: Estación Biológica Río Gualajito, in Qubeada Las Palmeras, Km 59 along road Chillogallo-Alluriquin, 00°14’S, 78°47’W, 1800-2000 m, 30 Nov-1 Dec 1991, Øllgaard 99946 (Holotype, QCA; isotypes, AAU, QCNE). (Fig. 1)

*Trunks* to 4 m high, 10(-12) cm diam., without old petiole bases or adventitious buds, appearing ruddy due to often long persisting spreading scales (Fig. 1A); frond scars round to weakly elliptic, crowded (Fig. 1A), weakly prominent, with an arch of several vermilion pneumathodes below them; trunk apices hidden in fascicles of the youngest petioles (Fig. 1A). *Petiole* bases sometimes with 1-2 pairs of small pinnae (Fig. 1B). *Petiole scales* lanceolate, concolorous brown to orange-brown or weakly bicolorous with the margins somewhat lighter. *Laminae* short pubescent on both sides, on and between the veins. *Sori* costal, indusia absent, paraphyses shorter than sporangia.

For full description see Moran & Øllgaard (1998).

The misunderstanding of *Cyathea pallescens* is based on a labeling error of a specimen in Paris which Tryon (1976) took for the type of this species. That specimen, however, belongs to *Cyathea tungurahuae* Sodiro. Under the same number and with identical label there is a pinna of the real *C. pallescens*, which Tryon did not see (at least it is not annotated), and a petiole of *C. conjugata* (Hook.) Domin. Evidently the Parisian Sodiro collections have been mixed up thoroughly. Hence I prefer to choose the specimen with an identical label at Q as holotype because the small number of Sodiro specimens there makes a similar error less likely. It is also supported by the discovery of an isotype at UC, which matches the holotype in specimen and label.

*Cyathea pallescens* sensu Sodiro (1883) and *C. tungurahuae* are easily distinguished as the first species is exindusiate, has concolorous orange brown scales, inconspicuous scurf of very small brown scales and trichomidia, and a strong pubescence on both sides of the lamina and leaf axes, the latter species is indusiate, has bicolorous brown scales with white margins, conspicuous scurf of whitish strongly dissected squamules, and glabrous axes and veins except for evanescent scurf and some scattered hairs on the veins abaxially.

Because of Tryon's misapplication of the name, the true *Cyathea pallescens* (Sodiro) Domin was newly described as *C. halonata* R.C. Moran & Øllg. (1998). The most remarkable feature of that species was the presence of small pinnae at the petiole base that form a halo around the trunk apex. Sodiro did not mention such a structure in his description (Sodiro 1883), but it is known from species like *Cyathea suprastrigosa* (H. Christ) Maxon (Tryon 1976), *C. brachypoda* Sodiro (this paper), and *C. brevistipes* R. C. Moran (pers. obs.) that these basal pinnae are sometimes missing. Apparently Sodiro had the bad luck to find only plants without basal pinnae, if not only one: He noted that the species occurs near Nanegal,



Prov. Pichincha, and appears to be rare. I have seen about six plants of *C. pallescens* in the field and all had aplebioid basal pinnae.

*Cyathea pallescens* can be confused with species of the *C. fulva* group sensu Tryon (1976) because of the similar petiole scales and pubescence of the fronds; one of them, *C. suprastrigosa*, commonly even has aplebioid pinnae, too. However, the whole group has sphaeropteroid indusia, and none of the species occurs in the small range of the exindusiate *C. pallescens*; *Cyathea delgadii* Sternb., the most widely distributed species of the *C. fulva* group, can generally grow from sea level to 2000 m, but has not been found above 800 m on the western Andean slope and hence is clearly separated from *C. pallescens*, which occurs here at 1550-2000 m. I cannot rule out that *C. pallescens* indeed belongs to the *C. fulva* group sensu Tryon (1976). Comparative field studies revealed that many species are nearly identical except for the presence or absence of indusia, and undoubtedly closely related, like *C. concordia* B. León & R.C. Moran and *C. palaciosii* R.C. Moran (León & Moran 1996), *C. brucei* M. Lehnert and *C. haughtii* (Maxon) R.M. Tryon (Lehnert, in press), or *C. colombiana* Domin and *C. pinnula* (H. Christ) R. C. Moran (pers. obs.).

**Distribution and habitat.** In moist montane forests of the western Andean slope at 1550-2000 m. Most collections have been made near Mindo and in the Maquipucuna Reserve, Ecuador, Prov. Pichincha, where the species occurs in small numbers; one collection is from southern Colombia, Prov. Nariño. Thus *Cyathea pallescens* seems to be small ranging and genuinely rare, with less than a dozen gatherings over the last century in a relatively well searched area.

**Additional specimens examined. COLOMBIA. Nariño:** Reserva Natural La Planada, 01°05'N, 77°25'W, 1800 m, 23 May 1994, *Bittner 2278* (MO).

**ECUADOR. Carchi:** Cerro Golondrinas, N-facing slope on S-side of upper Río Blanco valley, 00°52'N, 78°11'W, 1750-1800 m, 06 Feb 1993, *Boyle & Boyle 1466* (MO, QCNE).

**Pichincha:** Estación Biológica Gualajito, in Quebrada "Las Palmeras", Km 59 along road Chillogallo-Alluriquin, 00°14'S, 78°49'W, 1860 m, 01.-05 Apr 1995, *Ankersen & Kragelund 44* (AAU, QCA); Maquipucuna, 5 km E of Nanegal, 00°07'N, 78°37'W, 1550 m, 11 Feb 1991, *Gentry & Valencia 73245* (MO); Mindo Biological Station, 00°04.7'S, 78°43.9'W, 1550 m, 12 Oct 2002, *Lehnert 963* (GOET, QCA,UC); Santa Rosa, 18 km S of Nanagalito, 00°00'50"S, 78°29'10"W, 1900-2000 m, 1995, *Navarrete 820* (AAU, QCA); Pichincha, Estación Biológica Gualajito, in Quebrada "Las Palmeras", km 59 along road

Chillogallo-Alluriquin, 00°14'S, 78°47'W, 1800-2000 m, 30 Nov-01 Dec 1991, Øllgaard 99946 (AAU, QCA); along new road Nanegal-Mindo, 1600-1800 m, 03 Mar 1994, van der Werff *et al.* 13400 (AAU, MO).

***Cyathea brachypoda*** Sodiro, Sert. Fl. Ecuad. 2: 8. 1908. Type: ECUADOR. Pichincha: Sylv. suband. vulc. Atacatzo, *Sodiro s.n.* (Holotype, Q [designated herewith]; isotype, SI [N° 22795, 22707]). Syntypes: Atacatzo, Jul 1906, *Sodiro s.n.* (GH n.v., MO n.v.); Atacatzo, Jul 1907, *Sodiro s.n.* (NY, US).

*Cyathea asperata* Sodiro, Sert. Fl. Ecuad. 2: 9. 1908. Type: ECUADOR. Pichincha: Pichincha, Mar 1903, *Sodiro s.n.* (Holotype, SI [N° 22801] [designated herewith]; isotypes, NY, US).

*Cyathea asperata* var. *brevipes* Sodiro, Sert. Fl. Ecuad. 2: 10. 1908. ex char. No specimen cited.

*Cyathea muricatula* Sodiro, Sert. Fl. Ecuad. 2: 10. 1908. Type: ECUADOR. Pichincha: Corazón, Dec 1907, *Sodiro s.n.* (NY, P, US).

*Hemitelia subcaesia* Sodiro, Crypt. Vasc. Quit. 522. 1893. Type: ECUADOR. Prov. unknown: Bosques subandinos de la Cordillera Occidental hasta 2800 m, *Sodiro s.n.* (n.l.). Authentic specimens: ECUADOR. Pichincha: Niebly, *Sodiro s.n.* (NY), Canzacoto, Feb 1882, *Sodiro s.n.* (P, photo GH), Ecuador, Apr 1874, *Sodiro s.n.* (US), in silv. suband. m. Corazón, 2000 m, *Sodiro s.n.* (SI [N° 22872]). (Fig. 2).

*Trunks* to 4 (-5) m tall, to 8-12 cm diam., without old petiole bases, nevertheless appearing ruddy due to dark brown to blackish scales; frond scars circular to weakly elliptic, inconspicuous, with small round vermilion pneumathodes below them; trunk apices hidden in fascicles of the youngest petioles; adventitious buds lacking. *Petioles* 25-80 cm long, short-acute to verrucate, brown to tan, rarely stramineous, with plumbeous tinge; sometimes 1-2 pairs of small adventitious (aphlebioid) pinnae at the petiole bases, to 20 cm long; petiole scales narrowly lanceolate to lanceolate, 25-31 x 3-5 mm, their tips aristate, weakly to pronouncedly helically twisted, blackish to fuscous, the narrow margins lighter colored to whitish, not orange or rufescent (Fig. 2A); petiole scurf weakly developed, brown, consisting of small (0.2–0.3 mm) flat, round, appressed squamules with crested margins. *Fronde*s to 320 cm long, patent, arching. *Laminae* to 240 x 130 cm, bipinnate-pinnatifid, firm herbaceous, gradually reduced apically, widest at or below the middle, the basal pinnae significantly

reduced in fronds with short petioles; pale green abaxially, dark green abaxially, sometimes plumbeous when dried; pinnae sessile to short stalked. *Leaf axes* hairy adaxially (hairs 0.5-1.0 mm long), short pubescent abaxially, with white scurf consisting of small ciliate squamules and hairs, persisting in junctures of costae with costules and rhachis. *Pinnules* sessile to subsessile, 7.2-10.5 x 1.6-3.4 cm, truncate to weakly cordate at base, acute or short attenuate at tip, the segments weakly falcate with finely serrate to crenate margins, the sinuses narrow (Fig. 2B); sterile pinnules usually broader than fertile ones. *Veins* glabrous or 1–3 hairs on midveins adaxially, short pubescent abaxially, with downward-curved hairs 0.2 mm long or less, sometimes substituted by appressed white trichomidia, rarely glabrous and then only partially; no hairs between veins or only few beneath the sinuses abaxially; with small flattish to weakly bullate, whitish to tan or brown squamules (Fig. 2C). *Sori* subcostal to costal, indusiasphaeropteroid, usually with umbo, whitish-translucent, very fragile and evanescent (sometimes not detectible in mature sori); paraphyses as long as or shorter than sporangia. *Spores* not examined.

The most notable feature of *Cyathea brachypoda* is the small adventive pinnae at the petiole base; however, these are sometimes missing. It is very similar to *C. pallescens* (Sodi) Domin in laminar texture and pinnule shape, from which it differs in having very fragile indusia (no indusia in *C. pallescens*), dark brown to blackish, sometimes weakly bicolorous petiole scales (vs. concolorous orange-brown), and whitish to tan squamules on the lamina abaxially (vs. orange-brown).

Judging from the descriptions, *Hemitelia subcaesia* Sodi is the oldest name for this species. However, the type could not be located so far. There are no good matches of the type locality description with the label information of known Sodi specimens annotated with this name. The specimens I have seen have no petiole either; despite my confidence in the laminar indument as a reliable distinguishing character, I would prefer to have seen the petiole scurf and scales to separate this species from *Cyathea frondosa* H. Karst. confidently (see below). Instead of selecting an ambiguous specimen as reference, I prefer the second name in line, *Cyathea brachypoda* Sodi, for which complete specimens with matching references on the labels are available.

Included in *Cyathea brachypoda* are *C. asperata* Sodi and *C. muricatula* Sodi, which are identical judging from Sodi's description and the available type material in Paris and Quito. However, they have no adventive pinnae at the petiole base; *C. muricatula* is an extreme form whose petiole scales have more pronounced whitish margins.

*Cyathea frondosa* H. Karst. from Colombia and Ecuador is generally larger than *C. brachypoda*, has somewhat firmer indusia and wider pinnules. Both match in the scurf remnants on the leaf axes (white matted hairs or ciliate squamules), however, *C. frondosa* has the same type of dense scurf on the petiole while *C. brachypoda* shows here only scattered tan to brown squamules. The petiole scales of *C. frondosa* are nearly identical to those of *C. brachypoda* except that they are bicolorous only in the upper part of the petiole while they are concolorous or nearly so towards the petiole base, with a softer, more papery texture than those in the upper part; the scales of *C. brachypoda* are apparently always firm in texture.

Other species with basal aphlebioid pinnae are *C. brevistipes* R. C. Moran and *C. suprastrigosa* (H. Christ) Maxon, which can be easily distinguished by their plane petiole scales that are bicolorous brown and white in the former and concolorous dull orange-brown in the latter. Their distributions do not overlap with that of *C. brachypoda* in northern Ecuador: *Cyathea brevistipes* only occurs from southern Ecuador to Bolivia at 3000-3500 m; *Cyathea suprastrigosa* is known only from Costa Rica and northern Colombia.

Another similar tree fern is *C. caracasana* (Klotzsch) Domin s.s. which is identical in the sori and ephemeral indusia; it differs from *C. brachypoda*, however, in the wider sinuses between the segments, less hair abaxially on the lamina, and the lack of white scurf and remote basal pinnae on the petiole. The petiole scales of this species are broadly lanceolate with the apex not helically twisted (vs. narrowly lanceolate with apices helically twisted in *C. brachypoda*)

**Distribution and habitat.** Upper montane forest at 1200-2300(-2800) m, preferably along creeks in half shade. Restricted to northern Ecuador, to be expected in southern Colombia.

**Additional specimens examined. ECUADOR. Napo:** Valley of Río Oyacachi, 10 km W of El Chaco, ridge SE of Río San Juan Grande, 00°17'S, 77°52'W, 1950 - 2020 m, 13-14 Mar 1996, Øllgaard & Navarrete 1690 (AAU, QCA); Valley of Río Oyacachi, 10-15 km W of El Chaco, trail Río San Juan Grande to Santa Maria, 00°15'S, 77°52'W, 1850-1900 m, 15 Mar 1996, Øllgaard & Navarrete 1709 (AAU, QCA); Baeza, 12 ha de bosque poco disturbado y disturbado, 2 km antes de Baeza (carretera Papallacta - Baeza, parte alta de "Y"), 00°28'S, 77°54'W, 2000 m, 19-20 Mar 1993, Valencia, Navarrete & Quintana 2896, 2897, 2911, 2914, 2917 (AAU, QCA). **Pichincha:** Lloa valley, one hectare plot, Hacienda Las Palmeras del Lcdo. Fernando Sotomayor, 14 km below Lloa towards Mindo, 00°50'N, 78°38'W, 2900 m, 13-14 Oct 1990, Jørgensen & Yopez 92576 (AAU; QCA); Maquipucuna Biological Field

Station, ca. 5 km E of Nanegalito, 34 km NW of Quito, trail camino del Rio, 00°08'N, 78°37'W, 1300 m, 04 Apr 1996, *Moran et al.* 5988 (QCA); Reserva Maquipucuna, ca. 5 km (airline) ESE of Nanegal, Hda. El Carmen, trail along río Umachca, just W of research station, 00°07'N, 78°38'W, 1250-1350 m, 28 Feb-04 Mar 1995, *Øllgaard et al.* 904 (AAU, QCA); Tandayapa Cloud Forest Reserve, 1750-1880 m, 12 Sep 2004, *Lehnert & Kessler* 1222 (AAU, GOET, QCA, UC); Bosque Protector Maquipucuna, crest and upper slopes of Cerro Monte Cristi, ca. 9 km airline SE of Nanegalito, 00°03'N, 78°36'W, 2700 m, 08-09 Sep 1993, *Webster, Smith & Pastuzo* 30554 (QCNE). **Prov. unknown:** Limones subtropico, 2300 m, 19 Sep 1967, *Latorre-A.* 791 (Q)

***Cyathea austropallescens*** M. Lehnert, sp. nov. Type. BOLIVIA. La Paz: Prov. Nor Yungas, trocha al Valle de Coscapa, Parque Nacional Cotapata, 16°12'S, 67°53'N, 3250 m, 11 Sep 1997, *Kessler et al.* 11832 (Holotype, LPB; isotypes, GOET, UC).

*A Cyathea chimborazense* (Hook.) Domin var. *chimborazense fufure brunneo* (vs. *albido*), *squamis laminarum brunneis atrobrunneisque* (vs. *albis usque pallide brunneis*), *pilis creberioribus pagina adaxiali* (vs. *creberioribus pagina abaxiali vel neutra*), *absentia squamarum bullatarum* (vs. *squamis bullatis frequentibus*) differt.

Etymology. The name refers to the southern distribution (Latin *australis*, *austro-* = south) of this species in respect to the other species with which it had been included in *C. pallescens* (Sodirol) Domin.

*Trunks* to 6(-10) m high, to 15-20 cm diam., without persistent petiole bases when old, densely covered with them when young (less than 2 m high) and then to 25 cm diam.; trunk apices hidden in fascicles of the petioles; frond scars broadly ovate, gray-brown to blackish brown like the adjacent cortex, with an arch of small round pneumathodes below them; adventitious buds usually lacking, but multiple lateral sprouting possible after injury or loss of the apex. *Fronde*s to 300 cm long, patent to slightly erect, weakly arching. *Petioles* 30-100 cm long, muricate to spiny, brown, rarely blackish basally, often stramineous distally; scurf scattered, persistent, consisting of appressed to slightly erect, round to ovate, brown squamellae with somewhat paler, fringed or crested margins; petiole scales (10-)21-36(-41) x (2.8-)3.5-5.5(-7.5) mm, broadly lanceolate, discordantly bicolorous, or basal scales also

concordantly bicolorous, with brown to dark brown (never blackish) center, and white or yellowish margins; margins persistent, of the same firm texture as the center; apical scales broader and lighter in colour than the basal ones. *Laminae* 90-200 x 50-130 cm, ovate-elliptic, bipinnate-pinnatifid to tripinnate, green to dark green, sometimes blackish when dried adaxially, pale green abaxially; apices gradually reduced. *Rhachises* inermous to muricate, stramineous to light brown or yellowish, pubescent adaxially, the hairs 1 mm or less, white to tan, antrorsely curved; glabrous or glabrescent abaxially, with only few hairs to 1 mm long, and few to many squamellae like those of the scurf; sometimes persistent petiole scales reach up to the middle of the rhachises. *Pinnae* to 70 cm long, distally not or just weakly green alate, mainly alternate, rarely subopposite. *Costae* and costules inermous, stramineous to tan, short pubescent adaxially, glabrescent abaxially, with trichomidia, small thin scales (to 5 mm) and squamules; the insertions bearing a weakly raised elliptic aerophore, grayish to pale brown when fresh, black when dried. *Pinnules* to 50-82 x (8-)12-18(-25) mm, long-triangular to linear, the tips acute, the bases truncate to weakly rounded, basal segments may be remote from the following ones, but are connected by narrow green wings; segments with more hairs adaxially than abaxially, or sometimes equally hairy on both sides and then hairs sparse; hairs adaxially on and between veins mainly near the segment margins, evenly distributed on veins, rarely between them abaxially, here often substituted by appressed brown, unicellular trichomidia; small broad lanceolate to ovate, flattish scales of brown to dark brown colour present on midvein and veins; sterile veins forked or simple, fertile veins forked. *Sori* subcostal, in forks of veins; indusia sphaeropteroid, lustrous brown, transparent, with apical umbo, fragmenting irregularly at maturity, leaving an incomplete shallow cup or disc; paraphyses as long as or shorter than sporangia. *Spores* tetrahedral-globose, exospore smooth, finely porate near the laesura, exospore finely baculate.

**Distribution and habitat.** Grows in wet montane forests, elfin forests and *ceja de la montaña* in Bolivia and Peru at (2000-)2600-3500 m.

**Additional specimens examined. PERU. Cuzco.** Prov. Urubamba, Distr. Machu Picchu, Cedropata (Collpani), 13°06'S, 72°38'W, 2520 m, 071993, *Chávez Huamán 1002* (AAU); entre San Luis y Abra Málaga, 13°03'S, 72°23'W, 3050 m, 16 Oct 2002, *Lehnert 426* (GOET, UC, USM); entre San Luis y Abra Málaga, 13°03.61'S, 72°22.89'W, 3080 m, 16 Oct 2002, *Lehnert 431* (GOET, UC, USM). **Pasco.** Prov. Oxapampa, Río San Alberto valley E of Oxapampa, 10°34'S, 75°22'W, 2600 m, 25 Jul 1984, *Smith D. N. & Pretel 8014* (AAU, MO);

Río San Alberto valley E of Oxapampa, slopes of Cordillera Yanachaga, 10°34'S, 75°22'W, 2400 m, 23 Jul 1984, *Smith D. N. & Pretel 7972* (AAU, MO).

**BOLIVIA. La Paz.** Prov. Bautista Saavedra, Charazani, östlich von Chullina, 15°09'S, 68°56'W, 3150 m, 21 Jan 1994, *Herzog H521* (AAU, LPB); Charazani, Richtung Carijna, 15°12'S, 68°52'W, 2000 m, 19 Jan 1994, *Herzog H500* (AAU, LPB). Prov. Inquisivi, Abra Sitia - climbing 1 km to the W of the road between Sita and Licoma Pampa from where it crosses Loma El Abra, 5 km NW of Inquisivi, 16°51'S, 67°10'W, 3050-3250 m, 22 Dec 1989, *Lewis 36857* (MO); Comunidad Choquetanga-Valle Chimu, 8-9 km de Choquetanga, 16°48'S, 67°16'W, 3200 m, 26 Jan 1994, *Salinas 2318* (LPB); Comunidad Choquetanga - Wichupampa, serranias de Lulini, 13.5 km al N de Choquetanga, 16°45'S, 67°20'W, 3310 m, 03 Mar 1994, *Salinas 2509* (LPB); Comunidad Choquetanga - Cuchiwasi, bajando Pabellonani, a 7 km al NE de Choquetanga, 16°48'S, 67°17'W, 3300 m, 19 Jan 1994, *Salinas 2137* (LPB); Comunidad Choquetanga - Wichupampa, serranias de Lulini, 13 km al N de Choquetanga, 2-3 km al NW del Cerro Lulini, 16°45'S, 67°20'W, 3290 m, 17 Mar 1994, *Salinas 2698* (LPB). Prov. Murillo, Valle del Río Zongo, 24.2 km al N de la cumbre, 16°08'S, 68°07'W, 2900 m, 11 Apr 1987, *Solomon & Chevalier 16550* (LPB, MO, NY, UC). Prov. Nor Yungas, Parque Nacional Cotapata, Estación Tunquini, senda nueva del camino de la mina (curva al lado W) al pantanon, 16°11'S, 67°53'W, 2800 m, 13 Sep 2000, *Bach 1003* (GOET, LPB); Estación Biologica de Tunquini, senda al W del pantanon, 16°11'S, 67°53'W, 3000 m, 14 Jul 2002, *Bach et al. 1845* (LPB); Estación Biologica de Tunquini, camino de la mina, 16°11'S, 67°53'W, 2700 m, 06 Aug 2001, *Bach et al. 1437* (GOET, LPB); Estación Biológica de Tunquini, camino principal a la mina, 16°12'S, 67°53'W, 2700 m, 15 Aug 2002, *Bach et al. 1873* (LPB); Chuspipata, 5 km via Unduavi, 16°17'S, 67°50'W, 3150 m, 02 Apr 1982, *Beck 7576* (LPB); trocha al Valle de Coscapa, Parque Nacional Cotapata, 16°12'S, 67°53'W, 3400 m, 10 Sep 1997, *Kessler et al. 11765* (LPB, UC); 2 km de Chuspipata hacia Coroico, 16°22'S, 67°49'W, 2900 m, 14 Sep 1997, *Kessler et al. 11904* (LPB, UC); 5 km de Chuspipata hacia Coroico, 16°23'S, 67°48'W, 2750 m, 18 Sep 1997, *Kessler et al. 11996* (UC, LPB); Chuspipata, 2 km hacia Yolosa, 16°18'S, 67°48'W, 3000 m, 27 Jul 2000, *Lehnert 0* (UC, GOET, LPB); Chuspipata, 16°18'S, 67°49'W, 2950 m, 03 Aug 2000, *Lehnert 6* (GOET, LPB, UC); Carretera de Chuspipata a Yolosa, km 59, 16°17'S, 67°47'W, 2800 m, 03 Aug 2000, *Lehnert 9* (GOET, LPB, UC); Cotapata Santa Barbara, sobre la cumbre de la montana detras de la madona, 16°18'S, 67°52'W, 3100 m, 06 Aug 2000, *Lehnert 12* (GOET, LPB, UC); Entre Unduavi y Cotapata Santa Barbara, camino sobre la cumbre de la montana antes de la bifurcation, 16°18'S, 67°53'W, 3250 m, 07 Aug 2000, *Lehnert 13, 14 & 15* (GOET, LPB,

UC); 500 m de Chuspipata a Yolosa, sobre loma de montaña a Coroico, 16°18'S, 67°49'W, 3000 m, 19 Aug 2000, *Lehnert 31* (GOET, LPB, UC); Chuspipata - Sacramento, 16°18'S, 67°49'W, 2800 m, 10 Nov 2002, *Lehnert 492* (GOET, LPB, UC); entre Cotapata y Chuspipata, 16°18'S, 67° 50'W, 3100m, 06 May 1989, *Smith, D.N. & B. León 13134* (LPB, MO, UC); 1.2 km E of Cotapata on road between Unduavi and Chuspipata, 16°17'S, 67°50'W, 3100 m, 26 Jun 1986, *Solomon 15346* (LPB, MO, UC); Estrada de La Paz a Coroico, 72 km de La Paz, 3050 m, 28 Jul 1979, *Windisch 2446* (AAU). Prov. Sud Yungas, Cantón Yanacachi, Mina Chojlla, camino de acceso de vehiculos a Kacapi, 15°52'S, 68°07'W, 2182 m, 05 Aug 2000, *Siñani 246*, (LPB). **Cochabamba.** Prov. Ayopaya, Sailapata, 16°51'S, 66°56'W, 3500 m, Dec 1935, *Cárdenas 3150* (GH); Sailapata, 16°51'S, 66°56'W, 3250 m, Jan 1935, *Cárdenas 3059* (GH, US); Puiyani, 10 km Cotapata-Cotacajes, 16°38'S, 66°41'W, 2900 m, 07 May 1997, *Kessler et al. 9329* (LPB, UC); 10 km Cocapata - Cotacajes, 16°38'S, 66°41'W, 3000 m, 09 May 1997, *Kessler et al. 9407 & 9411* (GOET, LPB, UC). Prov. Carrasco, 108 km antigua carretera Cochabamba-Villa Tunari, 17°09'S, 65°38'W, 2950 m, 22 Jun 1996, *Kessler et al. 6548 & 6549* (LPB, UC); 116 km antigua carretera Cochabamba-Villa Tunari, 17°08'S, 65°38'W, 2400 m, 06 Jul 1996, *Kessler et al. 7047* (LPB, UC, US); Siberia, 220–222 km on the Cochabamba-Sta. Cruz highway (between Pojo and Comarapa), steep pass dividing the Dept. Cochabamba from that of Sta. Cruz, 17°50'S, 64°40'W, 2800 m, 20 Apr 1963, *Ugent & Ugent 5111* (GH, UC, US); Comarapa, aserradero Gualberto, Apr 1983, *Susanna 925* (LPB). Prov. Chapare, entre Villa Tunari y Cochabamba, detras Corani, arriba la montana, 17°11'S, 65°54'W, 2800 m, 09 Sep 2000, *Lehnert 61* (GOET, LPB, UC). **Santa Cruz.** Prov. Caballero, de Siberia 4 km al E, pequeña laguna por la cima (Laguna Tinqué?), 2600 m, 18 Mar 2003, *Lehnert 720* (GOET, LPB, UC); de Siberia 5 km al E, á Torecillos, ladera fuertemente inclinada, 2650 m, 18 Mar 2003, *Lehnert 721* (GOET, LPB, UC).

Identical in habit and undoubtedly closely related are *Cyathea chimborazensis* (Hook.) Domin and *C. tungurahuae* Sodiro. Both species grow sympatrically in Venezuela, Colombia, and Ecuador but show no geographical overlap with *C. austropallescens*. They can be easily distinguished by the petiole scurf which is scattered and pale brown in *C. austropallescens* and quite dense and whitish in the other two species. Structurally the scurf consists of appressed, irregularly crested flattish squamules in *C. austropallescens*, and of small erect multiciliate squamules in *C. tungurahuae* and *C. chimborazensis*, in latter species more variable in size than in the other. Usually *C. tungurahuae* and *C. chimborazensis* are less hairy



adaxially than abaxially (vice versa in *C. austropallescens*); however, in northern Peru *C. chimborazensis* var. *leonis* Lehnert is abundantly hairy on both laminar surfaces as well as on all leaf axes. It can be distinguished by the presence of white to tan bullate scales on the lamina abaxially which are common in all varieties of *C. chimborazensis* but are lacking in *C. austropallescens*. In both species the indument can be depauperate and virtually lacking the distinguishing lamina scales; these forms are best recognized by the petiole scurf and the geographic distribution, too. Glabrescent forms of *C. chimborazensis* are common in the var. *boreopallescens* M. Lehnert from southern Ecuador, Prov. Zamora-Chinchipec, while such forms of *C. austropallescens* have been often found in the Charazani region in Bolivia, Prov. La Paz. The northernmost collections of *C. austropallescens* in Peru, Prov. Pasco (*Smith D.N. & Pretel 7972, 8014*) do not only have almost glabrous laminae but also rather large petiole scurf squamules (to 1 mm); maybe they represent a local variety.

*Cyathea ruiziana* Klotzsch from Bolivia and Peru is distinguished from *C. austropallescens* by the fragile cretaceous petiole scale margins that are often abraded with age (vs. not fragile or abraded in *C. austropallescens*), dense white petiole scurf with the squamules intergrading to the larger scales (vs. scattered tan to brown scurf of only small squamules that do not intergrade to larger scales), and the presence of small white scales on the veins abaxially that always bear some distinct brown marginal teeth and often have a dark brown center, too (vs. concolorous brown to tan without distinct marginal teeth).

*Cyathea herzogii* Rosenst. from Peru and Bolivia grows in the same range and habitat like *C. austropallescens* and may appear similar, but this species is much hairier, with the hairs abundant and evenly distributed on and between the veins adaxially (vs. more frequent towards the segment margins in *C. austropallescens*) and has orange-brown, deeply bullate scales on the veins abaxially (vs. bullate scales lacking).

The species of the *Cyathea caracasana* alliance differ in the petiole scales which are either concolorous brown or bicolorous with brown margins (vs. white margins in *C. austropallescens*), or if the margins are whitish then the petiole scurf consists of erect, crested, dark brown squamules (vs. tan to brown and appressed).

**Cyathea chimborazensis** (Hook.) Hieron., Hedwigia 45: 230. 1906. *Alsophila chimborazensis* Hook., Syn. Fil. 37. 1866. Type. ECUADOR. Chimborazo: “Chimborazo, Ecuador, 3000-4000 ft”, *Spruce 5743* (Holotype, K; isotypes, P, B [frag.], US [frag.]

*Cyathea cystolepis* Sodiro. Rec. Crypt. Vasc. Prov. Quit. 15. 1883. Syntypes. ECUADOR.

Pichincha: “Crecen en la pendiente occidental del Atacazo y del Corazón, 1600, 2000 m,” Sodiro s. n. (NY). Authentic specimen: Ecuador, in sylv. apud Niebly, Jan 1883, Sodiro s.n. (P).

(Fig. 3, 4)

*Trunks* to 8-13(-15) m high, 7-14 cm diam., without persistent petiole bases when old, densely covered with them when young (less than 2 m high); trunk apices hidden in fascicle of the youngest petioles; frond scars broadly ovate, blackish brown like the adjacent cortex, with an arch of small round, brown to vermilion pneumathodes below them; adventitious buds lacking. *Fronde*s to 300 cm long, patent to slightly erect, weakly arching. Petioles 30-100 cm long, muricate to spiny (Fig. 3G), stramineous to brown, rarely blackish basally; scurf dense, persistent (Fig. 3G), consisting of erect, multiciliate, whitish squamellae (Fig. 3H); petiole scales 14.0-30.0 x (1.8-)2.0-4.0 mm, narrowly lanceolate to lanceolate (Fig. 3F), discordantly bicolorous, or basal scales also concordantly bicolorous, with brown to dark brown (never blackish) center, and white or yellowish margins; margins often fragmenting, of a more brittle texture than the center; apical scales broader and lighter in colour than the basal ones (Fig. 3F)). *Laminae* 90-200 x 50-130 cm, ovate-elliptic, bipinnate-pinnatifid to tripinnate, green to dark green, when dried sometimes blackish adaxially, pale green abaxially; apices gradually reduced. *Rhachises* inermous to muricate, stramineous to light brown, rarely brown or yellowish, pubescent adaxially, the hairs 1 mm or less, white to tan, antrorse and somewhat appressed; glabrescent abaxially, covered with easily abraded scurf of white to grayish bullate squamellae (Fig. 3A); sometimes persistent petiole scales reach up to the middle of the rhachises. *Pinnae* to 70 cm long (Fig. 3E), distally not or just weakly green alate, alternate to subopposite. *Costae* and costules inermous, stramineous to light brown, rarely brown or yellowish, often with plumbeous tinge, short pubescent adaxially, densely tomentose abaxially, with small white (rarely grayish or partly brown) flat and bullate squamules, also with some small trichomidia and thin scales (to 10 mm long); the insertions bearing each a weakly raised elliptic aerophore, grayish to black already in fresh material. *Pinnules* to 50-78 x (8-)12-17(-25) mm, sessile to subsessile (stalked to 1 mm), long triangular to linear, the tip acute, the base truncate to weakly rounded (Fig. 4D), basal segments may be remote from the following ones, but are connected by a narrow green wing; segments oblong, weakly falcate, tip obtuse, margins crenulated (Fig. 4A-C); segments with more hairs abaxially than adaxially, or sometimes equally hairy on both sides, or rarely hairs absent abaxially (Fig. 4A-

C); hairs to 0.5 mm long, appressed adaxially, mainly near the segment margin on veins, erect abaxially, evenly distributed on and between veins, and often substituted by appressed tan, unicellular trichomidia; squamules on midvein and veins similar to scurf on costules, mainly bullate squamules to 1 mm long, completely white or brown with white margins, some subbullate and flattish squamules between them, these discordantly bicolorous tan to brown with whitish margins or completely tan to whitish, margins often irregularly tinged brown (Fig. 3A-D); all squamules with one or few white apical processes; sterile veins forked or simple, fertile veins forked. *Sori* subcostal (Fig. 4A, B), in forks of veins; indusia sphaeropteroid, lustrous tan to light brown, transparent, with weak apical umbo, fragile, fragmenting irregularly at maturity, leaving a shallow cup or disc (Fig. 4A, B), sometimes completely missing; paraphyses as long as or shorter than sporangia. *Spores* tetrahedral-globose, perispore and exospore not examined.

Although *Cyathea cystolepis* Sodiro, which was listed as a synonym under *C. pallescens* (Sodiro) Domin by Tryon (1976), had not been revalidated properly before, it was cited by Moran (1998) as a valid species and treated as an endemic of the northern Cordillera Occidental in Ecuador by Valencia et al. (2000). It is considered here as a synonym of *C. chimborazensis*.

#### Key to the varieties

1. Hairs on the segments more abundant adaxially or equally dense on both sides, generally erect and abundant; bullate scales abaxially frequent, mainly pure white, rarely with brown body. ....  
var. **leonis**
1. Hairs on the segments more abundant abaxially than adaxially except if hairs generally few and appressed, then sometimes few hairs adaxially and almost no hairs abaxially; bullate squamules with brown body if abundant. .... 2
2. Hairs sparse, often appressed, bullate squamules abaxially few, only white, or lacking. .... var.  
**boreopallescens**
2. Hairs on the segments more abundant abaxially, sparse to abundant, mainly erect adaxially, appressed adaxially, bullate squamules few to many, always brown bodied and pure white ones mixed, the brown bodied squamules often prevailing. .... var.  
**chimborazensis**

**Cyathea chimborazensis** var. **chimborazensis** (Hook.) Lehnert, comb. nov. *Cyathea caracasana* (Kuhn) Domin var. *chimborazensis* (Hook.) R. M. Tryon, Contr. Gray Herb. 206: 19–98. 1976.  
(Fig. 4A, D)

*Cyathea chimborazensis* var. *chimborazensis* differs from the very similar and sympatrical *C. tungurahuae* Sodiro in having a concolorous whitish indument on the axes that can be easily abraded, and in having bullate scales on the laminae; *C. tungurahuae* lacks both and has generally wider pinnules than *C. chimborazensis*.

**Distribution and habitat.** Moist montane forests in western Venezuela, Colombia and Ecuador, south to Prov. Chimborazo, at 2450-2850 m.

**Additional specimens examined. COLOMBIA. Antioquia:** Prov. Jardín, Cuchilla de Ventanas, Alto de Ventanas, 2560 m, 09 Jun 2000, *Giraldo & Mejía 2131* (COL). **Bogotá:** "Nova Grenada", *Lindig 308* (B, COL); Fusugasugá, 2300/2600-2800 m, *Lindig 308* (B, COL). **Boyacá:** Valle del Río Cusiana, entre Sogamoso y Corinto, 2000-2200 m, 08 Dec 1970, *Murillo 1378* (COL); Arcabuco, 2700-2900 m, 07 Feb 1959, *Bishler 1908* (COL). **Cauca:** Puracé Parque Nacional de Puracé, 3050 m, 04 Oct 1984, *Lozano et al. 4490* (COL); Puracé, Parque Nacional de Puracé; via hacia la casacada, frente a la cancha de San Nicolás, 2800-2900 m, 14 Oct 1992, *Orozco & Mayorga 2641* (COL). **Cundinamarca:** Sibate, Alto de San Miguel, Km 31 de la carretera a Fusagasugá, 2730 m, 02 Mar 1974, *Acosta Arteaga 133* (COL); En Km 14.1 de la carretera Fómeque a Chingaza, 2770 m, 27 Apr 1974, *Acosta Arteaga 351* (COL); San Miguel (Caserio Mun. Sibate), 2500 m, 20 Oct 1972, *Hagemann & Leist 1249* (COL); Sibate, below Alto de Cuchuco, 7 km SW of Sibate, 2600-2650 m, 19 Oct 1961, *Tryon & Tryon 6113* (COL); Cordillera Oriental, quebrada la Virgen, Gazaunta valley, Cordillera de Heliconia, 15 km NW of Medina, 2560 m, 02 Oct 1944, *Grant 10345* (COL). **Huila:** Cordillera Oriental, at Hacienda Pensilvanica, 15 km E of Baraya, 8400 ft, 23 Jun 1944, *Little jr. 8120* (COL); Comisaria del Caquetá, Cordillera Oriental sobre el filo divisorio, en Gabinete, 2300-2450 m 21-22 Mar 1940, *Cuatrecasas 8418* (COL). **Nariño:** Páramo El Campanero, arriba de La Botana (region Pasto), 3200 m, 31 Oct 1972, *Hagemann & Leist 1382* (COL). **Santander:** Prov. Piedecuesta, Vereda Cristales, trocha que conduce al NE de la

estación, 2950 m, 07 Nov 1997, *Bustos et al. 178* (COL); carretera del páramo de Guantiva a Onzaga, 2970 m, 01 Dec 1967, *Jaramillo Mejia 4433* (COL).

**ECUADOR. Pichincha:** Quito, bei San Florencio, Exkursion nach dem Weg von Manabi, *Stuebel 806* (B); San Florencio, Camino de Manabi, 1500 m, *Stuebel 807* (B); Bellavista; entre Tandayapa y Mindo (vieja carretera Quito - Puerto Quito), 2300 m, 10 Sep 2004, *Lehnert & Kessler 1156* (GOET, QCA, UC). **Prov. unknown:** *Sodiro s.n.* (B); In silvis subandinis prope Alaspongo, Sep 1899, *Sodiro s.n.* (SI [N° 22864]).

***Cyathea chimborazensis* var. *boreopallescens*** M. Lehnert, var. nov. Type. ECUADOR. Zamora-Chinchipec: Reserva Tapichalaca, 2450-2550 m, 04°29'S, 79°07'W, 18-19 Sep 2004, *Lehnert 1296* (Holotype, QCA; isotypes, AAU, GOET, LOJA, UC).  
(Fig. 4B, E)

A var. *chimborazense* pilis paucioribus absentiaque squamarum bullatarum bicolorium differt.

Etymology. The name refers to the northern geographic position of this variety towards the similar *Cyathea austropallescens* M. Lehnert (Latin *borealis*, *boreo-* = North, northern).

Differs from the var. *chimborazensis* in lacking hairs on the veins abaxially as well as bicolorous bullate scales. The concolorous whitish indument on petiole and axes is often weakly developed; such plants resemble *C. austropallescens* from southern Peru and Bolivia, but this species can be distinguished by the concolorous tan to brown petiole scurf and the flattish to subbullate, concolorous brown squamellae and on the veins abaxially, which do not occur in *C. chimborazensis*.

**Distribution and habitat.** Moist montane forest in southern Ecuador, Prov. Zamora-Chinchipec, and northern Peru, Dept. Amazonas, at 2450-2850 m. This variety separates the var. *chimborazensis* in the north from the var. *leonis* in the south.

**Additional specimens examined. ECUADOR. Zamora-Chinchipec:** Reserva Tapichalaca, trail from the station to study plots 4-7, 04°29'S, 79°07'W, 2500 m, 31 Oct 2003, *Lehnert 1053* (GOET, LOJA, QCA, UC); Reserva Tapichalaca, study plot B1, near Sector Ventanillas, 04°29'S, 79°07'W, 2600 m, 02 Nov 2003, *Lehnert 1074* (GOET, LOJA, QCA, UC); road

Valladolid-Yangana, Km 10.4-12.3, 04°29'S, 79°10'W, 2450-2850 m, 18 Feb 1993, Øllgaard & León 100604 (AAU, QCA).

**PERU. Amazonas:** Prov. Bagua, Cordillera Colán SE of La Peca, 7500 - 7900 ft., 29 Sep 1978, Barbour 3611 (AAU, MO).

*Cyathea chimborazensis* var. *boreopallescens* appears to be smaller than the other two varieties. The largest plant I observed was 3.5 m high with 15 cm diam. including the persistent petiole bases. Most plants in the Reserva Tapichalaca, Ecuador, Prov. Zamora-Chinchipec, were fertile at just 2 m trunk height and 10 cm diam.

***Cyathea chimborazensis* var. *leonis*** Lehnert, var. nov. Type. PERU. Amazonas: Prov. Leymebamba, alrededor de la Laguna de Los Condores, 06°51.201'S, 77°40.958'W, 2500-2700 m, 16 Aug 1998, *Quipuscoa-S. et al.* 1234 (holotype, USM; isotypes, F, GOET). (Fig. 4C, F)

*A var. chimborazense pilis erectis in paginam superiorem crebribus absentiaque squamarum bicolorum in indumento laminarum differt.*

**Etymology.** This new variety is dedicated to Dr. Blanca León to merit her extensive work on Pteridophytes in the Río Abiseo National Park, Peru, where the paratype was collected. The epithet is a direct translation from Spanish “león” (= lion) to Latin *leo, leonis*.

Differs from the var. *chimborazensis* in being densely hairy with erect hairs on both sides of the lamina, and in having only white squamellae in the scurf on the pinnules. This variety reaches similar growth heights as var. *chimborazensis* and with 13-15 m, it belongs to the largest tree ferns worldwide.

**Distribution and habitat.** Growing in moist montane forest at 2700 m in northern Peru, Dept. Amazonas and San Martín; to be expected farther south.

**Additional specimens examined.** PERU. San Martín: Prov. Marsical Cáceres, Río Abiseo National Park, 07°XX'S, 77°XX'W, 2700 m, 01 Sep 1985, *Young 1546* (F, USM).

This variety can be mistaken for *Cyathea straminea* H. Karst. from Colombia, Ecuador and Peru because of the white laminar indument and the overall appearance. They can be distinguished by the flat bicolorous laminar scales with brown marginal teeth that are common in *C. straminea* but absent in *C. chimborazensis* var. *leonis*.

***Cyathea tungurahuae*** Sodiro, Sert. Fl. Ecuad. 2: 12. 1908. Type. ECUADOR. Tungurahua: “Sylv. suband. vulc. Tungurahuae, Ecuador”, *Sodiro s.n.* (Holotype, Q). Authentic specimens: “Tungurahua, Jul 1901”, *Sodiro s.n.* (P, SI).

*Cyathea fulva* Sodiro, Rec. Crypt. Vasc. Quit. 1883, not (M. Mart. & Gal.) Fée, 1857. Lectotype, chosen by Tryon (1976). ECUADOR. Riobamba: Tamboloma, Oct 1882, *Sodiro s.n.* (P; isolectotypes, B, K n.v., fragm. NY n.v.). Authentic specimen: “In suband. occid. prov. Bolivar, Ecuador, Sep 1888”, *Sodiro s.n.* (SI [N° 22806]).

*Cyathea ochroleuca* Sodiro, Sert. Fl. Ecuad. 2: 11. 1908. Type. ECUADOR. Pichincha: “Crescit in sylvis subandinis vulcani Atacazo, Ecuador, Jul 1907”, *Sodiro s.n.* (Holotype, QPLS; isotype, SI).

*Cyathea nitens* Sodiro, Sert. Fl. Ecuad. 2: 3. 1908. Type. ECUADOR. Pichincha: “Silvis subandin. vulc. Corazón, Ecuador, Jul 1907”, *Sodiro s.n.* (n.l.). Type collection (fide Tryon 1976): “Corazón, Aug 1907”, *Sodiro s.n.* (MO n.v., P, US)

*Cyathea subinermis* Sodiro, Sert. Fl. Ecuad. 2: 10. 1908. Type. ECUADOR. Pichincha: “Sylvis subandinis vulcani Atacazo, Ecuador, Jul 1907”, *Sodiro s.n.* (Holotype, Q).

*Cyathea sodiroi* H. Christ, Ind. Fil. 195. 1905. nom. nov. for *Cyathea fulva* Sodiro.

(Fig. 5)

*Trunks* to 10-12 m high, 12-20 cm diam., without old petiole bases, the frond scars usually tightly packed, rhomboid, the small parts of cortex between them blackish brown, without pneumathodes or with few small ones below the scars; adventitious buds lacking. *Petioles* 48-92 cm long, dark green to blackish, stramineous when dried, with strong spines; petiole scales large, to 30 x 8 mm, broadly lanceolate with long tips, discordantly bicolorous, dark brown to blackish with tan to white margins abaxially (Fig. 5A), discordantly bicolorous adaxially, brown, often streaked centres and yellowish to white margins; petiole scurf dense, whitish-grey to tan (Fig. 5B), consisting of clearly separated multiciliate squamellae with narrow bodies (Fig. 5C). *Fronde*s to 275 cm long, patent to weakly erect, arching from the middle. *Rhachises* inermous, or muricate in basal half, yellow to stramineous, glabrescent abaxially,

with dense indument of white to tan erect squamellae to 0.4 mm long, with many long marginal processes, no larger scales like petiole scales present. *Laminae* 175 x 90 cm, firm chartaceous to cartilaginous, bipinnate-pinnatifid, apices gradually reduced; dull green adaxially, pale green abaxially. *Costae* yellow to stramineous, inermous or rarely some short prickles basally, weakly hairy adaxially, the hairs white to tan, antrorsely curved, to 1 mm long; costules yellow to stramineous, inermous, moderately to densely hairy adaxially, the hairs white to tan, antrorsely curved, to 1 mm long. *Pinnules* to 12.0 x 2.5 cm, sessile to subsessile, linear lanceolate, the base truncate to slightly rounded, the apex long acute (Fig. 5E); segments to 3.5 mm wide, patent, straight to weakly falcate (Fig. 5F, G), the margins subentire to crenulated, basal segments sometimes even pinnatifid; sinuses narrow, pointed; basal segments never remote; veins glabrous adaxially, or with 1-3 white pluricellular hairs on the midvein distally, glabrous to densely hairy abaxially with white erect hairs 0.4-0.6 mm long (Fig. 5F, G), some scattered small flattish, round to broadly lanceolate, obtuse scales, light brown to tan with white entire margins; sterile veins forked or simple, fertile veins forked. *Sori* subcostal, in fork of vein; indusia subsphaeropteroid to sphaeropteroid, colourless or tan, translucent, fragile, fragmenting to a shallow cup or disc with lacerated margins at maturity, hardly recognizable as indusium; sometimes indusium stops growing before sorus is fully developed and may just be cyatheoid, or it may fall off before the sporangia open; paraphyses as long as or shorter than sporangia. *Spores* pale yellow, tetrahedral-globose; exospore and perispore not examined.

**Distribution and habitat.** Mainly in moist montane forest and elfin forest, in open spots like clearings and road cuts. Andes of Colombia and Ecuador at 2000-3200 m, to be expected in adjacent Venezuela and Peru.

**Additional specimens examined. COLOMBIA. Boyacá:** Villa de Leyva, Santuario de Flora y Fauna de Iguaque, Cabaña de Carrizal, 05°44'N, 73°28'W, 2820 m, 27 Mar 1993, *Betancur et al.* 4069 (COL); camino del Alto de Onzaga a Soatá, en valle lateral, 2800 m, 23 Nov 1967, *Jaramillo Mejia* 4183 (COL); entre Arcabuco y Villa de Leyva, camino de Las Coloradas, 2750 m, 28 Aug 1967, *Jaramillo Mejia et al.* 3001 (COL); Soatá, carretera a Onzaga, hoyo de la quebrada San Antonio, 2820 m, 03 Aug 1958, *Jaramillo Mejia, Hernández-Camacho & van der Hammen* 809 (COL); carretera de Chiquiquirá a Pauna, entre Los Curubitos y San Antonio, 2600 m, 02 Sep 1967, *Jaramillo Mejia, Murillo & van der Hammen* 3258, 3281 (COL); Villa de Leyva, Santuario de Flora y Fauna de Iguaque, alrededores de la Cabaña



Mamarramos, 2750 m, 09 Jun 2001, *Murillo J. et al. 2969* (COL). **Cundinamarca:** La Mesa, Laguna de Pedro-Palo, 2000 m, 14 Dec 1989, Acosta Artega et al. 2241 (COL); road from Bogotá to Sylvania, 20 km S of Bogotá., 22 Jul 1972, *Barrington 464* (COL); Arriba de La Mesa, 2600 m, 16 Nov 1964, *Jaramillo-U. s.n.* (COL); San Francisco, hacienda "La Laja", 2880 m, 26 Sep 2004, *Parra-O., Mieth & Vargas 596* (COL). **Santander:** Carretera del páramo de Guantiva a Onzaga, 2800 m, 01 Dec 1967, *Jaramillo Mejia & van der Hammen 4469* (COL).

**ECUADOR. Bolivar.** "In suband. occid. prov. Bolivar, Sep 1888," *Sodiro s.n.* (SI, N° 22806). **Cañar.** Tipococha, 3200 m, 17 Aug 1933, *Diels 592* (QCA). **Imbabura.** Cotacachi Canton, Parroquia Plaza Gutierrez, caserío Tablachupa, via a Apuela, NW de Cuicocha, 00°20'N, 78°26'W, 2800-3000 m, 13 Jun 1992, *Cuamacás, Gudiño & Tipaz 154* (QCNE). **Loja.** Between Argelia and La Palma, SW of Loja, along old road to Catamayo, 04°09.49'S, 79°16.86'W, 2600-2700 m, 03 Nov 2004, *Lehnert 1504* (AAU, GOET, LOJA, QCA, UC); Road La Argelia (southern Loja)-La Palma, along crest of the mountain range just SW of Loja, ca. 04°03'S, ca. 79°14'W, 2700-2900 m, 04 Mar 1989, *Øllgaard et al. 90829* (AAU, QCA); New road Loja-Saraguro, Km 17, 03°55'S, 79°15'W, 2600 - 2650 m, 19 Mar 1989, *Øllgaard & Feil 91113* (AAU, MO). **Napo.** Cuyuja, colecciones desde el Río Maspa siguiendo la carretera que va hacia Baeza, ca. 78°00'W, 2530 m, 19 Aug 1990, *Jaramillo, Grijalva & Grijalva 11933* (AAU, QCA); Oyacachi, camino Chalpi-Baños, 00°12'S, 77°58'W, 2500-2800 m, 24 May 1996, *Navarrete 1708* (AAU, QCA); Oyacachi, E of village, trail to Pueblo Viejo, 00°13'S, 78°02'W, 2900-3200 m, 28 Oct 1995, *Øllgaard & Navarrete 1296* (AAU, QCA). **Pichincha.** Reserva Geobotanica Pululahua, camino a Lulumbamba, 00°05'N, 78°30'W, 2500-2610 m, 29 Jun 1988, *Cerón 4288* (QCA); One hectare plot, Lloa valley, Hda. Las Palmeras del Lcdo. Fernando Sotomayor, 14 km below Lloa towards Mindo, 00°50'S, 78°38'W, 2900 m, 13-14 Oct 1990, *Jørgensen & Yepéz 92570* (QCA, AAU); One hectare plot, Lloa valley, Hda. Las Palmeras del Lcdo. Fernando Sotomayor, 14 km below Lloa towards Mindo, 00°10'S, 78°38'W, 2900 m, 07 Apr 1991, *Jørgensen et al. 92659, 93070, 93074, 93079 & 93085* (AAU, QCA).

The specimen at P annotated as type specimen of *Cyathea pallescens* by Tryon in 1974 belongs without any doubt to *C. tungurahuae* Sodiro. It consists of a petiole with well developed scurf and many scales, and a fertile pinna; a rare condition of such old a specimen. Sadly, it cannot be used as a type anymore because the label has been swapped, which has

been the cause of Tryon's error. The typical scurf is exquisitely pictured in the revision of the genus (Tryon 1976).

*Cyathea fulva* Sodiro is the name of priority; however, I tend to reject that name because it is a homonym (renamed *C. sodiroi* H. Christ) with insufficient type material. The priority of the other three combined names is not given by the publishing date as all three diagnoses follow one another in the *Sertula* (Sodiro 1908). I have chosen the name *Cyathea tungurahuae* Sodiro because of the condition and amount of the specimens. I have only found specimens of *C. subinermis* and *C. ochroleuca* once each in two herbaria in Quito, both with little scurf and scales remaining on the petioles. Furthermore, the label of *C. ochroleuca* has written on it "sive var. *C. tungurahuae*", indicating that Sodiro defined *C. tungurahuae* for himself prior to *C. ochroleuca* (although this has no value according to the ICBN).

The array of synonym types cover the whole variability of the species: *Cyathea tungurahuae* is a broad-leafed form with glabrous laminae, well developed spines and scurf; *C. ochroleuca* is a medium sized form with well developed indument on the lamina, strong spines and remnants of well developed petiole scurf; the specimens at hand of *C. fulva* and *C. nitens* are identical with *C. ochroleuca*, but they lack the petiole; *C. subinermis* has a very small leaf with the short petiole only muricate (thorns are worn off and thus only verrucate now), but the petiole scurf is typical.

The type of *C. tungurahuae* appears distinct by its glabrousness and broad segments from the types of the other names, which have generally some hairs abaxially and narrower segments, but intermediate forms that fill this morphological gap have been found in one population in southern Ecuador (*Ollgaard et al. 90829, Lehnert 1504*). They show that in one plant with broad pinnules short hairs may occur on one lamina while the other is completely glabrous.

*Cyathea tungurahuae* is defined by the combination of stellate scurf, glabrescent axes, fragile indusia and lack of bullate squamules. The pubescence may vary from no hairs on both sides to scattered hairs on veins adaxially and many hairs on and between veins abaxially; the hairs are always very short (to 0.5 mm) and may be replaced by evanescent appressed trichomidia; scales on the lamina are always few, broadly lanceolate to round, light brown with white subentire margins. The very similar *C. chimborazensis* (Hook.) Domin is best distinguished by the sessile bullate scales (vs. no bullate squamules in *C. tungurahuae*) which vary in colour from pure white to brown with white tips; they also form part of the easily abraded, dense scurf on rhachis, costae and costules which is otherwise formed of the same whitish squamellae as in *C. tungurahuae*. The petiole scales of *C. chimborazensis* tend

to be narrower and less contrastingly coloured than those of *C. tungurahuae*, and the scurf squamellae are not so uniform in size and shape, too. The rhachises of *C. tungurahuae* never have been found to bear persistent scales like it is sometimes the case of *C. chimborazensis*.

Other Andean *Cyathea* species are easily distinguished by the small stellate scurf squamules of *C. tungurahuae*: *Cyathea corallifera* Sodiro from Ecuador and *C. divergens* Kunze from the northern Andes, whose petiole scales match those of *C. tungurahuae* in size and colour, have generally larger erect flat squamules in the scurf and also larger and broader pinnules. *Cyathea patens* H. Karst. has brown to tan scurf of erect, round to oblong, fimbriate squamellae, and smaller, less contrasted petiole scales than *C. tungurahuae*. In *C. austropallescens* Lehnert of Peru and Bolivia, the scurf consists of irregularly dissected, flat squamellae that are generally browner than in *C. tungurahuae*; it can also be distinguished by the pubescence on the veins adaxially being denser than abaxially, and the presence of small flat, brown to tan squamules on the lamina abaxially.

Without petioles at hand for identification, one can rely on the laminar scales that can usually be found at the base of pinnae and basal pinnules: *Cyathea tungurahuae* has mainly flat, round, tan scales with white subentire margins; other species similar in leaf cutting have brown scales with dentate-ciliate margins (*C. patens*), or white scales with dark marginal teeth and sometimes also dark central stripes (*C. straminea* H. Karst, *C. corallifera* Sodiro, *C. boliviana* R. M. Tryon, *C. ruiziana* Klotzsch), or also bullate scales of white or brown color (*C. chimborazensis*).

#### EXCLUDED NAMES:

*Cyathea borjae* Sodiro = ***Alsophila cuspidata*** (Kunze) Conant. One specimen seen (*Sodiro s.n.*, SI [N° 22788]) clearly belongs to this species and fits Sodiro's (1893) description, which mentions the characteristic black spines and very narrow scales on the petiole.

#### ALLIED SPECIES:

***Cyathea atahuallpa*** (R. M. Tryon) Lellinger, Amer. Fern J. 74: 56. 1984.

*Sphaeropteris atahuallpa* R.M. Tryon, Rhodora 74: 442. 1972. Type: PERU. Amazonas. Prov. Chachapoyas, Cerros Calla Calla, above Balsas on road to Leimebamba, 3000-3100 m, 14 Oct 1964, *Hutchinson & Wright 6922* (Holotype, GH; isotype, UC). (Fig. 7B)

Distinguishing characters. - Trunks to 13 m x 12 cm diam., without persistent petiole bases when old, densely covered with them when young; fronds to 400 cm long, patent to ascending, arching; scurf on petioles and leaf axes dense, persistent, consisting of white erect scales 1-5 mm long (Fig. 7B), with long marginal cilia; scurf scales usually conglomerated to distinct tufts; pinnules to 120(-130) x 28(-30) mm, sessile to subsessile; squamules on veins mainly flat, white, translucent, 1-3 mm long, also with bullate squamules to 1 mm long distally on midveins, completely white or with brown bases; all squamules with many white marginal cilia; indusia firm, fragments persistent.

**Distribution and habitat.** In moist high montane forests in southern Ecuador and northern Peru at 2500-3000 m.

**Selected specimens examined. ECUADOR. Azuay.** Sevilla de Oro, old road 10 -12 km N of the village, 02°46'S, 78°37'W, 2750-2850 m, 11 Sep 1976, *Øllgaard & Balslev 9342* (AAU, QCNE). **Loja.** Cajanuma, sendero "Osos de Anteojos", 2740 m, 07 Aug 2003, *Lehnert 789* (GOET, LOJ, QCA, UC). **Morona-Santiago.** E of pass on Gualaceo-Limon road, 03°00.27'S, 78°39.10'W, 3000-3200 m, 15 Nov 2004, *Lehnert 1563* (GOET, QCA, UC). **Zamora-Chinchipe.** New road Loja - Zamora, ca. 5 km E of pass "El Tiro", above old landslide along road, 03°59'S, 79°08'W, 2500 m, 18 Nov 2004, *Lehnert 1573* (GOET, QCA, UC).

PERU. **Cajamarca.** Jaén, Sallique, localidad Quebrada Grande, 05°40'59"S, 79°55'W, 2700-2800 m, 20 Jul 1998, *Campos, Dia, & Guevara* (UC). **Libertad.** Patate, La Montañita (Dist. Buldibuyo), 08°06'S, 77°14'W, 3000 m, 15 Mar 2001, *Sagástegui, Zapata & Palacios 16321* (UC).

***Cyathea corallifera*** Sodiro, Rec. Crypt. Vasc. Prov. Quit. 11. 1883. Type: Ecuador. Pichincha: "Crece en los declives del Corazon y del Atacazo (Milligallí-S. Florencio), 1500-2000 m, *Sodiro s.n.* (n.l.), Authentic specimens: "Corazón, 1882," *Sodiro s.n.* (P, GH photo); "Atacazo, prop. Canzacoto," May 1882, *Sodiro s.n.* (NY).

For full synonymy see Tryon (1976). Fig. 6A-C.

Distinguishing characters. – Trunks to 5 m x 16 cm diam., without persistent petiole bases when old, densely covered with them when young (less than 2 m high); scurf dense, persistent on petioles, evanescent on leaf axes, consisting of erect, whitish squamellae with occasional

brown marginal cells, and a basal layer of appressed, matted squamellae with long marginal ciliae; petiole scales 18-30 x 3.0-6.0 mm, narrowly lanceolate to lanceolate, discordantly bicolorous, or basal scales also concordantly bicolorous, with brown to blackish center, and white to tan margins, these often fragmenting, of a brittle texture than the center; apical scales broader and lighter in color than the basal ones; pinnules to 120-160 x (12)25-45 mm, sessile or stalked to 6 mm), narrowly to broadly triangular to linear, tips long acute, bases truncate to weakly cordate, basal segments may be free but not remote from the other segments; indusia fragile, fragments ephemeral.

**Selected specimens examined. ECUADOR. Cotopaxi.** Reserva Ecológica Los Illinizas, sector II, sector Chuspitambo, W of Choasillí, Cordillera Occidental, W slope, 00°58'42"S, 79°06'22"W, 1900 m, 05 Aug 2003, *Silverstone-Sopkin et al.* 9829 (CUVC, UC). **Imbabura.** Catacachi, Parroquia Apuela, sector Cuellague, 00°15'N, 78°25'W, 1600 m, 10 Jul 1992, *Tipaz & Aulestina* 1684 (QCNE). **Pichincha.** Carretera Mindo – Nono, 00°01'N, 78°39'W, 2050 m, 02 Jul 2002, *Lehnert* 130 (GOET, QCA, UC).

This species is very similar to *C. tungurahuae* and *C. chimborazensis*. They share the same indusium type, i.e., it is sphaeropteroid, very fragile, and sometimes missing completely, though normally a disc with brown ring around the receptacle remains. Additionally, all have mainly white scurf on petioles and on the leaf axes abaxially (in *C. tungurahuae* only on young leaves, persistent in others). *Cyathea corallifera* differs, however, in its large, broad pinnules (max. 17 x 3.5 cm vs. 12.5 x 2.6 cm in *C. tungurahuae*) and the presence of brown marginal teeth in the concolorous white squamules of the scurf and the laminar indument (vs. no brown marginal teeth in *C. tungurahuae* and *C. chimborazensis*).

*Cyathea corallifera* is known only from northwestern Ecuador. It grows in the understory of moist montane forests and in clearings. Its habit with very long fronds drooping from their bases and with very large pinnules does not change with the different sun exposure (pers. obs.).

***Cyathea divergens*** Kunze, *Linnaea* 9: 100. 1834. Type: PERU. Huánuco. Pampayaco, Jul 1829, *Peoppig* s.n. (diar. 1163) (Holotype, LZ [destroyed]). Authentic specimens (fide Tryon 1976): *Poeppig* 219 (diar. 1152) (B, K n.v., P, photo GH n.v., NY [fragm. ex B, K]).

For full synonymy see Tryon (1976).

Tryon (1976) distinguished two varieties, var. *divergens* from Costa Rica and continental South America, and var. *türckheimii* from Mexico to Nicaragua. Only the var. *divergens* is considered here.

Distinguishing characters. - Trunks 5-8(-15) m tall, to 10-12 cm diam., including adventitious root mantle to 25 cm, without old petiole bases, upper parts invested in pale scales; fronds to 600 cm long, drooping; pinnules 14.0-17.0 x 3.5-5.0 cm, the largest ones long-stalked (14-19 mm), 1.5-4.0(-5.0) cm between the stalks, triangular, truncate at base, acute or short attenuate at tip, the basal segments alternately placed, often remote from each other; veins glabrous abaxially except for appressed white unicellular trichomidia, few small, flattish, brown, ovate squamules with elongated tips, and finely dissected dark brown squamules; indusia sphaeropteroid, firm, fragments persistent.

**Distribution and habitat.** In moist montane forests at 1000-2500 m in Costa Rica, Panama, Colombia, Venezuela, Surinam, Ecuador, and Peru.

**Selected specimens examined. COSTA RICA. Cartago.** Finca La Esperanza, ca. 3 km E of Muñeco and 2 km SW of Navarro, 1200-1300 m, 13 Jul 1970, *Lellinger 1120* (AAU).

**PANAMA. Panamá.** Cerro Jefe 100 m al N de la torre, 1000 m, 08 Nov 1986, *Valdespino & Aranda 247* (COL).

**COLOMBIA. Antioquia.** Amalfi, via principal hacia Medellín, sector de la Cascada, 1650 m, 15 Apr 2000, *Giraldo & Mejía 2034* (COL). **Cundinamarca.** Pacho, bosques de Patasía, 2300 m, 27 May 1949, *Uribe Uribe 1976* (COL). **Cauca.** Popayán, Río Molino, Vereda Santa Barbara, 1950 m, 14 Jul 2003, *Munar & Ceballos 152* (COL). **Huila.** La Argentina, Quebrada del Pueblo, 1850 m, 25 Sep 1984, *Lozano G. et al. 3996* (COL). **Nariño.** La Unión, Cerro La Jacoba, 1990-2440 m, 31 Jul 1977, *Díaz-P. S. et al. 872* (COL). **Norte de Santander.** Liso and vicinity (N of Toledo), 2200-2400 m, 06-07 Mar 1927, *Killip & Smith A.C. 20407* (COL). **Quindío.** Provincia de Mariquita, 1800 m, Jan 1852, *Triana 653* (COL). **Risaralda.** Santuario, Vereda Las Colonias, margen derecha del Río San Rafael, 2500 m 25 Feb 1983, *Torres et al. 2314* (COL). **Valle de Cauca.** Carretera Cali-Popayán, Reserva Natural El Guayabo, 1500 m, 12 Sep 1967, *Hagemann 353* (COL).

**ECUADOR. Carchi.** Tulcán, arriba de Maldonado, frontera con Colombia, sitio Chilma, 00°51'N, 78°02'W, 2000 m, 20 May 1991, *Palacios & Rubio 7275* (MO, QCNE). **Napo.** Quijos, Reserva Ecologica Antisana, Cordillera de los Guacamayos, sector oriente, cruce del oleoducto de la compañía ARCO, colección entre El Mirador y Camino de la Virgen, 00°38'S, 77°51'W, 2300 m, 12-14 Jan 1999, *Vargas & Navarrete 3489* (MO, QCNE).

*Cyathea divergens* may have remnants of brown scurf on the leaf axes, similar to *C. carolihenrici* M. Lehnert (2003) and *C. meridensis* K. Karst. However, the scurf of *C. divergens* consists of small, hyaline, thin bodied squamules whose numerous brown marginal teeth dominate the scurf color; in *C. carolihenrici* and *C. meridensis*, these squamules are entirely dark castaneous. The scurf is well developed the Peruvian material chosen as reference (Tryon 1976) and some specimens from Costa Rica and the Guyana Highlands in Venezuela; however, in most specimens from the northern Andes the scurf on the leaf axes is scarce or absent. *Cyathea divergens* (as well as *C. corallifera*) can furthermore be distinguished from *C. carolihenrici* and *C. meridensis* by the white margined petiole scales and the white petiole scurf containing different sized flattish squamules (vs. brownish to orange scale margins and dark brown, uniformly small scurf squamules in *C. carolihenrici* and *C. meridensis*).

***Cyathea ruiziana*** Klotzsch, *Linnaea* 20: 439. 1847. Type: PERU. Huánuco (Panatahuas). “In Peruviae Andium nemoribus,” *Ruiz 72* (Holotype, B; isotype, US).

*Cyathea boliviana* R. M. Tryon, *Contr. Gray Herb.* 206: 61. 1976. Type: BOLIVIA. Cochabamba. Chapare, Incachaca, *Steinbach 9512* (Holotype, GH n.s.; isotypes, BM, F, GH n.s., GOET, MO, NY, US).

Distinguishing characters. – Trunks to 15 m tall, to 12-25 cm diam., without persistent petiole bases when old, densely covered with them when young (less than 2 m high), then up to 40 cm diam. Petiole scurf dense, persistent, consisting of erect, multiciliate, whitish squamellae without marginal teeth; petiole scales to 50(-70) x 6 mm, narrowly lanceolate to lanceolate with attenuate tips, discordantly bicolorous, or basal scales also concordantly bicolorous, with dark brown to blackish centers and white to tan margins; margins often fragmenting, brittle than the center; fronds to 250-350 cm long, patent to slightly erect, weakly arching; pinnules to 120 x 17(-20) mm, well spaced, sessile to subsessile (stalked to 1 mm), linear, tips long

acute to attenuate, bases truncate, basal segments never remote from the following ones; only few hairs on the midrib adaxially, few white erect hairs to 0.5 mm long scattered on and between the veins abaxially, often replaced by appressed brown unicellular trichomidia; squamules on midvein and veins similar to scurf on costules, completely white or brown with white margins, some small (1-2 mm long), discordantly bicolorous tan to brown scales with whitish margins and dark brown to blackish marginal teeth; bullate scales to 1 mm long with ciliate to fimbriate margins mainly distally on the segments; indusia firm, fragments persisting.

**Distribution and habitat.** Cool montane forests at 2000-2600 m in southern Peru and Bolivia.

**Selected specimens examined. PERU. Pasco.** Prov. Oxapampa, P.N. Yanachaga Chemillén, sector San Alberto, 10°32'S, 75°21'W, 2600 m, 16 Mar 2003, *Vasquez & Francis 28036* (UC, US). **Cusco.** Prov. Paucartambo, carretera a Pilcopata, 2650 m, *León 2204* (USM).

**BOLIVIA. Cochabamba.** Prov. Carrasco, 116 km antigua carretera Cochabamba - Villa Tunari, 17°08'S, 65°38'W, 2400 m, 06 Jun 1996, *Kessler et al. 7040* (GOET, LPB, UC).

**La Paz.** Prov. Murillo, Valle del Río Zongo, along Río Jachcha Cruz, 32.2 km N of the pass, 16°07'S, 68°04'W, 2200-2300 m, 22 Oct 1987, *Solomon & Moraes 17221* (LPB, MO). **Santa Cruz.** Prov. Caballero, road Empalme-Karahuasi, ca. 3 km down from the main road, 17°50.53'S, 64°42.06'W, 2500 m, 19 Mar 2003, *Lehnert 724* (GOET, LPB, UC).

*Cyathea ruiziana* was separated from *C. boliviana* by Tryon (1976) by following differences: occurrence of some lanceolate black scales with white fragile margins at the costa bases; white bullate scales are scarce or lacking; the squamules on laminae have less, sometimes no dark teeth in the white fragile margin. All these characters can be found separately or combined in *C. boliviana*. As the name *C. ruiziana* has priority, I include here *C. boliviana* in that species.

This species is apparently very variable in amount of lamina indumenta, but small white or bicolorous squamules with dark marginal cells are always present. Small plants have more of the pure white squamules; these are often bullate. Larger plants, especially when fertile, have many bicolorous scales on the costules and concolorous dark brown flattish squamules on the midveins. The petiole scurf of *C. ruiziana* is similar to that of *C. corallifera* and *C. divergens*, pure white with transitions from small crested squamules to larger



lanceolate scales, but petiolar squamules with dark marginal teeth, which may be present in the other two species, are absent from the scurf of *C. ruiziana*.

**Cyathea simplex** R.M. Tryon, Contr. Gray Herb. 206: 60. 1976. Type: VENEZUELA. Amazonas. Cerro Yutaje, Serranía Yutaje, Río Manapiare, infrequent along left fork of Caño Yutaje, 1250 m, 12 Feb 1953, *Maguire & Maguire 35194* (Holotype, NY; isotypes, GH n.s., US).

Distinguishing characters. -Trunks ca. 1 m x 3 cm, without persistent petiole bases; fronds to 150-160 cm long, patent to slightly erect, weakly arching; scurf dense, persistent, consisting of appressed, multiciliate, whitish squamellae to 0.6 mm long; petiole scales to 25 x 3.0(-3.5) mm, narrowly lanceolate to ovate-lanceolate, discordantly bicolorous, or basal scales also concordantly bicolorous, with brown to dark brown (never blackish) centers and white margins with pale brown marginal cells; apices usually concolorous brown; apical scales broader and lighter in colour than the basal ones; pinnules to 47 x 10 mm, sessile to subsessile (stalked to 1 mm), linear oblong, tips acute to short attenuate, bases truncate, basal segments never remote; segments completely glabrous on both sides; indusia sphaeropteroid, rather fragile, fragments remaining.

**Distribution and habitat.** Only known from the type; there is no geographical overlap with any other species treated here.

**Cyathea straminea** H. Karst., Fl. Columb. II, 1869. Type. COLOMBIA. Quindio: “Crescit cum *Cyathea Quindiuensi* in declivitate montis glacialis vulcanici Tolima altitudine 2500 m,” *Karsten s.n.* (Holotype, n. l.; isotype, B [frag.]). (Fig. 6D-F, 7A)

Distinguishing characters. - Trunks to 5(-8) m tall, to 11(-15) cm diam., without persistent petiole bases when old, densely covered with them when young (less than 1.5 m high); fronds

to 210 cm long, patent, weakly to strongly arching distally, sometimes tips elongated and drooping; scurf on petioles loose, appearing flakey, not persistent, consisting of erect whitish squamellae 0.5-2.0 mm long with subentire margins; petiole scales to 30.0 x 5.0 mm, lanceolate, mostly cream-white to stramineous, concolorous with only a thin brown stripe at the apex and marginal brown teeth, always darker at the pseudopeltate insertion (Fig. 6F), basal scales also irregularly striped in the center, rarely also discordantly bicolorous, with brown to dark brown (never blackish) centers and pale brown margins; scales of a stiffly papery texture, also sitting on the spines where they are long persisting (Fig. 7A); segments without hairs on both sides, or with few white hairs on the midribs adaxially to 0.5 mm long, mainly with small, white, dissected squamules on midveins and veins (Fig. 6D), and some flat to bullate (Fig. 6E), lanceolate scales 1.0-4.0 mm long, entirely white to tan, with or without brown marginal teeth and basal brown spot, sometimes also with thin, elongate, concolorous white to brown scales; indusia sphaeropteroid with umbo (Fig. 6D), quite fragile, fragments remaining.

**Distribution and habitat.** In elfin forests and open páramo scrub, rarely in forest understories at 2400-3800 m in Venezuela, Colombia, Ecuador, Peru, and Bolivia.

**Selected specimens examined. VENZUELA. Trujillo.** P.N. Guaramacal, ridge Agua Fria, 09°16.70'N, 70°08.65'W, 2700-2800 m, Jan-Feb 1996, *Stergios & Zambrano 17736* (PORT, UC).

**COLOMBIA. Cauca.** Km 55 on road from Totoro to Inza, (E of páramo de Guanacas), 02 Aug 1972, *Barrington 482* (COL). **Nariño.** Pasto, "Selva El Campanero", 5 km SW of la Granja Botana, 08 Aug 1972, *Barrington 505* (COL); Pasto, Río San José, upper part of río Bobo, 3350 m, 13 Jul 1991, *Ramirez-P. & Cuayal 839* (COL). **Putumayo.** Comisariato de Putumayo, S side of Laguna de la Cocha, páramo of Sta. Lucia (source of río Alisales), 2900-3100 m, 09 Jan 1941, *Cuatrecasas 11856* (COL). **Quindío.** "Quindiu", *Karsten s.n.* (B).

**ECUADOR. Carchi.** About 1/2 h E of Huaca, past Colonia Huaceña, (ca. 00°35'S, ca. 77°42'W), 3100-3200 m, 19 Feb 1989, *van der Werff & Palacios 10605, 10611* (MO, QCNE); carretera Julio Andrade - El Carmen, Km 18, 00°38'N, 77°40'W, 3800 m, 16 May 1982, *Balslev et al. 2536* (AAU, QCA); road Tulcan-Maldonado, approx. 10 km from Maldonado, 00°52'N, 78°06'W, 2550 m, 05 Aug 1976, *Ollgaard & Balslev 8498* (AAU). **Loja.** Parque Nacional Podocarpus, carretera Yangana - Cerro Toledo, 04°23'S, 79°08'W, 2750 m, 01 Jan 1995, *Palacios & Tirado 12952* (MO, QCNE). **Morona-Santiago.** E of pass

on Gualaceo-Limon road, 03°00.27'S, 78°39.10'W, 3000-3200 m, 15 Nov 2004, *Lehnert 1565* (GOET, QCA, UC). **Napo.** Oyacachi, ca. 1.5 km SE of village, S of river, 00°13'S, 78°03'W, 3200 m, 27 Oct 1995, *Øllgaard & Navarrete 1244* (AAU, QCA). Reserva Ecológica Cayambe-Coca; Cuyuja-Quito Km 5, going up the slope NE of the Hacienda "La Flor del Bosque", 3250 m, 23 Jan 1993, *Gavilanes 1085* (QCNE); NE side of Cerro Sumaco, 00°35'S, 77°39'W, 3100-3300 m, 27 Apr 1979, *Løjtnant & Molau 12884* (AAU). **Pichincha.** Cayambe Canton, 00°07'N, 77°57'W, 3420 m, 27 Dec 1999, *Cuamacas & Gudiño 456* (QCNE).

**PERU. Amazonas.** Chachapoyas, carretera Leymebamba-Balsas, Km 16, 06°43.2'S, 77°50.7'W, 3300 m, 07 Aug 2002, *Lehnert 252* (GOET, USM, UC). **San Martín.** Prov. Mariscal Caceres, P.N. Río Abiseo, en valle de Chochos, 3300 m, 28 Jun 1988, *León & Young 2027* (F, USM); Prov. Mariscal Caceres, P. N. Río Abiseo, en valle de Chochos, 28 Jun 1988, *León & Young 2031, 2032* (USM); Prov. Huallaga, Distr. Saposoa, surroundings of La Canaán, Río Abiseo National Park, 28 Aug 2001, *Quipuscoa et al. 2626* (F).

**BOLIVIA. La Paz.** Prov. Franz Tamayo, PN-AMNI Madidi, trail Pelechuco-Mojos, Tambo Quenmado (camping site), going down trail to Chunkani, passing three crosses, 14°39'S, 68°57'W, 3470 m, 06 May 2003, *Jiménez 1872* (LPB, UC).

Specimens from north Peru have often bicolorous brown scales with white margins; plants with the typical white petiole scales are common in Ecuador and Colombia and also occur in southern Peru and Bolivia. The petiole scurf of *C. straminea* is rather poor; the few subentire squamules are whitish to pale tan and usually lack dark marginal teeth, which are typical of the larger scales.

Most closely related is *C. atahuallpa*, which can be distinguished by its concolorous, paler petiole scales, denser petiole scurf and lack of dark marginal teeth in scales and squamules.

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Fig 1. *Cyathea pallescens*: A. trunk apex; B. petiole base with adventitious pinnae. Photo M. Lehnert (*Lehnert 963*, Ecuador, Prov. Pichincha).

Fig. 2. *Cyathea brachypoda*: A. petiole scales; B. pinnule of medial pinna; C. segment abaxially, showing fragmented indusia and weakly bullate squamules. All from *Sodiro s.n.* (UC).

Fig. 3. *Cyathea chimborazensis*: A.-D. laminar indument; A. strongly bullate squamule B. weakly bullate squamules; C, D. flat squamules; E. medial pinna; F. petiole scales, showing variation in size and color on one petiole; G. basal part of petiole abaxially, with blunt spines and dense scurf. H. scurf squamules from one petiole; note variation in size and shape. All from *Lehnert & Kessler 1156* (GOET).

Fig. 4. *Cyathea chimborazensis*. A-B. variation of segments; A. var. *chimborazensis* (*Lehnert & Kessler 1156*, GOET); B. var. *boreopallescens* (*Lehnert 1053*, GOET); C. var. *leonis* (*Quipuscoa-S. et al. 1234*, GOET); D-F. variation in pinnules; D. var. *chimborazensis* (*Lehnert & Kessler 1156*, GOET); E. var. *boreopallescens* (*Lehnert 1053*, GOET); F. var. *leonis* (*Quipuscoa-S. et al. 1234*, GOET).

Fig. 5. *Cyathea tungurahuae*. A. lower petiole scale; B. detail of basal petiole adaxially, showing fine scurf; C. scurf squamules, strongly dissected; D. medial pinna; E. basal pinnule of medial pinna, adaxially; F. detail of pinnule abaxially, with relatively dense hair on the costule; G. segment abaxially, moderately hairy. A-E, G: *Lehnert 1504* (GOET); F: *Øllgaard & Feil 91113* (AAU).

Fig. 6 A-C. *Cyathea corallifera*: A. petiole scale; B. squamules from petiole scurf; C. basal segment of large pinnule abaxially. All from *Lehnert 130* (UC). D-F. *C. straminea*: D. segment of pinnule abaxially; E. weakly bullate squamule from midvein; F. petiole scales from pale variety. All from *Jiménez 1872* (UC).

Fig. 7. *Cyathea straminea*: A. basal part of petiole with sparse scales and scurf, the brown cortex is showing; near Gualaceo, Prov. Cuenca, Ecuador. B. *C. atahuallpa*: expanding crosier and petioles, with dense scales and scurf, the cortex is not showing; Cajanuma, Pro. Loja, Ecuador. Photos M. Lehnert.

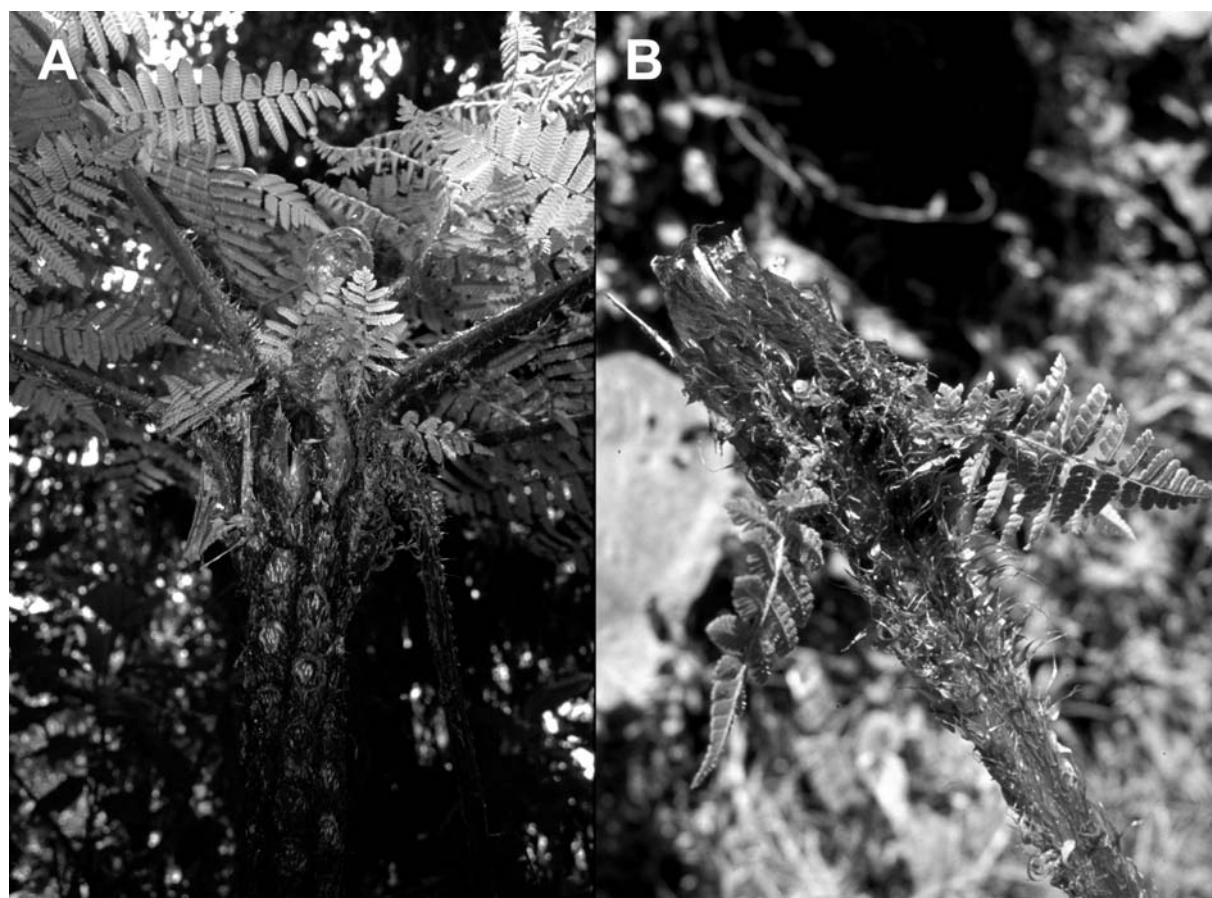


Fig 1. *Cyathea pallescens*: A. trunk apex; B. petiole base with adventitious pinnae. Photo M. Lehnert (*Lehnert 963*, Ecuador, Prov. Pichincha).

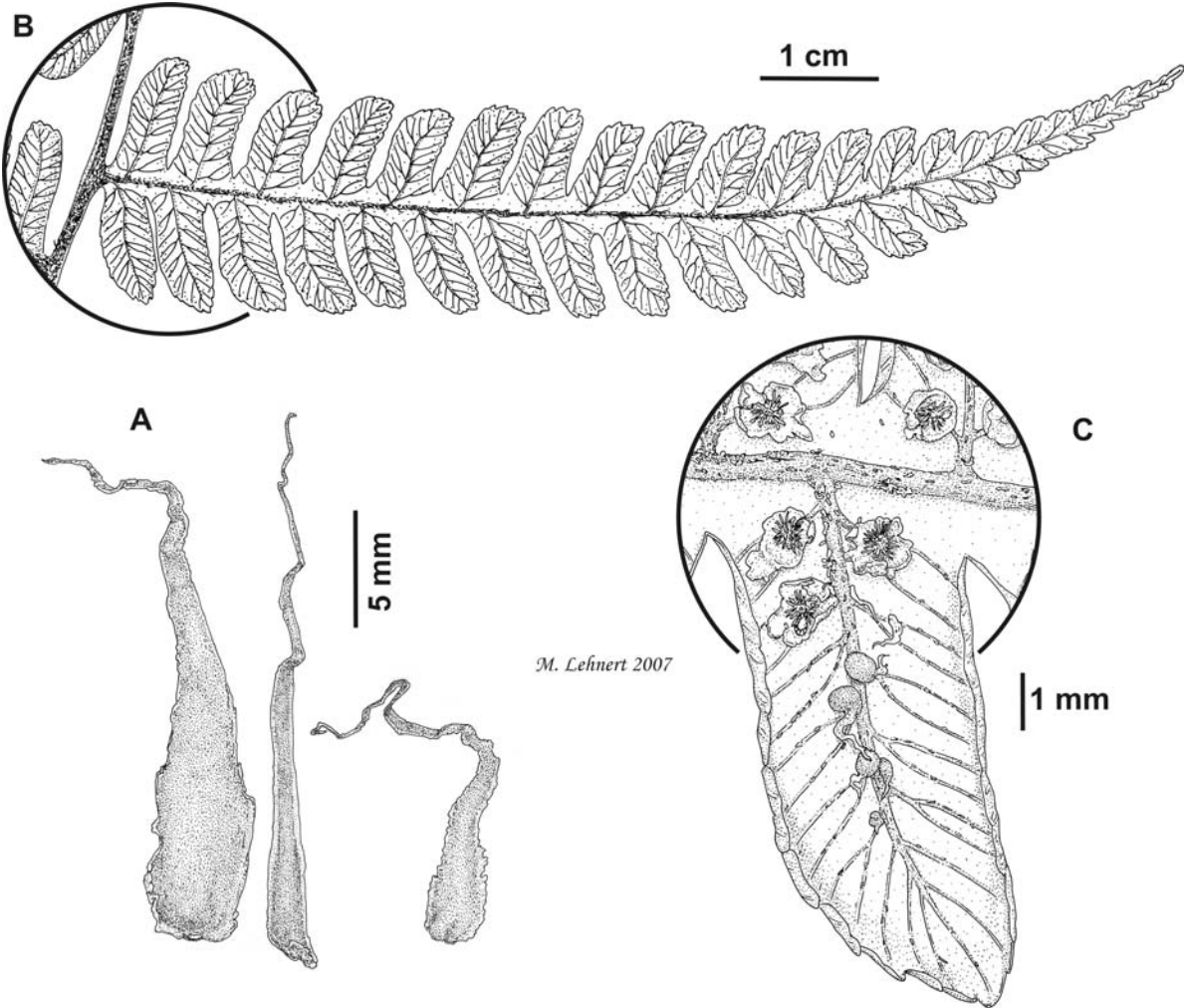


Fig. 2. *Cyathea brachypoda*: A. petiole scales; B. pinnule of medial pinna; C. segment abaxially, showing fragmented indusia and weakly bullate squamules. All from *Sodiro s.n.* (UC).



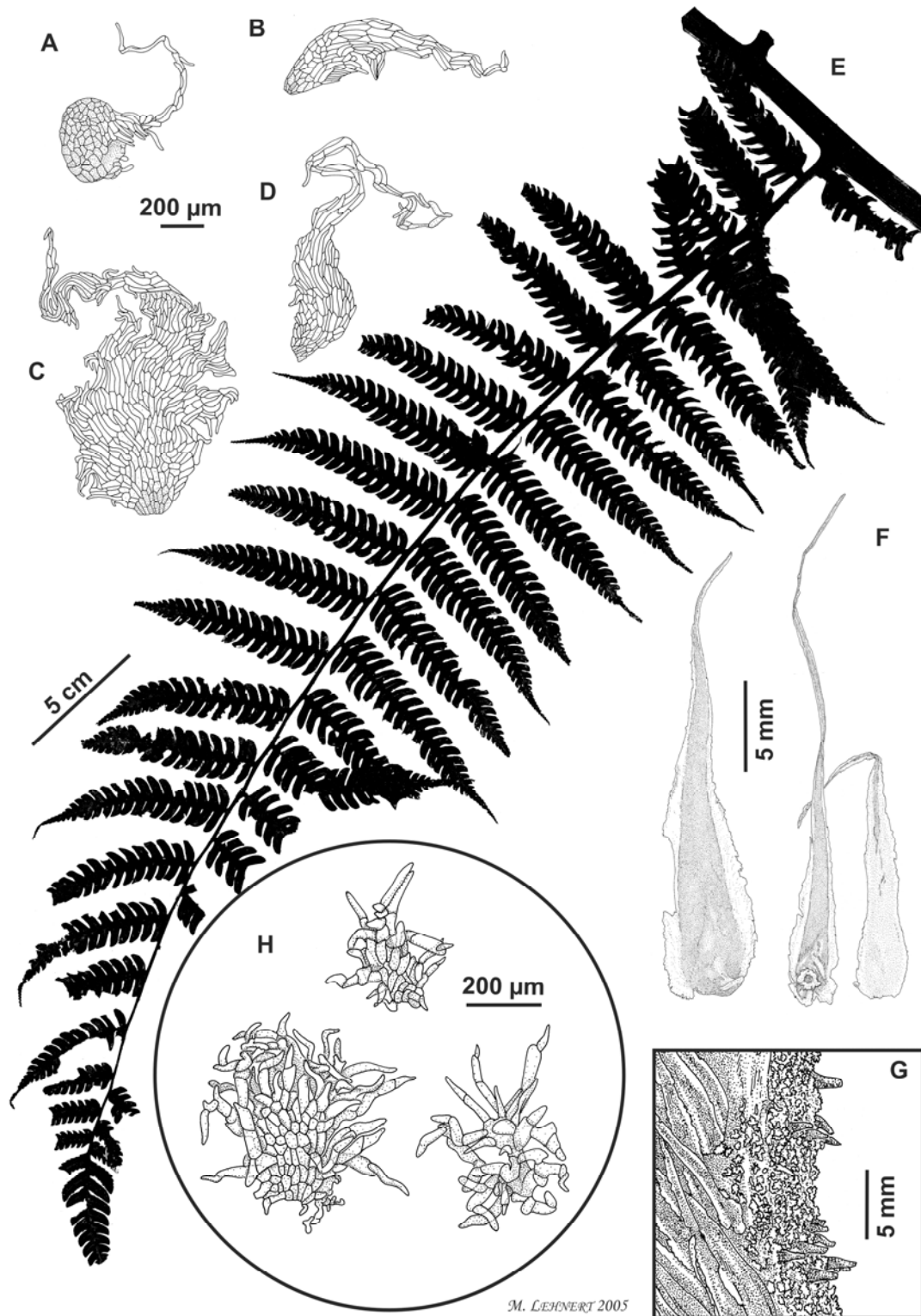


Fig. 3. *Cyathea chimborazensis*: A-D. laminar indument; A. strongly bullate squamule B. weakly bullate squamules; C, D. flat squamules; E. medial pinna; F. petiole scales, showing variation in size and color on one petiole; G. basal part of petiole abaxially, with blunt spines and dense scurf. H. scurf squamules from one petiole; note variation in size and shape. All from *Lehnert & Kessler 1156* (GOET).

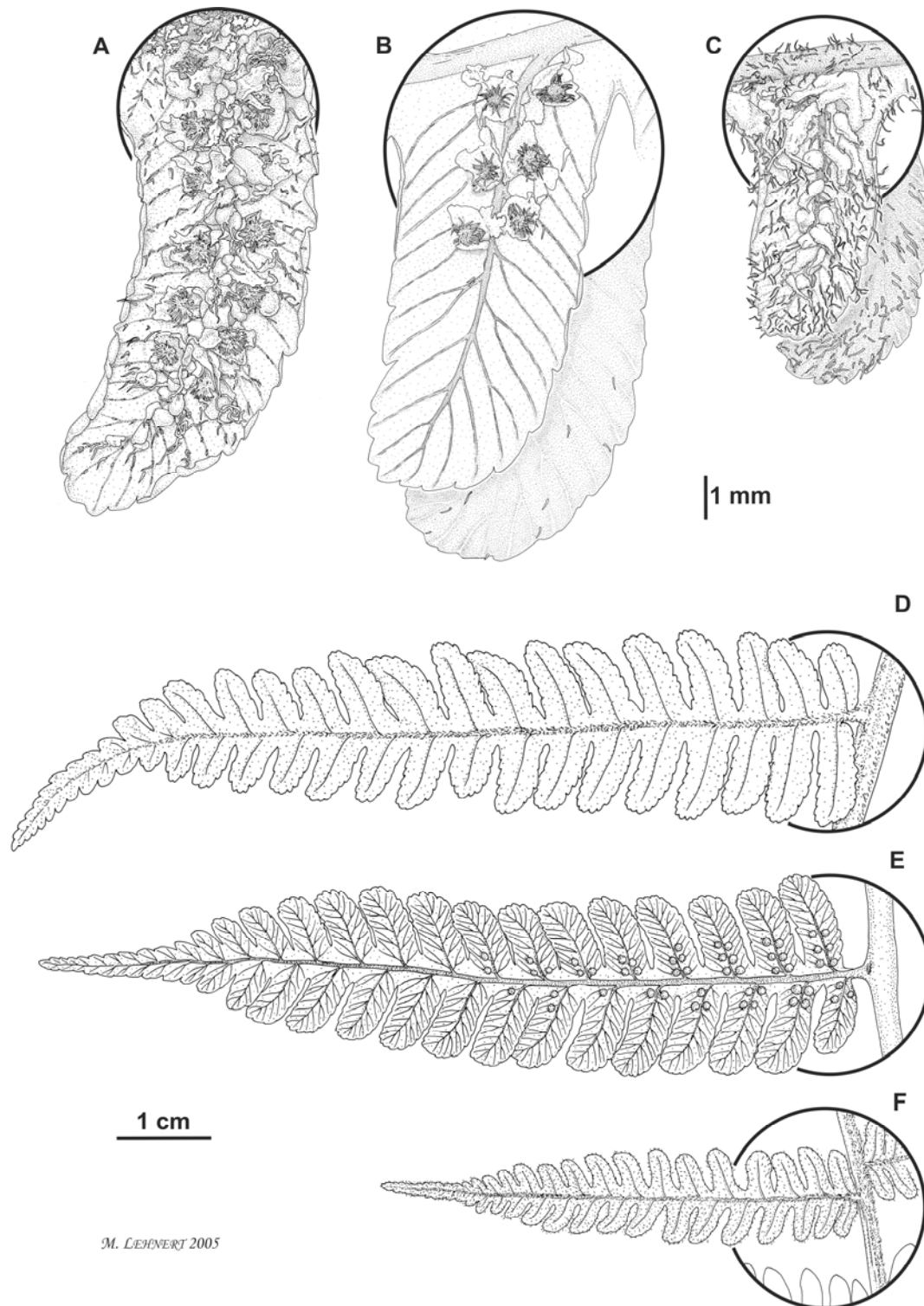


Fig. 4. *Cyathea chimborazensis*. A-B. variation of segments; A, var. *chimborazensis* (Lehnert & Kessler 1156, GOET); B, var. *boreopallescens* (Lehnert 1053, GOET); C, var. *leonis* (Quipuscoa-S. et al. 1234, GOET); D-F. variation in pinnules; D, var. *chimborazensis* (Lehnert & Kessler 1156, GOET); E, var. *boreopallescens* (Lehnert 1053, GOET); F, var. *leonis* (Quipuscoa-S. et al. 1234, GOET).

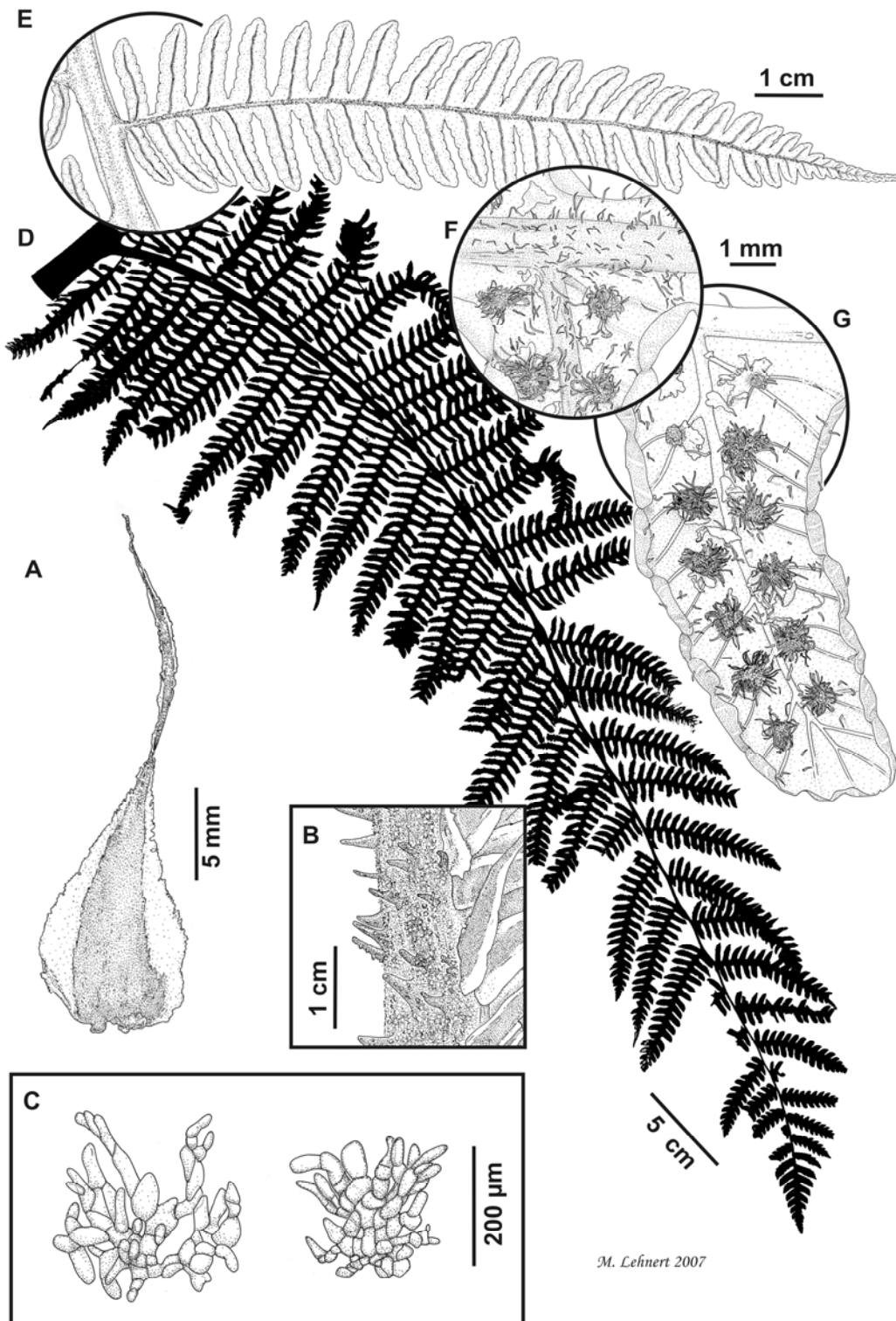


Fig. 5. *Cyathea tungurahuae*. A. lower petiole scale; B. detail of basla petiole adaxially, showing fine scurf; C. scurf squamules, strongly dissected; D. medial pinna; E. basal pinnule of medial pinna, adaxially; F. detail of pinnule abaxially, with relatively dense hair on the costule; G. segment abaxially, moderately hairy. A-E, G: *Lehnert 1504* (GOET); F: *Øllgaard & Feil 91113* (AAU).

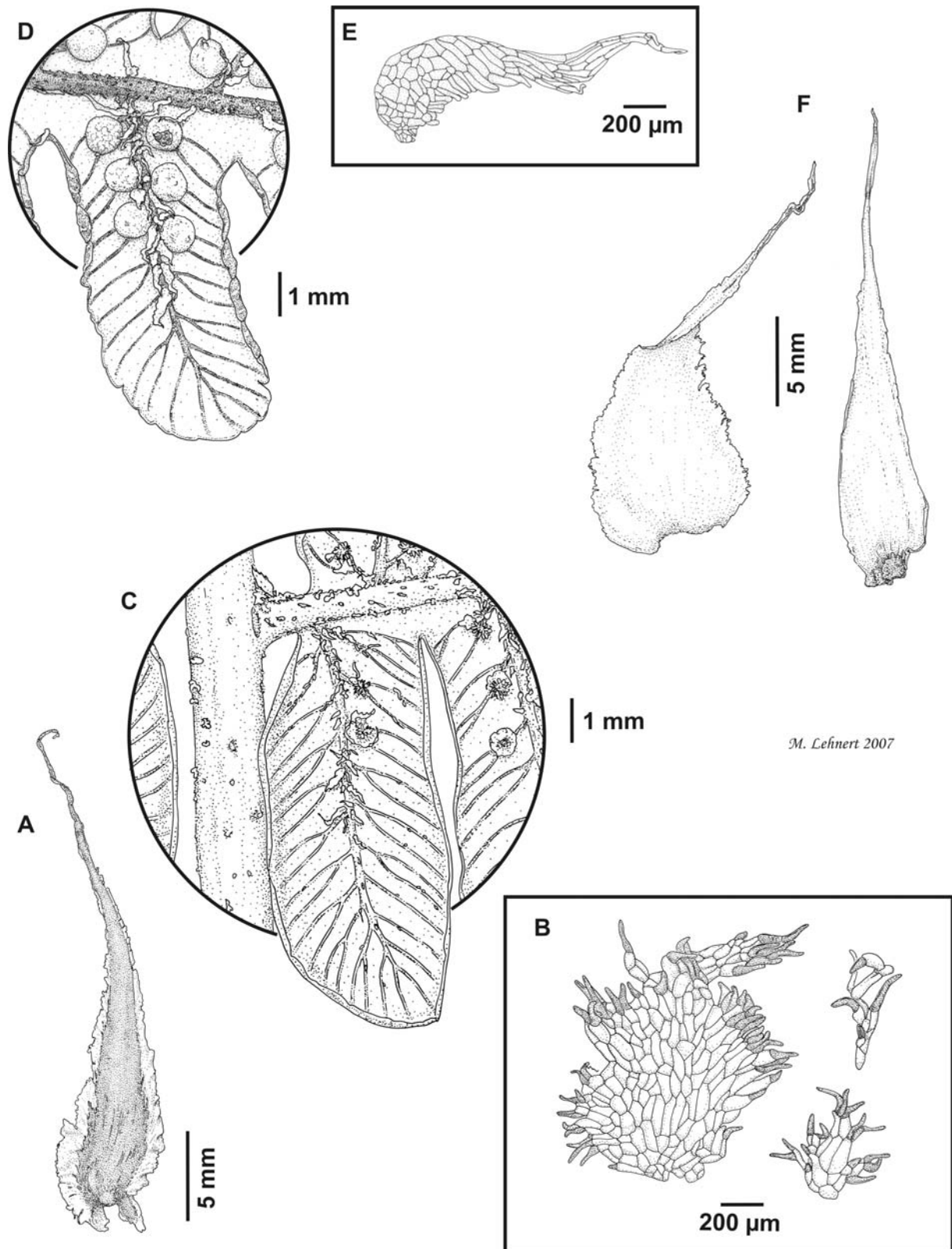


Fig. 6 A-C. *Cyathea corallifera*: A. petiole scale; B. squamules from petiole scurf; C. basal segment of large pinnule abaxially. All from *Lehnert 130* (UC). D-F. *C. straminea*: D. segment of pinnule abaxially; E. weakly bullate squamule from midvein; F. petiole scales from pale variety. All from *Jiménez 1872* (UC).

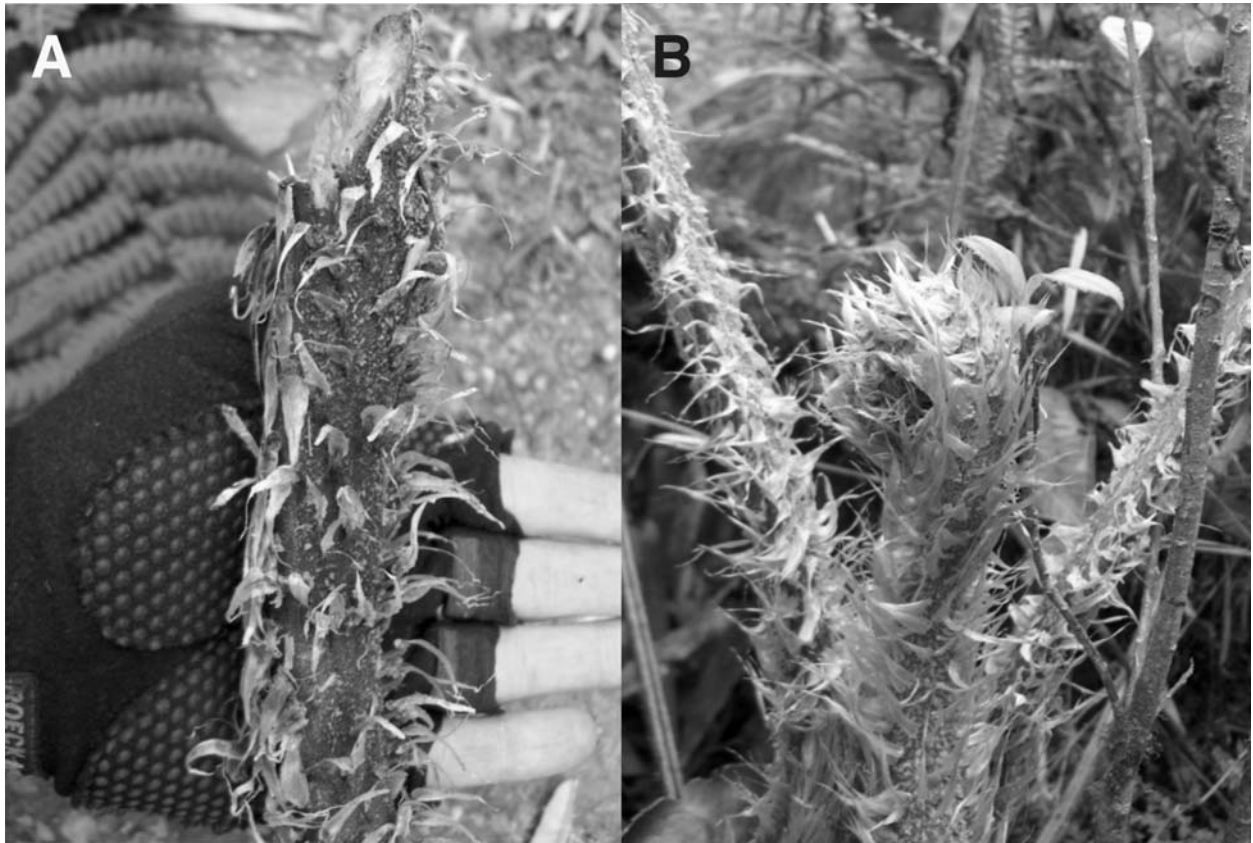


Fig. 7. A. *Cyathea straminea*: basal part of petiole with sparse scales and scurf, the brown cortex is showing; near Gualaceo, Prov. Cuenca, Ecuador. B. *C. atahuallpa*: expanding crozier and petioles, with dense scales and scurf, the cortex is not showing; Cajanuma, Prov. Loja, Ecuador. Photos M. Lehnert.

**FLORA NEOTROPICA MONOGRAPH XX**

Grammitid Ferns I (Polypodiaceae)

**Melpomene**

by

Marcus Lehnert

**Grammitid Ferns I (Polypodiaceae): *Melpomene***

M. LEHNERT

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ABSTRACT

Lehnert, M. (Herbarium GOET), Albrecht-von-Haller Institut für Pflanzenwissenschaften, Abt. Systematische Botanik, Untere Karspüle 2, D-37073 Göttingen, Germany). Grammitid Ferns I. *Melpomene*. Flora Neotropica XX: X-XX. 200X.- A systematic revision of the fern genus *Melpomene* is presented. In total 27 neotropical species and ten varieties are recognized. Ten species are new to science: *Melpomene albicans* Lehnert, *M. caput-gorgonis* Lehnert, *M. flagellata* Lehnert, *M. huancabambensis* Lehnert, *M. jimenezii* Lehnert, *M. michaelis* Lehnert, *M. sklenarii* Lehnert, *M. occidentalis* Lehnert, *M. personata* Lehnert, and *M. vulcanica* Lehnert. The following varieties are newly recognized: *M. pilosissima* var. *tsatchelae* (P. Labiak) Lehnert, *M. xiphopteroides* var. *acrodontium* (Fée) Lehnert, *M. moniliformis* var. **minor** (H. Christ) Lehnert, *M. moniliformis* var. *adnata* (Kunze) Lehnert, *M. moniliformis* var. *tepuiensis* Lehnert, and *M. moniliformis* var. *paradoxa* Lehnert.

The genus is distributed in the mountainous regions of Mesoamerica and tropical South America, with one disjunction (*M. flabelliformis* (Poir.) A. R. Sm. & R. C. Moran) to Africa, Madagascar, and the Mascarenes. Several natural groups are morphologically and phylogenetically recognized and discussed. A key to the species and varieties as well as figures of all species are provided.



## INTRODUCTION

The grammitid ferns comprise about 750 species (Parris, 2003) with a pantropical – southern temperate distribution (Smith in Moran & Riba, 1995; Parris in Kubitzki & Green, 1990; Parris, 2003). They are small plants that prefer epiphytic and saxicolous habitats (Smith in Moran & Riba, 1995; Parris 1998, 2003). Grammitid ferns were part of the broadly defined genus *Polypodium* for a long time because of the overall similarity in the habit (Christensen, 1938; Copeland, 1947). Many species look like miniature *Polypodium* with pinnatisect fronds and round sori (Smith in Moran & Riba, 1995). Some characters, however, define them clearly as a separate group, i.e., green, usually trilete spores and petioles without phyllopodia (vs. monolet spores mostly without chlorophyll and with petioles often on distinct phyllopodia) (Ranker et al., 2004). Based on these characters, the grammitid ferns were sometimes regarded as a subfamily Grammitideae within the Polypodiaceae (Presl, 1836) or as family Grammitidaceae (as Grammitaceae, Ching, 1940), but latest phylogenetic results show that this family is just another clade within a monophyletic family Polypodiaceae (Schneider et al., 2005). Thus the family Grammitidaceae is treated again as part of the Polypodiaceae (Smith et al., 2006). In the following it is referred to as grammitids or grammitoid ferns. The clade of grammitid ferns has probably evolved in the Neotropics, from where it spread to the Paleotropics (Schneider et al., 2004).

The subdivision of the grammitid ferns has a changeful history. A universal genus *Grammitis* (Morton, 1967, 1969; Tryon & Stolze, 1993) was alternatively divided in eight genera (Copeland, 1947), six sections (Tryon & Tryon, 1982), or four genera (Parris in Kubitzki & Green, 1990). The availability of more and better-preserved specimens allowed L. E. Bishop to recognize more natural genera than before. Starting with the neotropical species, his work lead to the separation of several new genera from a more narrowly defined genus *Grammitis* (Bishop, 1977). Since then, the taxonomy of the grammitoid ferns is still changing, with new collections bringing evidence for new species (León & Smith, 2004) and even new genera (*Luisma*, Murillo & Smith, 2003; *Chrysogrammitis*, Parris, 1998). Currently, 11 genera are recognized in the New World (Parris, 2003): *Ceradenia* L. E. Bishop (Bishop, 1988), *Cochlidium* Kaulf. (Bishop 1978), *Enterosora* Baker (Bishop & Smith, 1992), *Grammitis* Sw. sect. *Grammitis* (Bishop 1977), *Lellingeria* A. R. Sm. & R. C. Moran (Smith et al., 1992), *Lomaphlebia* J. Sm. (Smith, 1875), *Luisma* M. T. Murillo & A. R. Sm. (Murillo & Smith, 2003), *Melpomene* A. R. Sm. & R. C. Moran (Smith & Moran 1992), *Micropolypodium* Hayata (Smith, 1992), *Terpsichore* A. R. Sm. (Smith 1993), and *Zygophlebia* L. E. Bishop (Bishop, 1989). Phylogenetic studies on grammitid ferns (Ranker et al., 2003, 2004) support

the currently accepted genera in part as monophyletic (e.g., *Adenophorus*, *Ceradenia*, *Enterosora*, and *Melpomene*), but indicate paraphyly or polyphyly in other genera which thus have to be rejected as unnatural, or further divided and redefined (e.g., *Lellingeria*, *Terpsichore*).

This notwithstanding, Bishop's genera have been applied in modern floristic treatments on neotropical ferns (Moran & Riba, 1995; Mickel & Smith, 2004; Kessler & Smith, in prep.). Most of the genera have not been thoroughly revised since their instatement, exceptions being *Adenophorus* (Bishop, 1974) and *Cochlidium* (Bishop, 1978). In this fascicle of the Flora Neotropica series, I present the first taxonomic monograph of *Melpomene*. The supposed and confirmed relationships of each species and variety are discussed in the systematic treatment.

A total of 2100 collections from following herbaria were consulted: AAU, B, BHCB, C, COL, COLO, CUZ, GOET, K, LOJA, LPB, QCA, QCNE, RIO, S, SP, UC, US, USM. Among them 251 were collected by myself in Ecuador, Peru, Bolivia, and Argentina, with separate samples in silica gel, which were the base for the molecular studies. Samples and field observations from areas not visited by myself were kindly provided by colleagues: Jürgen Kluge (Costa Rica), Thomas Janssen (Madagascar), Andreas Hemp (Tanzania), and Michael Kessler and Thorsten Krömer (Mexico).

#### HISTORICAL SURVEY

*Melpomene* was established as a genus in 1992 by Smith and Moran. The name was based on annotations by L. E. Bishop, who was working intensively on the Grammitidaceae until his death in 1991. The first species now known as *Melpomene* was described in 1804 as *Polypodium flabelliforme* by Poiret; its typification has been controversial (Bishop, 1989). The species of *Melpomene* were soon known as a distinct group within the Polypodiaceae because of their strong aromatic smell and their property to discolor the paper with which they were pressed or on which they were mounted. In the descriptions of species with similar properties, *M. moniliformis* was often used as standard for comparison. The widespread species were described first, with species often defined broadly to incorporate specimens from the whole range. This made determinations relatively easy but also resulted in very heterogenous assemblages in the herbaria. After the establishment of the most common species i.e., *M. moniliformis*, *M. flabelliformis*, *M. pilosissima*, *M. xiphopteroides*, *M. peruviana*) in the first half of the 19<sup>th</sup> century, there was a long period without new

discoveries. Recognition of new, relatively widely distributed species started in the early 20<sup>th</sup> century, e.g., *Melpomene sodiroi* and *M. pseudonutans* (H. Christ & Rosenstock, 1908). New species of *Melpomene* were described irregularly (Copeland, 1955; Tryon & Stolze, 1993), sometimes among historic collections, e.g., *Melpomene erecta* was described from a collection made by R. Spruce more than 100 years earlier (Morton, 1971).

In recent phylogenetic analyses (Ranker et al., 2004; Lehnert et al, in prep. a), *Melpomene* appears monophyletic, based on 24 species sampled. This supports the current morphological concept of the genus.

The present study is the first revisional study of *Melpomene*.

### MORPHOLOGY AND ANATOMY

Plants of *Melpomene* are usually small to minute ferns with rather stiff fronds (one exception being *M. leptostoma* (Fée) A. R. Sm. & R. C. Moran with lax fronds). The fronds are erect, patent, arching downward, or pendent with respect to the substrate but this is hardly detectible in herbarium specimens because usually specimens are mounted with the blade tips pointing upwards. This led to the assumption that most species have their fronds stiffly erect (Smith & Moran, 1992). This is true for the *M. moniliformis*-, *M. firma*- and *M. pseudonutans*-groups, but other species have their fronds usually patent (*M. xiphopteroides* and allies, *M. melanosticta*) to pendent (*M. pilosissima* and allies; *M. gracilis*, *M. allosuroides*; *M. personata* and allies).

The rhizome is either erect and short creeping, or horizontally creeping; in latter case the rhizome can be contracted with the fronds tightly bunched and seemingly fasciculate to long creeping with the fronds widely separated; both growth habits may look the same if the plants form dense mats. The rhizome cortex is dark and sclerenchymatous and the fronds are continuous with the rhizomes. The roots insert only ventrally; in species with erect rhizomes the roots may grow around the rhizomes and thus point radially in all directions. Root insertion could not be ascertained in the small compact rhizomes of *M. gracilis* and *M. allosuroides*. Small phyllopodia have been reported for *M. gracilis* (Tryon & Stolze, 1993) but could not be confirmed from the material examined in this study. In any case, they do not function as articulations because in this and any other *Melpomene* species, the dead fronds remain attached to the rhizomes until they wither or break off at any point along the petioles.

The rhizome scales are the most important character for both delimiting the genus as a whole and circumscribing the individual species. They are clathrate in all species of

*Melpomene* and may be strongly iridescent. Clathrate scales occur also in the genera *Lellingeria* and *Terpsichore*. The main difference is that *Melpomene* has glandular cells or hairs on the margins and these are mostly restricted to the scale tips; the other two genera usually have acicular hairs on the scale margins. In all three genera the marginal hairs may be reduced. Apical glands are present in all *Melpomene* species, but are usually are dislodged with age. The scales of some species of *Melpomene*, e.g. *M. michaelis*, are then hardly distinguishable from those without marginal hairs of *Lellingeria* or *Terpsichore*, and vice versa. Scales of *Melpomene* are usually proximally cordate and pseudopeltately attached while they are only weakly cordate and proximally attached in the other two genera. Marginal glands and setae are also known in other grammitid genera (*Zygophlebia*, *Micropolypodium*) and may occur together on one scale (group of *Terpsichore lanigera*) but in these cases the scales are not clathrate.

Within *Melpomene*, there is a tendency towards reduction of the marginal glands and also a tendency towards increased of scale width from the phylogenetically basal species to the derived ones. Scales that measure more than 26 cells wide across their base are found only in the derived groups of *M. moniliformis* and *M. pseudonutans* (including *M. erecta* with scales to 60 cells wide across the base). The utility of the cell number across scale bases was discovered by C. V. Morton (1971) but not adopted by other researchers in subsequent studies.

Fronds of *Melpomene* are firm-chartaceous to subcoriaceous; blade dissection varies only from pinnatifid to pinnatisect; in some species, larger pinnae may be crenate or even pinnatifid (e.g., Fig. 6D). The pinnae are never stalked and usually fully adnate (exceptions are *M. allosuroides* and *M. gracilis*); their position with respect to the rhachis may be measured as the angle between the rhachis and the costa (Fig. 1A-C), from ascending (80-60°) (Fig. 1A), to patent (85-95°) (Fig. 1B), to deflexed (100-120°) (Fig. 1C). The visibility of the black costae, although quite variable in some species (e.g., Fig. 25D, F), is an important character. The veins are simple, free and end in an adaxial hydathode in most species (e.g., Fig. 7E). Veins are usually not visible in the uncleared pinnae, although sometimes illustrated as such (de la Sota et al., 2000; Labiak & Prado, 2005a). There is a trend within the *M. pilosissima*-group toward reduction of the hydathodes so that they are partially lacking (*M. michaelis*) or entirely lacking (*M. huancabambensis*, *M. jimenezii*); they are present in all other species of *Melpomene*. The laminae may be covered abaxially with a white wax-like deposit in some species (*M. albicans*, *M. youngii*; to a lesser extend *M. sodiroi* and *M. erecta*). The deposit often turns yellow when dried and dissolves in alcohol; hence it is not readily

seen in most herbarium specimens. Other species of *Melpomene* have pale green abaxial laminae that may appear whitish (e.g., *M. xiphopteroides*). To test for the presence of a wax-like layer on the epidermis, a lacquer film peeling of the abaxial laminae should be made: if the wax-like substance is present, the pattern of the epidermal cell pattern is obscured. Stomata of some species are regularly dark brown to reddish in herbarium specimens. This lead to the name *M. melanosticta* for a species in which this trait is most common (Fig. 21F). Other species with dark stomata include *M. xiphopteroides*, *M. jimenezii*, *M. firma*, *M. occidentalis*, and rarely *M. moniliformis*. The fact that the stomatal color may be indistinct from the lamina in all of these species suggests that this phenomenon is caused in part by environmental factors then to genetic predisposition. The increase in frequency of pigmented stomata from *M. moniliformis* to *M. melanosticta* in the above cited sequence follows a gradient from high to low habitat elevation, which means an increase of mean ambiental temperature. This suggests that certain compounds are released in plants grown in warmer conditions which turn brown during the drying process. Unlike the white wax, the darkening of the stomata is not influenced by alcohol conservation.

Pinnae or segments are of various shapes: most common are rounded to oblong segments that are patent to the rhachis, and long-deltate segments that are weakly to strongly ascending. Linear or truncate to trapezoid segments occur only in few species (e.g., *M. wolfii*, *M. flagellata*) and are thus important character states. The dimensions of the segments are measured with the costae as cardinal points (Fig. 1D). The often obscure costae are assumed as medial lines in the central parts of the segments between the sori; segment length is measured along the costa from segment tip to rhachis; segment width is taken as orthogonal line at half of the length (Fig. 1D). This is important because deltate segments are usually strongly decurrent onto the rhachises in their proximal half; thus the base line of the segments is hard to define and width taken here may vary considerably. The dimensions are more useful if the width is taken in the central part of the segment, because it is clearer to delimit and hence better for comparative purposes.

There are two common types of hairs. Aglandular hairs are multicellular, usually dark brown to castaneous, and rather stiff (Fig. 1E). Their variation in length is characteristic: *M. firma* and *M. occidentalis* have short (0.5-0.8 mm) hairs that have a firm insertion and are held erect (*strigose* sensu Lellinger, 1985) (Fig. 12F); the *M. pilosissima* group has similar, stiff but much longer hairs (1.0-3.0 mm) (*pilose* sensu Lellinger, 1985) (e.g., Fig. 16C-E). In most species the hairs are 0.8-1.5 mm long. They can be evenly distributed on the abaxial

lamina or clustered in the sori; *Melpomene gracilis* and *M. allosuroides* lack acicular hairs completely (e.g., Fig. 15C).

Glandular hairs are only 0.2-0.6 mm long and are either simple or branched (Fig. 1F). They are structurally identical with the apical scale glands. Glandular hairs cover the crosiers and young petioles. An actual excretion by the hairs was not observed; however, the apical cells are often darkened, indicating different cell chemistry, and young petioles of *M. moniliformis* may have a greasy touch by the hairs. On fully developed fronds, the glandular hairs are scattered on petioles and abaxial laminae. Depending on the environmental conditions, the glandular hairs may be persistent or ephemeral. In one species, *M. vernicosa*, a special hair type is found: a branched glandular hair with one branch developed as a brown acicular hair (Fig. 1G). Such hairs are common in other grammitid genera (group of *Terpsichore lanigera*) but unique in this species within *Melpomene*.

Sporangia are globose with a broad annulus and lack hairs (Fig. 1H-J); the walls are usually colorless and do not obscure the spores (Fig. 1H). Hence, developing sporangia change color from whitish or yellowish to dark to bluish green while the spore mature, with the ripe spores ultimately outlined in white. This is due to a granular deposit on the spores (Tryon & Tryon, 1982; Tryon & Lugardon, 1991). The spores are trilete with the laesurae reaching almost the length of the radius (Tryon & Lugardon, 1991). The perispore is described as either finely papillose or verrucate; the term colliculate (i.e., finely and shallowly verrucate; see Murley in Stearn, 2004) is also applicable. As they contain chlorophyll, the spores have a short viability (Kramer et al., 1995); germination is quick and often occurs within the sporangia but prothallial growth *in vitro* is very slow (pers. obs.; Stokey & Atkinson, 1958). Cultures may take several years before archegonia and antheridia are developed. The prothallia are laminarioid and characterized by marginal hairs of the same types that occur on the sporophytes, i.e., branched hairs with papillose tips, and uni- to multicellular acicular hairs (Stokey & Atkinson, 1958). Vegetative reproduction of gametophytes by means of plate-like outgrowths is reported for *M. xiphopteroides* (as *Grammitis rigens*), but this seems to be less important than mere fragmentation of the filamentous prothallium stage (Stokey & Atkinson, 1958).

#### KARYOLOGY

Only one chromosome count is known for *Melpomene*. Walker (1966) reported  $n = ca. 74$  for *Melpomene moniliformis* (as *Grammitis moniliformis*) from Jamaica. This seems to be

a tetraploid with the base number  $n = 37$ , which is common in grammitid genera. Within *Melpomene*, no indications for a deviance from this polyploidy have been recorded during this study. Measurements of the stomatal size as a proxy for the karyological state (Barrington et al., 1986) has not yielded relevant data in any recognized species (data not shown). Tryon and Lugardon (1991) report that different spore sizes among the grammitids do not reflect ploidy levels.

#### CHEMOTAXONOMY

Probably all species of *Melpomene* contain a chemical compound, of yet undetermined nature that causes paper to turn yellow or brown. The property of coloring is connected with a sweet, aromatic, sometimes pungent smell that has often been compared with that of pine needles, and perhaps originates from the same component. This chemical is localized in the adaxial epidermis, including the hyaline cell rows along the segment margins, and the brown acicular hairs. This conclusion is derived from two observations. First, folded leaves that have lain for some time between two sheets of paper leave a pattern, with a brown outline where the leaves have touched the paper abaxially, and a brown silhouette where they touched the paper adaxially. Second, in rarely observed cases of herbivory in herbarium material, the abaxial epidermis as well as the mesophyll are devoured, but the hairs and adaxial epidermis are spared. This also shows a potential function of these compounds as repellents against insect herbivores, although it may not be very efficient in dried plants.

The odor can persist for long time periods. Stolze (Tryon & Stolze, 1993) reported that the smell was detectible in an isotype of *Melpomene gracilis* at GH after over 130 years. Smith (Mickel & Smith, 2004) gave a similar report for *M. firma*. Further species with a strong scent are *M. occidentalis*, *M. xiphopteroides*, *M. vernicosa*, *M. albicans*, *M. personata*, *M. erecta*, and large plants of *M. moniliformis*. The smell is rather weak in *M. pseudonutans*, *M. vulcanica*, *M. wolfii*, *M. sklenarii*, *M. flabelliformis*, and *M. peruviana*.

#### PHYLOGENY AND EVOLUTION

Recent attempts to unravel the phylogeny of the polygrammoid ferns (Schneider et al. 2003; Ranker et al., 2004) have revealed that the Grammitidaceae are monophyletic but nest within the Polypodiaceae. The relationship of grammitid ferns to neotropical clades of the Polypodiaceae sensu stricto and the species richness and diversity in South America, point to

a neotropical origin of the whole group, with subsequent long-distance dispersals to the Paleotropics (Ranker et al., 2004). The genus *Melpomene* was highly supported as monophyletic by the analysis of Ranker et al. (2004) but its sister taxon remains uncertain. Ranker et al. (2004) included only four samples of three rather similar species of *Melpomene* in their phylogeny, but their results suggest that *Melpomene* is close to parts of *Lellingeria* or of *Terpsichore*, which share certain synapomorphies with *Melpomene*, i.e., hydathodes and clathrate rhizome scales.

I conducted a phylogenetic analysis using the same gene loci (Lehnert et al., unpubl. data), covering nearly all Mexican and Andean *Melpomene*-species as well as two populations of *M. flabelliformis* from East Africa and Madagascar, respectively. In the Ranker et al. analysis, the *Terpsichore taxifolia*-group appeared as basal paraphylum to *Melpomene*, with *Lellingeria* as sister clade. In my analysis, a part of *Lellingeria* is sister to *Melpomene*, and the *Terpsichore taxifolia*-group is sister to them (Fig. 2). In any case, a relationship of *Melpomene* to these groups is undoubted because the basalmost *Melpomene* species, which appear on well supported branches in my analysis, still have marginal hairs on their rhizome scales as it is characteristic of many genera of Grammitidaceae, but which are usually absent (except for the scale tips) in *Melpomene*. In *Lellingeria* and *Terpsichore*, these hairs are long, acicular and usually unicellular, whereas they are short, glandular, and often multicellular in *Melpomene*. The glandular hairs on the clathrate rhizome scales seem to be the best synapomorphy of *Melpomene*. Their evolution from originally unicellular acicular hairs seems probable; in the course of evolution, the marginal hairs have been then restricted to the scale tips. Unfortunately, there are *Lellingeria* and *Terpsichore* species whose scales lack marginal hairs entirely. These have been often confused with *Melpomene*, but luckily they have other features that distinguishes them, like calcareous deposits in hydathodes or fungal infections, which are not typical of *Melpomene*.

Basal and of still dubious relation to the rest of the genus are *Melpomene gracilis* and *M. allosuroides*, which are small, specialized páramo ferns. Their morphology with thin wiry petioles and small, proximally cuneate segments makes them very distinct from their nearest relatives (according to the phylogenetic results either *M. firma* and *M. occidentalis*, or *M. sodiroi*), which are rather large plants with fully adnate linear segments. Both share narrow rhizome scales with regularly present marginal glands. The group of *M. firma* resembles most closely certain species of the *Terpsichore taxifolia* group (Smith, 1993) in habit, and the latter is a putative sister clade to *Melpomene*. *Melpomene gracilis* and *M. allosuroides* look



superficially like *Ceradenia intricata* (C. V. Morton) L. E. Bishop ex A. R. Sm., but a closer relationship is doubtful.

The core group of *Melpomene* is characterized by clathrate scales with glands restricted to the scale tips. Within this group, some morphologically clearly defined groups are retrieved in the molecular analyses: The *M. pilosissima* group and the *M. xiphopteroides* group are sister clades characterized by short ascending to erect rhizomes and long hairs. The *M. personata* group is similar in leaf dissection to the *M. pilosissima* group but differs in horizontally creeping rhizomes; genetic data show a stronger affiliation to the *M. moniliformis* group than to *M. pilosissima*. The species around *M. pseudonutans* can be separated from the *M. moniliformis* aggregate as a new group, defined by evenly distributed laminar hairs and rather stout, long-creeping rhizomes.

#### DISTRIBUTION AND DISPERSAL

*Melpomene* is clearly centered in the Neotropics, with the highest diversity in the Andes. Only one species, *M. flabelliformis* (Poir.) A. R. Sm. & R. C. Moran, occurs scatteredly in tropical Africa, Madagascar, and the Mascarenes, but is also widely distributed in the Neotropics. Centers of endemism are the northern Andes (6 spp.), the Huancabamba depression (2 spp.), and the central Andes (3 spp.). Other typical biodiversity hot spots (Myers, 2003, and references therein) have few (Brazil, 2 var.; Guayana Highlands, 1 var.) or no endemics (Costa Rica). *Melpomene leptostoma* is the only species to be restricted to Mexico and Central America. Other previously recognized endemics for that region have been found in other regions as well, or are included in more widespread species.

The patterns formed by the distribution of *Melpomene* are commonly observed in many Andean taxa (Simpson, 1975; Molau, 1988). The group of *M. firma* occurs only in the northern and central Andes; its range matches the presence of páramo and puna vegetation (Luteyn, 1999). This group has one widely distributed species *M. firma* (range of the genus without Paleotropics and SE Brazil). The other species, *M. occidentalis*, is narrowly distributed (northern Andes) and may have evolved under the influence of the last uplift of the Andes. The other clades are also centered in the Andes. *Melpomene* species of SE Brazil, the Greater Antilles and Mesoamerica are conspecific with or closely related to Andean species.

One exception is *M. leptostoma*, which is confined to Mexico and Guatemala. It is likely to have evolved from a progenitor similar to *M. firma* or *M. pilosissima*, but its distinctness suggests that this was long ago and under the forces of vicariance. It is possible

that it has been dispersed from South America to Mexico before a continuous land bridge between them allowed more frequent gene flow between the populations as occurs today.

In the other groups of *Melpomene*, many species are restricted to the northern Andes, like *M. pseudonutans*, *M. sklenarii*, and *M. vulcanica* (*M. pseudonutans* group), and *M. sodiroi* (*M. personata* group). Typical of the Amotape-Huancabamba region are *M. huancabambensis* (*M. pilosissima* group) and *M. youngii* (*M. personata* group). Species restricted to the Central Andes belong either to the *M. personata* group (*M. albicans*) or the *M. moniliformis* group (*M. caput-gorgonis*, *M. flagellata*). The great similarity of the southeastern Brazilian *Melpomene* populations to Andean populations indicates a relatively recent colonization; morphological differences are absent or so few that only varieties of some species (*M. moniliformis* var. *subdicarpon*, *M. xiphopteroides* var. *acrodontium*) can be separated. The Caribbean was colonized by the widespread species *M. firma*, *M. xiphopteroides*, *M. melanosticta*, *M. moniliformis*, and *M. flabelliformis*. The last is the only one to occur also in Africa and Madagascar, too. Throughout its range it shows a specific morphological and genetic variation of a kind that does not allow separating subspecies or regional varieties. On the contrary, the genetic analysis suggests the possibility of several colonization events of Africa (Lehnert et al, in prep. a), and maybe recolonization of South America, too. This is remarkable as only *Melpomene flabelliformis* seems to have been able to disperse over the Atlantic. A distribution similar to the pattern found in *M. flabelliformis* is known in other grammitid genera (Smith & Moran, 2001).

The limiting factor in dispersal of *Melpomene* is the viability of the spores. The green spores of the grammitid ferns are usually viable for no longer than two weeks (Kramer et al., 1997), and they are not as drought resistant as spores without chlorophyll. However, these green spores germinate early and grow up to long-lived and vegetatively reproducing prothallia. This may be of advantage when colonizing new areas and may compensate for the short viability. It has been claimed that the establishment of a sound population of ferns is facilitated by fragmentation of long-lived prothallia (Stokey & Atkinson, 1966). One spore of a grammitid fern may thus produce a small population of prothallia, giving a higher chance of cross-fertilization compared to the single prothallia that grow from non-chlorophyllous spores.

No matter under what circumstances, fact is that *Melpomene flabelliformis* has reached Africa, Madagascar and the Mascarenes Islands by long distance dispersal. Separation of a prehistoric continuous population by continental drift can be ruled out because South America and Africa were separated (ca. 100 Mya) long before the evolution of the whole Polypodiaceae took place (ca. 60 Mya) (Collinson, 1996). Furthermore, my phylogenetic

results (Lehnert et al., in prep. a) show that *Melpomene flabelliformis* belongs to the crown group of the genus, so the species is likely to be of relatively young origin. The problem with the long distance dispersal model is that the main wind direction within the tropics is from east to west and thus contrary to the supposed migration direction of many fern taxa (Smith & Moran, 2001). For example, Rouhan et al. (2004) postulated at least 13 separate long distance dispersal events from South America to Africa in *Elaphoglossum* in order to explain the phylogenetic relationships they have found. This disequilibrium may have its cause in the severely depleted African fern flora, where 1000 pteridophyte species (A. R. Smith, pers. com.) stand against 3000 neotropical species (Tryon & Tryon, 1982). Thus the long distance dispersal of a given species to an area where it was previously not present is statistically more probable from South America to Africa than into the opposite direction, against the odd of the prevailing winds. *Melpomene flabelliformis* is just another example of this phenomenon.

#### ECOLOGY

Most *Melpomene* species occur between 2000 m and 4000 m in moist montane forests. Many species grows side-by-side on the same substrate. Only few species occur at lower elevations: *Melpomene firma* may be found around 1500 m but is more frequent at higher elevations; *M. xiphopteroides* is usually found below 2000 m, and *M. melanosticta* rarely grows higher than 1500 m.

Some *Melpomene* species are characteristic páramo elements. *Melpomene moniliformis* is listed in nearly every ecologic study on páramos (e.g., Luteyn, 1999); *Melpomene gracilis* and *M. allosuroides* are saxicolous plants occurring only at or above timberline in moist punas and páramos. *Melpomene peruviana* has the highest recorded growth elevation (5200 m, Peru, Dept. Ancash, Prov. Huaraz) in the genus; its adaptation seems to be mainly to withstand desiccation as it also occurs in relatively dry areas at lower elevations, e.g., in Mexico and Argentina. The páramo species are mainly terrestrial or saxicolous, but always prefer moss cushions to bare soil or rock. *Melpomene erecta* apparently grows best in seepage areas. Most species (23 of 27 spp.), however, are potentially or even strictly epiphytic.

A survey of eight *Melpomene* species showed the presence of Ascomycetes in the root hairs and cortical cells (Lehnert et al., in prep.b). This is interpreted as a kind of mycorrhiza similar to the Ericoid type (Kottke, 2002). The fungi enter via the root hairs; from here, the septate hyphae grow directly into the cortical cells, which respond to the infection with a local reinforcement of the cell walls and a thickening of the cytoplasm (as shown for other fern

genera by Schmid et al., 1995). The infection can spread laterally in the cortex and is visible as dense hyphal coils. In some samples (i.e., *M. pseudonutans*, *M. gracilis*, *M. erecta*, all from Ecuador, Prov. Azuay) the infection was restricted to the root hairs, which may be related to the environment. *Melpomene gracilis* grows almost directly on rocks with only a thin moss cover over it; it is known that saxicolous species usually have no or a low rate of fungal infection (Olsson & Tyler, 2004). The other two grew in soggy *Sphagnum* cushions, and had few but thick roots with dense persisting root hairs, a condition similar to many Polypodiaceae which are known to be free of mycorrhiza (Boullard, 1979). Probably, these environments are not favorable for the establishment of mycorrhizae, with the cost of hosting fungi being greater than the benefit of increased mineral uptake of the plants.

Although ascomycete infections of this type are not yet generally regarded as symbiosis (Schmid et al, 1995), the complete failure of a transplantation experiment with different *Melpomene* species in Bolivia suggests that mycorrhizae may be important (data not shown). Over 15 months, even control plants, which had only been uprooted once and then put back on the same spot, gradually died like all other transplanted plants. This suggests that factors other than abiotic ones condition the growth of *Melpomene*.

## CONSERVATION

The genus is not specifically protected by any law. Considering the lack of any known intensive use, a direct threat to the genus cannot be seen. However, species with a limited distribution may be endangered by habitat destruction. This is imminent in countries like Ecuador and Mexico, which have experienced severe deforestation during the last century (Dodson & Gentry, 1991; Deiniger & Minten, 1999). Potentially endangered species with a small range include *Melpomene leptostoma* (Mexico, Guatemala), *M. huancabambensis* (northern Peru), *M. flagellata*, and *M. caput-gorgonis* (both southern Peru and western Bolivia).

## USES

Macía (2004) reported that plants of *Melpomene melanosticta* (Kunze) A. R. Sm. & R. C. Moran are used as material for necklaces by the Tacana Indians of Bolivia. The women of this tribe wear these plants for the long-lasting sweet smell. No economical uses are known.

## TERMINOLOGY

Acicular: needle-like, unbranched, pointed; applied to the dark brown to castaneous, non-glandular hairs in *Melpomene* which are also sometimes called → setae (Bishop, 1989c; Mickel & Smith, 2005).

Angle: the position of a frond with respect to the rhizome is taxonomically relevant and may be described in degrees. The angle may be very acute (10-20°) resulting in fronds appressed to the short straight rhizomes, which is the case in species with vertically growing rhizomes (i.e., in specimens appearing to be erect, but in vivo growing downwards with pendent fronds); sometimes the angle is wider when the rhizomes had been brought out of the original position and tries to compensate this by curved-up growth (Fig. 8A). In such specimens the angle is still more acute than in species with generally horizontally creeping rhizomes which have the fronds held in a more or less right angle (80-100°) (Fig. 9A), at least near the insertion into the rhizomes. However, in such species, the rhizomes follow the substrate contours while the fronds are geotropic; thus the angles may be exceptionally acute if the relief is steep. For clarity in this valuable but hard to describe character, references to figures should be made and followed.

Clathrate: Lattice pattern formed by the dark tangential cell walls in otherwise transparent tissue; characteristic of rhizome scales of *Melpomene* species.

Glands: small globose hyaline cells, single or on a simple or branched stalk (→ glandular hairs), occurring on young fronds and the scale margins, here mostly restricted to scale tips.

Glandular: small, often branched hyaline (rarely pale brown) multicellular hairs (compare with → acicular hairs).

Habit: appearance in the field; largely determined by the fronds which can be either held upright, patent or pendent in respect to the substrate.

Hairs: multicellular structures of one cell row; single or branched; either → eglandular or → glandular.

Pinnae: applied to the → segments of the pinnatisect laminae; often used synonymously.

Rhizomes: diameter is measured without the investing sheath of scales, which can more than double the rhizome diameter.

Scales: restricted to the rhizome (sometimes also on petiolar bases), usually clathrate in *Melpomene*; width measured in cell rows across base.

Segments: lobes of the pinnatifid to pinnatisect laminae, always adnate, never stalked. They may be patent (held at 85-95° to the rhachis), ascending (held at 30-80°), or deflexed (held at 100-120°).

Setae: sometimes applied to the → acicular hairs.

#### SYSTEMATIC TREATMENT

***Melpomene*** A. R. Sm. & R. C. Moran, Novon 2: 426-432. 1992.

Type. *Polypodium moniliforme* Lagasca ex Sw. (= *Melpomene moniliformis* (Lagasca ex Sw.) A. R. Sm. & R. C. Moran).

The name of the genus is taken from Greek mythology: Melpomene was the muse of tragedy.

Plants perennial; epiphytic, saxicolous, or terrestrial, rhizomes (0.6-)0.8-2.0(-2.5) mm diam., erect to decumbent, compact to short and unbranched, or horizontally creeping to ascending, short to long and often regularly branching, solenostelic, dorsiventral anatomy with the fronds originating alternately and dorsally (upper half), the roots inserting ventrally (lower half); roots black to dark castaneous, crowded in the posterior parts in erect rhizomes, evenly distributed along horizontally creeping rhizomes, with many root hairs to 1.0 mm long; rhizome scales 1.0-7.5 x 0.4-1.6 mm, broadly to very narrowly lanceolate, (8-)10-40(-60) cells wide across the cordate to pseudopeltate bases, apices attenuate to acute, usually only 1-2 cells wide (*M. caput-gorgonis* with scale apices 3-4 cells wide) before ending in a glandular cell or simple to branched glandular hairs, these hyaline and ephemeral; scale margins entire, without hairs, or sometimes with glands like those on the scale apices; scales clathrate, weakly to strongly iridescent, cell walls auburn, brown, castaneous or even blackish, in some species cell lumina occluded by thick cell walls and then central parts of the scales not clathrate. Crosiers densely packed with simple and branched glandular hairs (0.2-0.6 mm) similar to scale glands. Fronds 5-35 cm long, stiffly erect or pendent, straight to arching, rarely laxly pendent. Petioles (2-)5-95 mm, 0.4-1.5 mm diam, dark brown to black, terete, marginate (laminar strand one cell row wide), or alate (several cell rows wide), glabrous or glabrescent to densely and persistently hairy with brown to castaneous, pluricellular acicular hairs (= setae), and with many hyaline, yellowish to pale brown, glandular hairs, these ephemeral to persistent, giving a greasy feel to young petioles. Blades pinnatisect to pinnate

in most parts, pinnatifid at the apices; bases long-decurrent to broadly truncate, mostly short-cuneate to round, apices acute to long-attenuate; fertile from the tips downwards over 1/2 to 3/4 of the blade. Rhachises the color as the petioles, dark brown to black, glabrous to densely hairy with acicular hairs, usually less hairy adaxially than abaxially. Pinnae usually 1-10 times longer than wide, rarely shorter than wide, rounded to oblong, often deltate, rarely linear, the tips acute to obtuse or rounded, sometimes truncate to erose; pinnae adnate, usually decurrent onto the costa and connected by a thin laminar strand, rarely proximally cuneate, sinuses very narrow to wide, sometimes basal pinnae remote, margins entire or in larger specimens of a given species also weakly auriculate proximally to undulate or even pinnatifid along the whole length, in some species last marginal 1-2 cell rows hyaline. Costae dark brown to black, visible from both sides or just abaxially, or not visible; lateral veins simple, not visible; hydathodes present at the ends of veins, rarely reduced in some parts of the fronds or lacking completely, some species with white wax-like deposit on abaxial lamina; glabrous to densely hairy on both laminar sides and along pinna margins; stomates superficial, ca. 30-40 x 65-70  $\mu\text{m}$ , sometimes visible as clear green or darkened, then reddish to black spots abaxially. Sori 1-2 mm diam., single or in 1-15 pairs per pinna, opposite to each other or rarely alternating, borne on a vein, immature sori elliptic like the receptacles, more or less round when mature, glabrous or with dark castaneous hairs; sporangia 0.15-0.20 mm diam., more or less globose, on a thin stalk one cell row wide (except for the two-cell-wide insertion to the capsule) and 3-5 cells long, lacking hairs, releasing ca. 32 spores at maturity (based on *M. gracilis*, *M. firma*, *M. leptostoma*, and *M. moniliformis*); spores globose, 30-40  $\mu\text{m}$  diam., trilete, green, sometimes germinating in sporangia.

A genus of 27 species and ten varieties occurring mainly in the mountainous regions of tropical America, with one species also present in Africa, Madagascar, and the Mascarene Islands. In this treatment, the species are in alphabetical order.

#### KEY TO THE SPECIES OF *MELPOMENE*

1. Scales regularly with marginal glands. 2.
2. Costae not visible, segments proximally cuneate or contracted. 3.
3. Scales large, more than 1 mm long, 38-60 cells wide across their bases.

**5. *M. erecta***

3. Scales small, usually less than 1 mm long, 8-12 cells wide across their bases. 4.
4. Petioles marginate to alate, short (less than 1/4 of frond length).  
**13. *M. melanosticta***
4. Petioles terete, rather long (ca. 1/3 to 1/2 of frond length). 5.
5. Segments entire to incised halfway to the costa, gibbose, margins not  
revolute. **9. *M. gracilis***
5. Segments entire, not gibbose, the margins revolute. **2. *M. allosuroides***
2. Costae visible, segments at least acroscopically surcurrent along rachis. 6.
6. Petioles persistently hairy adaxially; lamina bases truncate; proximal pinnae patent to  
deflexed; hairs clustered in sori and along costae, few or absent between sori.  
**6. *M. firma***
6. Petioles completely glabrous, lamina bases cuneate to rounded, proximal pinnae  
patent to weakly ascending; hairs between the sori in fertile parts but absent in sori.  
**16. *M. occidentalis***
1. Scales without marginal glands. 7.
7. Costae clearly visible as continuous dark lines from the rachises. 8.
8. Petioles 1/3 to 2/5 of frond length, terete to decurrently marginate from lowest  
pinna pair. **17. *M. personata***
8. Petioles 1/4 of frond length or less, marginate to alate to the blade bases. 9.
9. Laminae broadest at or above the middle; rhizomes 1.5 - 2.0 mm diam.;  
moderately to short creeping with fronds clustered to caespitose; scales 32-42  
cells across. **20. *M. pseudonutans***
9. Laminae broadest below the middle; rhizomes to 1.5 mm diam.; fronds well  
spaced on long-creeping rhizomes, scales 20-32(40) cells across.  
**24. *M. vulcanica***
7. Costae not clearly visible as dark lines, either discontinuously or completely obscured. 10.
10. Costae irregularly visible as discontinuous lines only abaxially; laminae  
chartaceous and flat. 11.
11. Scales broadly cordate and 22-40 cells wide at their bases. 15.
15. Petioles 1/2 to 1/3 of frond length, semiterete to marginate; segments  
oblong, 2-3 times longer than broad, obtuse to rounded.  
**7. *M. flabelliformis***



15. Petioles usually 1/4 or less of frond length, alate; segments deltate, 3-4 times longer than broad, acute **24. *M. vulcanica***
11. Scales narrowly lanceolate, subcordate and 10-20 cells wide at their bases; segments ascending. 12.
12. Hairs evenly distributed on laminae, not clustered in sori, regularly on margins. **19b. *M. pilosissima* var. *tsatchelae***
12. Hairs clustered in sori, rarely some on margins. 13.
13. Petiole marginate to alate, segments to 3 times longer than broad **18. *M. peruviana***
13. Petiole terete to marginate; segments to 6-8 times longer than broad. 14.
14. Laminae abaxially pale green, costae with scattered hairs; fronds pendent. **17. *M. personata***
14. Laminae abaxially whitish; costae without hairs; fronds patent to ascending **1. *M. albicans***
10. Costae not visible, sometimes protruding in dried specimens; laminae chartaceous and flat to coriaceous and gibbose. 16.
16. Apical glands on each scale as dense mass of branched hairs at the truncate scale apex (multicellular base). **3. *M. caput-gorgonis***
16. Apical glands as single, simple or branched hair on each scale, originating from one basal cell at the acute scale apices. 17.
17. Rhizomes horizontally creeping with well-spaced fronds. 18.
18. Scales 40-60 cells wide across their bases; rhizomes 1.5-2.0 mm diam.; segments oblong, weakly contracted proximally. **5. *M. erecta***
18. Scales 10-32 cells wide across their bases; rhizomes usually 1.5 mm diam. or less; segments deltate or rounded, rarely oblong, always fully adnate. 19.
19. Sori without hairs. 20.
20. Segments long-deltate, acute, ascending; petioles terete, glabrous. **27. *M. youngii***
20. Segments rounded to short-deltate, obtuse, patent to weakly ascending; petioles alate, hairy to glabrous. 21.
21. Petioles glabrous; segments deltate and ascending. **4. *M. deltata***

21. Petioles hairy to glabrescent; segments oblong to rounded at apices, strictly patent. 22.
22. Segments hairy on costae and between sori, proximal segments often remote, never alariform. **21. *M. sklenarii***
22. Segments not hairy on costae or between sori; proximal segments only remote if alariform. 23.
23. Segments as long as broad, each with 1(-3) sori, petioles ususally glabrous in older fronds; small terrestrial or saxicolous plants (Mesoamerica, Andes, SE Brazil). **15b. *M. moniliformis* var. *minor***
23. Segments to twice as long as broad, each with 6-8 sori, petioles usually hairy in older fronds; rather large terrestrial or epiphytic plants of elfin forests (Mesoamerica, northern Andes).
- 15c. *M. moniliformis* var. *adnata***
19. Sori with hairs. 24.
24. Segments rounded, to twice as long as broad. 25.
25. Laminar hairs restricted to sori; fronds linear; proximal pinnae not remote. 26.
26. Hairs in sori 3-5; petioles marginate to alate throughout.
- 15a. *M. moniliformis* var. *moniliformis***
26. Hairs in sori 5-10; petioles decurrently marginate, often terete at base. 27.
27. Rhizomes moderately to long-creeping; scales to 32 cells wide across their bases; segments round, patent. (Bolivia, Peru). **15e. *M. moniliformis* var. *paradoxa***
27. Rhizome short-creeping; scales 24-28 cells wide across their bases; central segments obtuse to truncate apically, weakly ascending. 28.
28. Central segments weakly oblong-deltate with obtuse to truncate tips; scales usually 20-24 cell rows wide; Venezuela.
- 15d. *M. moniliformis* var. *tepuiensis***

28. Central segments oblong-deltate with obtuse to weakly acute tips, scales to 20 cell rows wide, ususally less; SE Brazil.

**15f. *M. moniliformis* var. *subdicarpon***

25. Laminar hairs usually also between sori, blades long lanceolate, the basal pinnae sometimes remote. 29.

29. Rhizome scales ovate to broadly lanceolate, brown; laminar hairs more or less evenly distributed abaxially, fronds erect, proximal pinnae usually remote.

**21. *M. sklenarii***

29. Rhizome scales narrowly lanceolate, dark brown to blackish, hairs clearly clustered in sori, fronds stiffly pendent, proximal pinnae usually not remote.

**18. *M. peruviana***

24. Segments long-deltate to oblong, largest ones 2-3 times or more as long as broad. 30.

30. Scales 20-32 cells across base; pinnae patent.

**7. *M. flabelliformis***

30. Scales 10-20 cells wide across their bases; pinnae ascending. 31.

31. Petioles decurrently alate, or at least marginate throughout; segments ca. twice as long as broad.

**18. *M. peruviana***

31. Petioles terete, or decurrently marginate; segments at least 3 times as long as broad 32.

32. Segments gibbose, sori weakly to strongly immersed in tissue, scales 24-30 cells wide across their bases.

**22. *M. sodiroi***

32. Segments not gibbose; sori not immersed in tissue, scales 12-20 cells wide across their bases. 33.

33. Abaxial laminar surface pale green; costae ususally visible abaxially, at least partially.

**17. *M. personata***

33. Abaxial laminar surface white; costae usually not visible. 34.
34. Sori each with at most 8 hairs; petioles always with some hairs. **1. *M. albicans***
34. Sori with up to 2 hairs or glabrous; petioles always glabrous. **27. *M. youngii***
17. Rhizomes ascending to erect with caespitose fronds. 35.
35. Proximal segments obtuse to erose, basal ones often alariform. 36.
36. Petioles alate, always glabrous; hairs 0.5-1.0 mm long, few to many in sori, sometimes also evenly distributed between them; blades to 15 mm wide. **25. *M. wolfii***
36. Petioles terete to marginate, densely hairy; hairs 1.5-2.0 mm long, on petiole and in sori, not between them, blades to 5 mm wide. **8. *M. flagellata***
35. All segments deltate to rounded, not alariform. 37.
37. Petioles terete (rarely weakly decurrently marginate). 38.
38. Hairs evenly distributed on laminae, not crowded in sori, regularly on segment margins. 39.
39. Segments long-deltate to oblong, patent, hydathodes small and often absent; petioles 0.8-1.2 mm diam.; hairs to 3.5 mm long. **10. *M. huancabambensis***
39. Segments long deltate, weakly ascending; hydathodes well developed; petioles 0.5-0.8 mm diam.; hairs to 2.5 mm long. 40.
40. Petioles terete, or very narrowly decurrently marginate from the laminar bases, segments rounded to obtuse at tips. **19a. *M. pilosissima***
40. Petioles terete to narrowly marginate, sometimes alate, segments obtuse or acute, rarely rounded at tip. **19b. *M. pilosissima* var. *tsatchelae***
38. Hairs crowded in sori, rarely on segment margins. 41.
41. Rhizomes short-creeping, ascending; fronds erect to patent, hairs to 2 mm long; hydathodes always present. 42.

42. Petioles 0.8-1.2 mm diam., terete; laminae adaxially glabrous, often shiny; terrestrial or epiphytic.

**23. *M. vernicosa***

42. Petioles 0.5-0.8 mm diam. marginate to alate; laminae adaxially opaque, sometimes with some hairs; epiphytic.

**26a. *M. xiphopteroides***

41. Rhizomes erect; fronds fasciculate, pendent; hairs to 3 mm long; hydathodes in part to completely absent. 43.

43. Hairs restricted to sori and rhachises, some scattered on costae; hydathodes missing, rarely some developed; adaxial surface opaque; stomates sometimes visible as red dots. **11. *M. jimenezii***

43. Hairs abundantly between sori; hydathodes irregularly present in some fronds or parts of them; adaxial laminar surfaces shiny; stomates not visible as red dots.

**14. *M. michaelis***

37. Petioles marginate to alate. 44.

44. Segments rounded to short-oblong; scales short-lanceolate, 0.8-1.2 x 0.2-0.5 mm, petioles and sori without hairs.

**13. *M. melanosticta***

44. Segments oblong to elongate; scales long-lanceolate, 1.2-1.4(-4.5) x 0.3-0.8 mm, petioles and sori with at least some hairs. 45.

45. Hairs evenly distributed on laminae, dark brown to castaneous; segment tips acute to obtuse.

**19b. *M. pilosissima* var. *tsatchelae***

45. Hairs crowded in sori, brown, flaccid, often twisted; segment tips rounded to obtuse. 46.

46. Petioles marginate to alate; segments oblong to long-deltate, patent to weakly ascending.

**26a. *M. xiphopteroides***

46. Petioles usually alate; segments long-deltate, ascending.

**26b. *M. xiphopteroides* var. *acrodontium***

1. *Melpomene albicans* Lehnert, sp. nov. Type. Bolivia. Santa Cruz: Prov. Caballero, Comarapa, ca. 1 km de Siberia hacia Torecillos, 17°49'S, 64°40'W, 2650 m, 18 Mar 2003, Lehnert 714 (holotype, GOET; isotypes, LPB, UC). Figs. 4, 5A.

A *Melpomene personata* laminis abaxialiter albicantibus, a *M. youngii* pilis confertis in soris praestans.

Etymology: The name refers to the white wax-like deposit on the abaxial laminae (Latin, *albicans* = whitish).

*Plants* predominately epiphytic or epilithic, growing in moss layers. *Rhizomes* moderately to short-creeping, horizontal (Fig. 4A), 0.8-1.2 mm diam., sometimes with short branches (5-10 mm) going off at right angles. *Fronds* erect (Fig. 4A) or patent, inserted onto the rhizome in acute angles, but often held at nearly right angles to the rhizome, closely placed (2-5 mm) (Fig. 4). *Scales* 3.0-5.0(-7.5) x (0.3-)0.6-0.8(-1.0) mm, (12-)16-20(-22) cells wide, clathrate (Fig. 4B), dark brown to brown, strongly iridescent, cordate to broadly cordate, acute to attenuate at tip; apical glands 3-8, in a nodding cluster or palmate arrangement (Fig. 4C). *Petioles* (24-)35-85 mm long, 0.5-0.8 mm thick, marginate from the lamina bases, most parts terete, glabrous to glabrescent with few (rarely many) short (0.75-1.2 mm) dark brown acicular hairs (Fig. 4D); simple and branched glandular hairs (0.1-0.3 mm) of crosiers and young fronds often persist in older fronds. *Laminae* to 120-175 x 18-35 mm (2/3 to 4/5 of frond length), narrow elliptic to elliptic (widest in the middle), rarely obovate (widest above the center), cuneate or somewhat tapering at base, acute to attenuate at tip (Fig. 4A). *Rhachises* dark brown to black, planar and slightly sunken between leaf tissue adaxially (Fig. 4F), hemispherically protruding abaxially (Fig. 4E), with few to many branched glandular hairs like on petioles, otherwise glabrous or with scattered acicular hairs. *Pinnae* to 9.0-16.0 x 1.2-2.6(-3.0) mm (6-8 times as long as broad), weakly ascending (80-70°), equilateral at bases or weakly decurrent basiscopically, fully adnate, linear-oblong to long-deltate, the tips obtuse or short-acute; costae not visible, or obscurely so abaxially in dried specimens (Fig. 4E, F); proximal 1-7 pinna pairs markedly smaller than subsequent pinnae, sometimes the lowermost 1-4 pinna pairs alariform; surfaces abaxially whitish to white, often yellow or ochre when dried, usually eliminated if treated with alcohol; stomata sometimes visible as rusty red dots;

pinna margins without hairs; hydathodes present (Fig. 4F). *Sori* 2-8(-9) pairs per segment, with 4-10 dark castaneous hairs 0.5-0.8 mm long (Fig. 4E).

**Distribution and habitat.** Elfin forests, cloud forests, and moist montane forests at 2500-3400 m in Bolivia and eastern Brazil (Fig. 5A).

**Selected specimens examined: BRAZIL. Minas Gerais:** Alto Caparaó, Parque Nacional do Caparaó, along trail to Pico da Bandeira, 2600 m, ca. 20° 31' 0S, 41°53'60W, 21 Mar 1999, *Salino & Morais 4538* (UC). **Paraná:** Curibita, Serra Ibitiraque, Morro Camapuá (Mun. Campina Grande do Sul), 25°18' 0S, 49°04' 60W, 02 Mar 2000, *Ribas et al. 3080* (UC). **Rio de Janeiro:** Teresopolis, ca. 22° 25'S, ca. 42° 58'W, Oct 1929, *Brade 9094* (NY); boundary between municipio de Teresopolis and Municipio de Petropolis, Serra dos Orgaos National Park, ca. 5 km SW of city of Teresopolis, 22°27-28'S, 43°01-02'W, 30 Nov 1965, *Eiten & Eiten 7168* (US).

**BOLIVIA. Cochabamba:** Prov. Ayopaya, San Cristobal, climbing along the trail that leads to San Miguel, 16°39'S, 66°43'W, 3100 m, 06 Jun 2002, *Jiménez I. 1107B* (GOET, LPB, UC); Prov. Carrasco, on the way from Comarapa to Siberia, 17°50'64"S, 64°42'W, 3000 m, 22 Jan 2000, *Jiménez I. 283* (LPB, UC); 10 km from Siberia to Comarapa, 17°48'S, 64°42'W, 2600 m, 20 Oct 1996, *Kessler et al. 9164* (LPB, UC); Prov. Carrasco, 10 km Cocapata-Cotacajes, 16°38'S, 66°41'W, 3000 m, 09 May 1997, *Kessler et al. 9401* (GOET, LPB, UC); road Cochabamba-Villa Tunari, below Corani, 17° 10.58'S, 65° 53.67'W, 2700 m, 26 Nov 2002, *Lehnert 512* (GOET, LPB, UC); road Cochabamba-Villa Tunari, below Corani, 17°10.58'S, 65° 53.67'W, 2700 m, 26 Nov 2002, *Lehnert 514* (GOET, LPB, UC); Prov. Chapare, Cochabamba 54 km hacia Villa Tunari, 2750 m, 30 Apr 1979, *Beck 1424a* (LPB). **La Paz:** Prov. Inquisivi, "Kinpaya," at the mouth of the Río Jancha Kaihua where the Aquilani-Choquetanga trail crosses the Río Ocsalla, 10 km N of Choquetanga, 16°45'S, 67°17'W, 3400 m, 07 Sep 1991, *Lewis 39952* (LPB); comunidad Choquetanga-Wichupampa, Serranías de Lulini 13 km al N de Choquetanga, 2-3 km al NW del cerro Lulini, 16°45'S, 67°20'W, 3290 m, 17 Mar 1994, *Salinas 2783* (US); Prov. Nor Yungas, Coscapa, on prehispanic trail Sillutinkara, 16°12'S, 67°53'W, 3100-3300 m, 07 Jan 2001, *Jiménez I. & Vidaurre 526* (LPB, UC), *559* (GOET, LPB, UC); Unduavi; trench to the Valle de Coscapa, 16°17'S, 67° 51'W, 3350 m, 04 Feb 2003, *Lehnert 599, 601, 602* (GOET, LPB, UC). **Santa Cruz:** Prov. Caballero, Comarapa, between Torecillos and Siberia, 17°49.65'S, 64°40.14'W, 2600-2700 m, 18 Mar 2003, *Lehnert 696, 707* (GOET, LPB, UC); from Siberia 4 km to the E,

small laguna on the ridge (Laguna Tinqué?), 2600 m, 18 Mar 2003, *Lehnert 717* (GOET, LPB, UC); by small lake at summit of pass ca 4 km E of Siberia, 2800 m, 04 Jan 2000, *Wood & Goyder 15792* (LPB).

There are only few other species of *Melpomene* with whitish abaxial laminae. *Melpomene youngii* differs from *M. albicans* in being completely glabrous (vs. at least some hairs in sori) and the more strongly ascending pinnae. *Melpomene sodiroi* matches *M. albicans* in the hair distribution, but has thicker rhizomes (to 2.0 mm vs. 1.2 mm in *M. albicans*) and gibbose pinnae with the sori slightly to decidedly sunken (vs. laminae planar with superficial sori).

*Melpomene albicans* belongs to a complex comprising *M. personata*, *M. youngii*, and *M. peruviana*, which all have horizontally creeping rhizomes, downward pointed fronds and dark, lanceolate scales. All except *M. youngii* have hairs in the sori. *Melpomene personata* and *M. peruviana* differ from *M. albicans* in their green laminae (vs. white wax-like undersurfaces; *M. peruviana* sometimes has whitish green laminae but lacks a wax-like layer) and adaxially hairy rhachises; they often have hairs along the costae and sometimes single hairs along the pinna margins. Additionally, *M. peruviana* is generally much smaller than *M. albicans* (and *M. personata*) (5-10 cm vs. to 25 cm), tends to form dense tufts or cushions (vs. single plants or loose groups), and is generally saxicolous in drier or cooler habitats than the other two (mostly epiphytic in elfin forests and wet montane forests).

The specimens from Brazil are less variable in size than the Bolivian specimens. They are in average smaller and have shorter petioles than the latter; *Ribas et al. 3080* (UC) has also rather densely hairy petioles. These Brazilian plants are much easier to confuse with *M. xiphopteroides* var. *acrodontium* than the Andean population because the white laminar layers are less developed and the scales are smaller, and thus closer to the morphological spectrum of *M. xiphopteroides*. However, even weakly hairy *M. xiphopteroides* var. *acrodontium* have more hairs on the rhachises than *M. albicans*, in which the rhachises may be sparsely hairy abaxially but usually are glabrous. Furthermore, both varieties *M. xiphopteroides* often have dark stomata, a character not observed in *M. albicans*.

- 2. *Melpomene allosuroides*** (Rosenst.) A. R. Sm. & R. C. Moran, *Novon* 2: 430. 1992.  
*Polypodium allosuroides* Rosenst., *Meded. Rijks Herb.* 19: 16. 1913. Type. Bolivia.



Cochabamba (?): Lagodos Valley, 4000 m, Oct 1911, *Herzog 2373* (holotype, S; isotypes, UC, US). Figs. 6, 7A.

**Etymology:** The name refers to the similarity of the fertile segments of this species with those of *Cryptogramma crispata* (L.) R. Br. ex Hook. [= *Allosurus crispus* (L.) Bernh.], in which the margins are also revolute.

*Plants* saxicolous, forming dense mats. *Rhizomes* very short-creeping, compact, 0.8-1.5 mm diam. *Fronds* to 140 mm long, erect or pendent (Fig. 6A), inserted onto the rhizomes at right angles, caespitose, closely placed (1 mm or less); dead fronds forming a dense persisting mass. *Scales* 1.0 x 0.4-0.6 mm, (10-)12-16 cells wide across their bases, clathrate, dark brown to blackish, weakly iridescent, weakly cordate to adnate, acute to attenuate at tips; apical glands with 1 (-3 in a linear arrangement) cells, marginal glands unicellular (Fig. 6B). *Petioles* 20-35 mm long, 0.2-0.4 mm thick, terete, glabrous to glabrescent; simple and branched glandular hairs of croziers and young fronds sometimes persist in older fronds. *Laminae* to 120 x 8-10 mm, linear to narrow lanceolate (broadest in the middle), cuneate to decurrent at bases, shortly acute at tips. *Rhachises* dark brown to black, terete like the petiole, hemispherically protruding abaxially and adaxially (Fig 4C, D). *Pinnae* 5.0-10.0 x 1.5-2.5 mm (3-4 times as long as broad), strongly ascending (45- 30°) (Fig. 6A), rhomboid to oblong, cuneate and inequilateral basally, weakly to strongly basiscopically decurrent, the tip obtuse; costae not visible (Fig 4D); all segments free except for the distal pairs (Fig 4A); proximal segments much smaller than preceding pairs; margins revolute in fertile segments (Fig. 6C), not hairy except for glandular hairs (Fig. 6D); hydathodes present (Fig. 6C). *Sori* 2-4 pairs per segment, without setae.

**Distribution and habitat.** Wet places in punas of Bolivia, Depts. La Paz and Cochabamba at 3600-4200 m (Fig. 7A).

**Specimens examined. BOLIVIA. La Paz:** Prov. Murillo, Valle de Zongo (E slope) going down via Botijlaka to Cuticucho, 16°06'S, 68°07'W, 3600 m, 19 Mar 1995, *Gonzales et al. 1915* (LPB, UC); vicinity of Mina San Francisco, 10 km NE of Ventilla along Río Choquekkota, 16°29'S, 67°54'W, 4200 m, 24 Nov 1984, *Solomon 12829* (LPB, MO, UC).

Apparently *Melpomene allosuroides* is most closely related to *M. gracilis*; in fact, both may be regarded just as one variable species, but the lack of morphological transitions between the two taxa justifies their separation. Both have small, broadly lanceolate scales with unicellular marginal glands. Only the group of *M. firma* shares the character of marginal glands; these species, however, have larger, long lanceolate scales and linear to long deltate entire pinnae (vs. elliptic to oblong pinnae, or if linear then crenate in *M. allosuroides*) with visible costae (vs. not visible) and adnate bases (vs. cuneate, weakly perpendicular bases). *Melpomene allosuroides* is best characterized by the small stature (to 5 cm tall), the remote pinnae, and the strongly revolute margins of the otherwise planar pinna; in the usually larger (to 10 cm) *M. gracilis* the pinnae are often gibbose with the margins not revolute.

**3. *Melpomene caput-gorgonis*** Lehnert, sp. nov. Type. Bolivia. La Paz: Prov. Nor Yungas, Cotapata, detras del gasolinero, 3200 m, 16°17'S, 67°51'W, 25 Sep 2002, *Lehnert 367* (holotype, LPB; isotypes, GOET, UC). Figs. 5B, 8.

A *Melpomene flabelliforme* petiolis brevioribus, glandulis apicum squamarum crebrioribus in basibus latioribus (1-2 vs. 3-4 celulis), absentia pilorum inter soris differt.

Etymology: The name refers to the multiple apical glands on the scale tips; these glands resemble the head of Medusa, one of the Gorgons in Greek mythology, which had snakes instead of hair (Latin, *caput* = head).

*Plants* predominatly epiphytic, growing in moss layers, rarely epilithic. *Rhizomes* moderately to short-creeping, horizontal (Fig. 8A), 1.0-1.5 mm diam. *Fronds* to 350-420 mm, arching to pendent, inserted onto the rhizome at right angles, closely placed (1-4 mm) (Fig. 8A). *Scales* to 6.5 x 0.8-1.0 mm, (18-)20–26(-32) cells wide, clathrate, auburn to brown, strongly iridescent, broadly cordate to pseudopeltate, with blunt to truncate tips ending in rows of 3-4 cells (Fig. 8B); apical glands numerous, sitting clustered on the wide tips (Fig. 8C). *Petioles* 15-50(-70)mm long, 0.6-0.8(-1.0) mm thick, decurrently marginate from the lamina base, with brown flaccid hairs (1.0-2.0 mm) on both sides (Fig. 8D), simple and branched glandular hairs of crosiers and young fronds sometimes persistnet in older fronds, but generally glabrescent. *Laminae* to 300(-350) x 14-22 mm, narrow-elliptic (broadest in the middle), decurrent at bases, acute to attenuate at tips (Fig. 8A), chartaceous, rarely coriaceous (*Lehnert 781*).

*Rhachises* dark brown, planar and slightly sunken adaxially (Fig. 8E), weakly hemispherically protruding abaxially (Fig. 8F), glabrous except for the proximal part, with hairs as on petioles. *Pinnae* 4.5-9.0(-12.0) x 3.2-3.8(-5.0) mm (1.5-3 times as long as broad), weakly ascending (80-70°), equilateral at bases or weakly decurrent towards the base, fully adnate, oblong to rounded, the tips obtuse (Fig. 8E, F); costae not visible, or obscurely so abaxially (Fig. 8F), especially in dried specimens; proximal pairs markedly smaller than the central segments (Fig. 8A), inequilateral at bases, basalmost alariform (e.g., *Lehnert 368*), but never trapezoid; hairs in and around sori (Fig. 8F), rarely scattered hairs along the segment margins; hydathodes present (Fig. 8E). *Sori* 2-4 pairs per segment, with 3-10 hairs (1.0-1.5 mm) (Fig. 8F).

**Distribution and habitat.** Wet montane forests and elfin forests at 2680-3200 m in southern Peru and Bolivia (Fig. 5B).

**Additional specimens examined. PERU. Cuzco:** Abra de Chaupimayo, Hacienda Pintubamba, 2700 m, Sep 1932, *Bües 1945* (CUZ).

**BOLIVIA. La Paz:** Prov. Franz Tamayo, PN-ANMI Madidi, trail Keara-Mojos, below Chunkani, 2870 m, 14°38'S, 68°57'W, 08 Nov 2001, *Jiménez I. & Gallegos 917* (LPB, UC); Prov. Larecaja, toll house above Mapiri, 2000 m, 12 Sep 1901, *Williams 1154* (NY); Prov. Nor Yungas, Estación Biológica Tunquini, Bajo Hornuni, senda del campo de Don Pedro al camino de la mina, 2550 m, 16°11'S, 67°53'W, 17 Aug 2000, *Jiménez I. et al. 488* (LPB, UC); Coscapa, along the prehispanic trail Sillutinkara, 16°12'S, 67°53'W, 3100 m, 07 Jan 2001, *Jiménez I. & Vidaurre 534* (LPB, UC); trench to the Coscapa valley, Parque Nacional Cotapata, 16°12'S, 67°33'W, 3000 m, 12 Dec 1997, *Kessler et al. 1871* (LPB); 2 km from Chuspipata to Coroico, 16°22'S, 67°49'W, 2900 m, 19 Sep 1997, *Kessler et al. 11921* (GOET, LPB, UC); Cotapata, behind the gas station, 16° 17'S, 67° 51'W, 3150-3200 m, 25 Sep 2002, *Lehnert 367, 368, 369, 372, 373, 386, 392* (GOET, LPB, UC); Chuspipata-Sacramento, 16°18'S, 67°49'W, 2680 m, 10 Nov 2002, *Lehnert 496a* (GOET, LPB, UC); 1.2 km E de Cotapata-Santa Barbara, trail to the Chuspipata electricity station, 16°17'S, 67°50'W, 3200 m, 02 Feb 2003, *Lehnert 586* (GOET, LPB, UC); Chuspipata, old trail to Unduavi, 3200 m, 07 May 2003, *Lehnert 781* (GOET, LPB, UC).

The most distinguishing feature of this species is the broad scales with the abundant apical papillae. No other species has scale apices that provide a base for glandular papillae

several cells wide. *Melpomene flabelliformis* can be distinguished furthermore by its distant fronds and glabrous or glabrescent petioles (vs. fronds close and petioles persistently hairy in *M. caput-gorgonis*). *Melpomene flagellata* is generally more slender in habit and most features, i.e., laminae to 16 mm wide (vs. to 22 mm), thinner and ascending rhizomes, narrower petiole scales, and longer hairs in sori.

*Melpomene caput-gorgonis* grows together with *M. moniliformis* var. *paradoxa*, which can be distinguished by its longer, glabrescent petioles and shorter pinnae; the latter species also grows in patches with the fronds erect to arching whereas *M. caput-gorgonis* forms solitary plants with arching to pendent fronds.

**4. *Melpomene deltata*** (Mickel & Beitel) A. R. Sm. & R. C. Moran, Novon 2: 429. 1992.

*Grammitis deltata* Mickel & Beitel, Mem. New York Bot. Gard. 46: 198. 1988. Type. Mexico. Oaxaca: Dtto. Mixe, NW slope of Cerro Zemoaltépetl, *Mickel 4637a* (holotype, NY). Figs. 9, 10A.

*Plants* predominately epiphytic, growing in moss layers, rarely saxicolous. *Rhizomes* moderately to short-creeping, 0.8 mm diam. *Fronds* to 180-230 mm, erect, inserted onto the rhizome in about right angles, closely placed (2-4 mm apart) (Fig. 9A). *Scales* 4.0-4.5 x 0.8-1.0 mm, (10-)14-18(-20) cells wide, clathrate, dark brown to brown, weakly iridescent, cordate to pseudopeltate, acute to attenuate at tips; apical glands 3-8, in nodding clusters or palmately arranged. *Petioles* 18-35 mm long (Fig. 9A), 0.6-0.8 mm diam., decurrently alate to marginate throughout, glabrous; simple and branched glandular hairs of crosiers and young fronds sometimes persistent in older fronds. *Laminae* 150-190 x 8-16 mm, narrow-elliptic (broadest in the middle), decurrent at bases, long acute at tips (Fig. 9A). *Rhachises* dark brown to black, planar and slightly sunken adaxially, hemispherically protruding abaxially (Fig. 9B), only with ephemeral glandular hairs, otherwise glabrous. *Pinnae* 4.5-6.0 x 2.5-4.0 mm (1-2 times longer than wide), weakly ascending, inequilateral at base, weakly decurrent towards the base, fully adnate, oblong to broadly deltate, the tips obtuse to rounded; costae not visible (Fig. 9B), or weakly protruding in dried specimens; hairs absent; proximal 1-3 pinna pairs markedly smaller than the following segments, sometimes alariform; hydathodes present, planar to slightly sunken in tissue. *Sori* 2-4 pairs per segment, without hairs (Fig. 9B).

**Distribution and habitat.** Montane forests at 1000-3000 m in Mexico, Honduras, Salvador, and western Venezuela (Fig. 10A).

**Specimens examined. MEXICO. Chiapas:** N of San Cristobal las Casas on top of Cerro Zontehuitz, 9400 ft, 27 Jul 1963, *Mickel & Hellwig 1247D* (NY). **Oaxaca:** Dtto. Mixes, SE shoulder of Cerro Zempoaltépetl, 8200 ft, 22 Sep 1970, *Mickel & Leonard 4894* (NY, UC). **Prov. unknown:** “Tropical North America, Herbar Hart 2,” Aug 1912, *Hart 20* (P).

**HONDURAS. Lempira:** Celaque National Park; along Río Arcágual, upstream from base camp 2, 10.5 km WSW of the town of Gracias, 14°34'05"N, 88°41'05"W, 2500 m, 16 Nov 1991, *Moran 5586* (UC)

**EL SALVADOR. Chalatenango:** Cerro El Pital, 2600 m, 16 Nov 1978, *Seiler 758* (NY); E slope of Los Esesmites, 2430 m, 15 Mar 1942, *Tucker 1065* (P, UC).

**VENEZUELA. Táchira:** Dtto. Uribante, between Pregonero and Laguna de los García, locality known as La Pradera, 5 km W of Pregonero, 08°01'N, 71°43'W, 1300 m, 22 Nov 1985, *Ortega & van der Werff 2861* (UC). **Trujillo:** Dtto. Boconó, mountains and páramo of Guaramacal, 09°12'N, 70°09'W, 2500-3000 m, 22 Nov 1984, *Ortega & van der Werff 2246* (UC); páramo of Guaramacal, 1000 m, 03 Feb 1987, *van der Werff et al. 8823* (AAU); mountains and páramo of Guaramacal, 09°12'N, 70°09'W, 2500-3000 m, 01 May 1985, *Ortega 2650* (UC).

This species is a segregate of *Melpomene moniliformis* from which it only differs in the complete glabrousness and the decidedly deltate segments. Mixed occurrences of *M. deltata* and *M. moniliformis* show that they are not simply varieties or ecotypes of one species (Mickel & Smith, 2004). The Venezuelan specimens are morphologically not distinguishable from Mesoamerican specimens. Larger plants of *M. deltata* may be mistaken for glabrous *M. pseudonutans* but that species has much thicker rhizomes (to 0.8 mm in *M. deltata* vs. 2.8 mm in *M. pseudonutans*) and larger scales (14-18 cells vs. 24-40 cells wide across the bases).

**5. *Melpomene erecta*** (C. V. Morton) A. R. Sm. & R. C. Moran, *Novon* 2: 429. 1992.  
*Grammitis erecta* C. V. Morton, *Phytologia* 22: 72. 1971. Type. Ecuador. Tungurahua: Mt. Tungurahua, *Spruce 5279A* (holotype, K; isotypes, GH n.s., GOET).

*Polypodium moniliforme* Lagasc. ex Sw. var. *bogotense* Hieron., Hedwigia 48: 249. 1909.

Type. Colombia. Cundinamarca, Bogotá region, *Stübel 431* pro parte (holotype, B). Fig. 5C, 11.

Etymology: Named for the ascending, tough rhizomes (Latin, *erectus* = upright)

*Plants* terrestrial or epilithic, growing in moss layers. *Rhizomes* long-creeping and often ascending, (1.5-)2.0-2.4 mm diam. (Fig. 11A), hard and woody; roots with dense cover of ferruginous to castaneous root hairs to 3 mm long. *Fronde*s erect, inserted onto the rhizome in a narrow to right angle, widely placed (10-15 mm) (Fig. 11A). *Scales* 7.0 x 2.8 mm, (28-)38-60(64) cells wide across bases, clathrate, light brown to brown, strongly iridescent, broadly cordate, acute and often undulate at tips (Fig. 11B); apical glands 1-2(-3), in nodding clusters. *Petioles* 7-30(-54) mm long, ca. 0.8 mm thick, marginate from the laminar bases to terete, glabrous (Fig. 11C) to glabrescent, simple and branched glandular hairs of crossiers and young fronds sometimes persistent in older fronds. *Laminae* to 200 x 15(-25) mm, broadly linear to narrow elliptic (broadest from below to above the middle), rounded to truncate at bases, acute to rostrate at tips (Fig. 11A); completely glabrous, abaxially white. *Rhachises* dark brown to black, glabrous, planar and slightly sunken adaxially (Fig. 11D), hemispherically protruding abaxially (Fig. 11E). *Pinnae* to 7(-17) x 1-2 mm (4-5(-15) times as long as broad), planar to weakly gibbose, smaller ones patent, larger ones ascending (80-70°), equilateral at base or weakly decurrent towards the base, fully adnate, linear-oblong, the tip acute; costae not visible (Fig. 11E), or obscurely so in dried specimens; proximal 1-4 pinna pairs markedly smaller than the following segments, the lowest ones sometimes alariform; hydathodes present. *Sori* 1-4 per segment, without setae, placed alternately or just on one side of the costae (Fig. 11E), their size (1-2 mm) exceeding the width of the pinnae/segments (Fig. 11D).

**Distribution and habitat.** Moist montane forests and elfin forests, on rock outcrops, along road cuts and small streams at (2400-)2900-3500 m in Venezuela, Colombia, Ecuador, Peru, and Bolivia (Fig. 5C).

**Selected specimens examined.** **VENEZUELA. Táchira:** Upper Río Quinimari, surroundings of "Las Copas," at base of Peña de Pata de Judío (below Páramo de Judío), 15 km S of San Vicente de la Revancha, 30 km S of Alquitrana, SW of Santa Ana, 2400 m, 10-11 Jan 1968, *Steyermark et al. 100548* (NY, UC); *ibid.*, *Steyermark et al. 100597* (NY).

**COLOMBIA. Huila:** Cordillera Central, Cordillera del Buey, hike from Finca Loyola over the páramo down to San Antonio, 2400 m, 14 Dec 1975, *Bishop 1987* (UC).

**ECUADOR. Azuay:** Sector Maylas, near the pass on Gualaceo-Limon road, 03°00.08'S, 78°39.70'W, 3300 m, 15 Nov 2004, *Lehnert 1570* (GOET, QCA, UC). **Morona-Santiago:** E of pass on Gualaceo-Limón road, 03°00.27'S, 78°39.10'W, 3000-3200 m, 15 Nov 2004, *Lehnert 1560* (GOET, QCA, UC); road Plan de Milagro-Gualaceo, 03°02'S, 78°35'W, 3000-3200 m, 06 Feb 1989, *Palacios & van der Werff 3763* (AAU, UC); road Plan de Milagro-Gualaceo, 03°02'S, 78°35'W, 3000-3200 m, 06 Feb 1989, *van der Werff & Palacios 3763* (UC), road Gualaceo-El Limón, on the E side of the pass, 2900-3200 m, 07 Feb 1989, *van der Werff & Palacios 10456* (AAU, UC). **Tungurahua:** Cordillera de lo Llanganetes, Patate-El Triunfo Km 16, 3000 m, 01 Mar 1998, *Schwerdtfeger 98030103* (UC). **Prov. unknown:** "In Andibus Ecuadoriensibus," 1857-1859, *Spruce 5413* (AAU, B, GOET, P).

**PERU. Cuzco:** La Convención, Cordillera Vilcabamba, 3100-3500 m, *Dudley 11062* (GH).

**BOLIVIA. Cochabamba:** Prov. Carrasco, 8 km from Empalme towards Siberia, 17°46'S, 64°48'W, 2900 m, 22 Oct 1996, *Kessler et al. 9198* (GOET, LPB, UC). **La Paz:** Prov. Nor Yungas, passing Unduavi, end of asphalt, Cotapata, down the trail (1 h), 3100 m, 29 May 1994, *Beck 21393* (LPB, UC). **Santa Cruz:** Prov. Caballero, 1.5 km on the road SE of the community of Siberia, 17°50'12"S, 64°44'00"W, 2970 m, 29 Nov 2002, *Nuñez-C. 25* (MO, NY); 2 km SE of the community of Siberia, 17°50'14"S, 64°43'45"W, 2957 m, 08 Apr 2004, *Nuñez-C. 626* (MO, NY, UC)

This species is unmistakable because of the combination of following unique characters: thick rhizomes with wide scales (to 60 cells across bases) together with glabrous, relatively small fronds with narrow segments. One Bolivian collection (*Beck 21393*, LPB) has exceptionally long petioles and wide laminae; this is possibly related to the low elevation at which it was found (2400 m). It could also represent a hybrid between this species and *M. personata*, which is very common at that locality.

The closest relationship of *M. erecta* is with *M. pseudonutans*, which is similar in rhizome thickness as well as scale form and size (but not number of cells). However, that species has much larger fronds, shorter creeping rhizomes, at least some hairs on the lamina, and grows mainly epiphytically. Other similar terrestrial species include *M. vulcanica* and *M. sklenarii*, but these species have much smaller scales and are hairy to some extent.

*Melpomene erecta* clearly prefers thick moss cushions in seepage areas. At the few spots in the Andes where it has been found, it grew in large quantities, which is reflected by the large amount of duplicates to each collection.

**6. *Melpomene firma*** (J. Sm.) A. R. Sm. & R. C. Moran, *Novon* 2: 430. 1992. *Polypodium firmum* Klotzsch, *Linnaea* 20: 378. 1947, (non Kaulf., 1827). *Ctenopteris firma* J. Sm., *Hist. Fil.* 184. 1875. *Grammitis firma* (J. Sm.) C. V. Morton, *Contr. U.S. Natl. Herb.* 38: 110. 1967. Type. Guyana. *Schomburgk 1170* (lectotype, designated by Looser, *Rev. Univ. Chile* 36:75. 1951; B; isolectotype, K).

*Polypodium aromaticum* Maxon, *Proc. U.S. Natl. Mus.* 27: 743. 1904. *Ctenopteris aromatica* (Maxon) Copel., *Philipp. J. Sci.* 84: 418. 1955 (1956). *Grammitis aromatica* (Maxon) Proctor, *Brit. Fern Gaz.* 9: 218. 1965. *Xiphopteris aromatica* (Maxon) Crabbe, *Brit. Fern Gaz.* 9: 318. 1967. Type. Jamaica. Blue Mt. Peak, *Underwood 1449* (holotype, NY, fragment US).

*Polypodium herzogii* Rosenst., *Repert. Spec. Nov. Regni Veg.* 6: 176. 1908. Type. Bolivia. Cochabamba: Incacorral, *Herzog 783* (holotype, S; isotypes, UC, US). Figs. 7B, 12.

*Plants* predominately epiphytic, sometimes terrestrial or epilithic, growing in moss layers. *Rhizomes* moderately long to short, ascending to erect (Fig. 12A), (0.8-)1.2-1.8(-2.2) mm diam. *Fronde*s to 350 mm, erect (Fig. 12A), often arching, inserted onto the rhizomes at an acute angle, closely placed (3-5 mm) (Fig. 12A). *Scales* (3.0-)4.2-6.0(-12.0) x 0.4-0.6 mm, (12-)14-22(-26) cells wide across their bases, clathrate (Fig. 12B), dark brown to brown, iridescent, cordate at bases, acute to attenuate at tips; margins with small hyaline retrorse papillae 1-3 cells long (Fig. 12B); apical glandular cells 3-8, in a linear arrangement or nodding cluster (Fig. 12C). *Petioles* (5-)35-80(-100) mm long, (0.5-)0.8-1.0 mm thick, alate to marginate throughout, with few to many short (0.2-0.8 mm) dark brown acicular hairs, usually hairier adaxially than abaxially (Fig. 12D), often glabrescent abaxially; simple and branched glandular hairs of crosiers and young fronds sometimes persistent in older fronds. *Laminae* (80-)120-280(-310) x (14-)50-70(-80) mm, lanceolate or broadly elliptic (broadest at or above the middle), acute to attenuate at tips; laminar bases truncate with proximal pinnae usually remote (Fig. 12A). *Rhachises* dark brown to black, planar to weakly protruding adaxially (Fig. 12E), hemispherically protruding abaxially (Fig. 12F); few to many short brown acicular hairs 0.2-0.8 mm long on both sides, usually hairier adaxially than abaxially (Fig. 12E, F). *Pinnae*



(6-)22-35(-40) x (1.2-)1.8-2.8(-3.0) mm (5-10 times as long as broad), patent to reflexed proximally (120-90°) (Fig. 12A), patent or weakly curved towards laminar tips distally (90-80°), fully adnate, inequilateral at bases, weakly decurrent acroscopically, rounded basiscopically (Fig. 12E, F), linear-oblong, tips obtuse, margins entire (Fig. 12E, F) or dentate proximally in large segments; costae visible on both sides, weakly hairy abaxially; proximal pinna pairs smaller than the central ones, but not alariform (Fig. 12A); stomata sometimes visible as dark brown to reddish dots; margins sometimes with ephemeral glandular hairs or cells, but other hairs lacking; hydathodes present (Fig. 12E). *Sori* 5-14(-25) pairs per segment, each with 4-10 short hairs 0.4-0.8 mm long (Fig. 12F).

**Distribution and habitat.** Elfin forest and moist montane forest at 1300-3400 m from Mexico, El Salvador, Nicaragua, Costa Rica, Panama, Cuba, Jamaica, Dominican Republic, Colombia, Venezuela, Guyana, Ecuador, Peru, Bolivia, and northern Brazil (Fig. 7B).

**Selected specimens examined. MEXICO. Chiapas:** Tenejapa, Paraje Kurus Ch'en, 2200 m, 29 Sep 1972, *Breedlove 28212A* (NY); Sierra Madre de Chiapas, along trail to E from high point on road between Finca Liquidambar and Nueva Colombia, 2500 m, 15°40'N, 92°44'W, 18 Jun 1985, *Luteyn & Lebrón-Luteyn 11599A* (NY). **Oaxaca:** Ixtlán, 65-58 km N of Ixtlán, 41-44 km S of Valle Nacional, 2000 m, 28 Oct 1969, *Mickel & Hellwig 4287B* (NY).

**EL SALVADOR. Chalatenango:** Cerro El Pital, 2500 m, 16 Nov 1978, *Seiler 737* (NY). **Morazan:** El Zancudo, 1900 m, 23.03.1979, *Seiler 998* (NY). **Santa Ana:** Bosque Montecristo, 2150 m, 16 Sep 1977, *Seiler 96* (NY). **Sonsonate:** Cerro Los Naranjos, 1900 m, 05.10.1978, *Seiler 603* (NY).

**COSTA RICA. Heredia:** Vara Blanca, 2000 m, 17 Aug 1967, *Bishop 882* (UC); Cerro Chompipe, N of San Rafael, 2000 m, 29 Aug 1964, *Lems 640829* (NY); 1 km W of Vara Blanca on the slopes of Volcán Poás, 1800 m, 06 Jul 1967, *Mickel 2150* (NY). **San José:** about 10 km N of San Rafael de Heredia on Volcán Barba, 1950 m, 09 Jul 1967, *Bishop 825* (UC); 25 km S of Villa Mills on the way to San Isidro on the Interamerican Highway, 1450 m, 10 Aug 1967, *Bishop 873* (UC); National Park Braulio Carrillo, transect trail between OTS-Station La Selva and Volcan Barva, 2100 m, 15 Feb 2003, *Kluge 5230* (GOET); S of Cartago, ca. 3 km NNW of Trinidad along the Interamerican Highway, 2500 m, 16 Jul 1970, *Lellinger & White 1190* (UC).

**PANAMA. Chiriquí:** along Río Caldera (Boquete region) and on slope to the E, ca. 3,5 km NW of Bajo Mono, 08°50'N, 82°28'W, 1600 m, 08 Feb 1986, *Smith A. R. et al. 2454* (UC).

**DOMINICAN REPUBLIC. Peravia:** 48 km S of Costanza (on road to San José de Ocoa), in area of La Nevera, 18°41'N, 70°35.5'W, 2200 m, 03 Apr 1981, *Zanoni & Mejía-M. 122209A* (US).

**VENEZUELA. Amazonas:** Cerro Neblina, camp No. 7, S slopes of Cañon Grande, 00°55'N, 66°00'W, 1800 m, 19 Nov 1984, *Croat 59469* (UC). **Anzoátegui:** Dtto. Libertador, ridges and tops of Montañas Negras, along the Sucre and Anzoátegui border, 20 airline km NE of Bergantín, NE of Buenos Aires, Serranía de Turimiquire, 10°04'30"N, 64°11'W, 2350 m, 28 Nov 1981, *Davidse & Gonzáles A. C. 19604* (UC). **Aragua:** Tovar, *Moritz 437* (P). **Bolívar:** Dtto. Roscio, mostly along the trail that leads to the top of Cerro Roraima, 05°15'N, 60°42'W, 2200-2600 m, 27 Mar 1984, *Aymard & Luteyn 2452* (UC). **Mérida:** San Javier valley, slope at La Altura de La Caña (Serranía Escorial), 08°43'N, 71°05'W, 2700-2750 m, 09-10 Mar 1999, *Schneider & Zipp 2154* (UC); Los Piedras, Km 37, carretera Apartaderos-Barinas, 13 Aug 1980, *Stergios & Taphorn 2090* (UC). **Portuguesa:** Dtto. Sucre, Los Paramitos, at 20 km by air SE of Biscucuy, 09°20'N, 69°05'W, 1000-1500 m, 17 Sep 1983, *Ortega F. et al. 1891* (UC). **Trujillo:** Dtto. Boconó, ca. 10 mi SW of Batatal on road to Boconó, Laguna de Aguas Negras, 09°71'N, 70°12'W, 2000 m, 03 Nov 1982, *Smith A. R. et al. 945* (UC); 24-28 km SE of Boconó, road to Guaramacál, 09°12'N, 70°08'W, 1700-2000 m, 25-26 Nov 1982, *Smith A. R. et al. 1592* (UC). **Vargas:** Cordillera de la Costa, serranía Litoral, Monumento Natural Pico Codazzi, Carretera Arco de la Colonia Tovar-Pto. Cruz, 1 km desde el Arco, Urb. Residencial Jenjibrillar, Sector La Neblina, final Avda. La Neblina, 10°26'N, 67°14'30"W, 2280 m, 07 Feb 2000, *Mostacero et al. 442* (UC).

**COLOMBIA. Cundinamarca:** Junin, towards La Cumbre, 2650 m, 15 Jan 1967, *Murillo M. T. 997* (COL); vereda San Antonio, 2500-2800 m, Jul 1994, *Rodriguez-B. 113* (COL). **Risaralda:** Santuario, vereda Las Colonias, 400 m arriba del Campamento, 2910 m, 02 Feb 1983, *Torres J. H. et al. 1497* (COL).

**ECUADOR. Loja:** new road Loja-Saraguro, Km 17, 03°55'S, 79°15'W, 2600-2650 m, 19 Mar 1989, *Øllgaard & Feil 91147* (AAU); Parque Nacional Podocarpus, road Yangana-Cerro Toledo, 04°23'S, 79°08'W, 2600 m, 27 Feb 1985, *Øllgaard et al. 58346* (AAU); Parque Nacional Podocarpus, around entrance to the park on road Yangana-Cerro Toledo., 04°23'S, 79°08'W, 2600-2800 m, 03 Jun 1988, *Øllgaard et al. 74561* (AAU); trail ca. 5 km ENE of San Pedro de Vilcabamba, Loma Solamaco to upper Quebrada Romerillos, 04°14'S, 79°10'W,

2300-2400 m, 01 Dec 1994, *Øllgaard et al. 105983* (AAU). **Morona-Santiago:** along road Gualaceo-El Limon, 2500 m, 15 Aug 1989, *van der Werff & Gudiño 11105* (UC). **Napo:** Quijos Canton, trail through pastures and up into jungle S from the town of Quijos, just E of Baeza, 00°28.5'S, 77°53.5'W, 2100 m, 04 Aug 1992, *Fay & Fay 3832* (UC). **Tungurahua:** Volcán Tungurahua, 01°25.6'S, 78°25.3'W, 2200 m, 11 Jul 2002, *Lehnert 196* (GOET, QCA, UC). **Zamora-Chinchipe:** road Loja-Zamora, Km 24-25, 03°59'S, 79°05'W, 1950-2100 m, 15 Apr 1973, *Holm-Nielsen et al. 3507* (COL, UC); Estación Científica San Francisco, around refuge, study plot A 6, 03°59'21.0"S, 79°04'20.5"W, 2470 m, 23 Sep 2003, *Lehnert 871* (GOET, QCA, UC); Reserva Tapichalaca, trail down into the Quebrada Honda, passing N of Cerro Tapichalaca, 04°29'S, 79°07'W, 2480 m, 27 Oct 2003, *Lehnert 1003* (GOET, QCA, UC); new road Loja-Zamora, ca. 4 km E of pass "El Tiro," 03°59'S, 79°08'W, 2650 m, 23 Sep 2004, *Lehnert 1328* (GOET, QCA, UC), new road Loja-Zamora, ca. 4 km E of pass "El Tiro," 03°59'S, 79°08'W, 2650 m, 23 Sep 2004, *Lehnert 1332a* (GOET, QCA, UC); limit of Parque Nacional Podocarpus, new road Loja-Zamora, E of the pass, 03°58'S, 79°07'W, 2500-3000 m, 25 Mar 1990, *Madsen 87101* (AAU).

**PERU. Cuzco:** Prov. Urubamba, Machu Picchu, on rocks of Waina Picchu, 2400 m, 20 Jan 1976, *Bishop 2505* (UC); Calca, height above Río Lachac, Valle de Lares, 7000 ft, 05 Apr 1932, *Bües 1820* (CUZ); summit of Huayna Picchu, 2900 m, 05 Nov 1957, *Hutchinson 1759* (UC); Aguas Calientes, behind thermal baths, 2100-2200 m, 12 Oct 2002, *Lehnert 415* (GOET, UC, USM); between San Luis and Abra Malaga, 3050-3250 m, 16 Oct 2002, *Lehnert 425, 428, 436* (GOET, UC, USM); between San Luis and Abra Malaga, Km 154, 13° 05, 4'S, 72° 22, 2'W, 3300 m, 16 Oct 2002, *Lehnert 438* (GOET, UC, USM). **Huanuco:** Prov. Huanuco, Mirador, road Acomayo to Chinchao, 2400 m, 05 Nov 1935, *Mexia 4142* (UC). **Junin:** Prov. Tarma, Agua Dulce, 1900 m, 16 Mar 1948, *Woytkowski 35480* (UC). **Pasco:** Prov. Oxapampa, Palmazu, Cooperativa Navarra, 2000 m, 05 Mar 1986, *van der Werff et al. 8411* (MO, UC, USM). **San Martín:** Prov. Rioja, Buenos Aires, along road Pedro Ruiz-Rioja, 05°42'09"S, 77°53'06"W, 2000 m, 21 Mar 1998, *van der Werff et al. 15351* (UC).

**BOLIVIA. Cochabamba:** Prov. Ayopaya, 10 km Cocapata-Cotacajes, 16°38'S, 66°41'W, 2900 m, 11 May 1997, *Kessler et al. 9464* (LPB, UC); Prov. Carrasco, Sehuencas, crossing the bridge over Río Fuerte, first camping site behind the river, 17°30'S, 65°17'W, 2100 m, 13 Sep 1993, *Ibisch 93-1024* (LPB); 134 km old road Cochabamba-Villa Tunari, 17°07'S, 65°34'W, 1650 m, 26 Aug 1996, *Kessler et al. 7797* (LPB, UC); Prov. Chapare, 163 km W of El Sacta (Proyecto Valle de Sacta), 56 km E of Cochabamba, 17°20'S, 65°50'W, 2460 m, 15 Jul 1989, *Fay & Fay 2380* (LPB, MO); Prov. Chapare, 80 km old road Cochabamba-

Villa Tunari, 17°71'S, 65°51'W, 2200 m, 05 Sep 1996, *Kessler et al.* 8206 (LPB, UC); Prov. Sacaba, Yucachaca, 2500 m, *Steinbach* 5822 (B). **La Paz:** Prov. Bautista Saavedra, 15 km de Charazani hacia Apolo, 15°11'S, 68°46'W, 2400 m, 30 Jun 1997, *Kessler et al.* 10437 (GOET, LPB); 13 km from Charazani to Apolo, 15°11'S, 68°46'W, 2500 m, 02 Jul 1997, *Kessler et al.* 10488 (GOET, LPB, UC); Prov. Franz Tamayo, PN Madidi, trail Keara-Mojos, below Fuertecillos, 14°36'S, 68°58'W, 1970 m, 06 Nov 2001, *Jiménez I.* 864 (LPB, UC); Prov. Inquisivi, "Loma Linda-Turculi" along the road between Loma Linda and Turculi, this road runs N from Cajuta off of existing maps, 16°38'S, 67°10'W, 1850 m, 26 Dec 1989, *Lewis M.* 36879 (LPB, MO); Prov. Murillo, Valle de Zongo, going up from the village Zongo, 2250-2350 m, 15 Feb 1981, *Beck* 6128 (LPB); 31.7 km N (below) dam, at lago Zongo, Valle Zongo, trail up to Río Jachcha Cruz, 16°07'S, 68°05'W, 2200 m, 17 Mar 1984, *Solomon et al.* 11924 (LPB, UC); Prov. Nor Yungas, above Coroico, on top of Cerro Uchumachi, 2550 m, 25 Feb 1990, *Beck* 17494 (LPB); 8 km from Chuspipata to Coroico, 16°23'S, 67°48'W, 2600 m, 19 Sep 1997, *Kessler et al.* 12144 (GOET, LPB, UC); Unduavi, 16°15'S, 67°51'W, 3400 m, 12 Sep 2002, *Lehnert* 354 (GOET, LPB, UC); Cotapata, behind gas station, 16° 17'S, 67° 51'W, 3200 m, 26 Sep 2002, *Lehnert* 391 (GOET, LPB, UC); Sacramento Alto, between Chuspipata and Yolosa, 2500 m, 07 May 2003, *Lehnert* 783 (GOET, LPB, UC); Cantón Pacollo, Cerro Omuni, 16°11'S, 67°52'W, 1870 m, 27 Nov 1998, *Portugal et al.* 507 (LPB, UC); Prov. Sud Yungas, Huancané, 7.5 km hacia S sobre el camino nuevo, 2410 m, 09 Mar 1980, *Beck* 3133 (LPB).

This species is recognized by the combination of deflexed linear segments and black costae visible on both laminar sides (Fig. 7E, F). *Melpomene firma* and few other *Melpomene* species regularly have scales with marginal glandular cells and hairs, in addition to having glands at the scale tips (Fig. 7B). Other species with this feature, namely *M. gracilis* and *M. allosuroides*, may be distinguished by their short pinnae that lack visible costae, and by their terete petioles; *Melpomene firma* has clearly visible costae and marginate to narrowly alate petioles. *Melpomene melanosticta* and *M. erecta* sometimes have small secondary apices near the scale bases (Figs. 14B, 21B), but these species differ in being completely glabrous and having no visible costae (*M. firma* has some hairs and visible black costae).

A new segregate of this species, *M. occidentalis* Lehnert, may be distinguished by having patent to ascending pinnae (vs. proximally patent to deflexed pinnae in *M. firma*), and the glabrous, terete petioles (vs. marginate to weakly alate, adaxially hairy petioles).

The scales of *Øllgaard & Navarrete 1650* (AAU) from Ecuador are exceptionally long with 12 mm, but their width is normal.

- 7. *Melpomene flabelliformis*** (Poir.) A. R. Sm. & R. C. Moran, *Novon* 2: 430. 1992. *Polypodium flabelliforme* Poir., *Encycl.* 5: 519. 1804. *Grammitis flabelliforme* (Poir.) C. V. Morton, *Contr. U.S. Natl. Herb.* 38: 57. 1967. *Xiphopteris flabelliforme* (Poir.) Schelpe, *Bol. Soc. Brot.*, sér. 2, 41, 217. 1967. Type. Réunion. *Commerson s.n.* (holotype, P-JU 1098-C).
- Polypodium rigescens* Bory ex Willd., *Sp. Pl. ed. 4, 5*: 183. 1810. *Ctenopteris rigescens* (Bory ex Willd.) J. Sm., *Hist. Fil.* 184. 1875. *Xiphopteris rigescens* (Bory ex Willd.) Alston, *Bol. Soc. Brot.*, sér. 2, 30: 27. 1856. *Grammitis rigescens* (Bory ex Willd.) Lellinger, *Proc. Biol. Soc. Wash.* 89: 383. 1985. Type. Réunion. *Bory s.n.* (holotype, B W-19668; isotype, P JU1098-C).
- Polypodium rigescens* var. *setulosa* Rosenst., nom. illeg. Specimen labelled as type: Madagascar. Haute Monia, Roaullu, Ni-Tsilonduin, 01 May 1920, *de la Bathe 13190* (P).
- Grammitis katasophistes* Mickel & Beitel, *Mem. New York Bot. Gard.* 46: 200. 1988. Type. Mexico. Oaxaca: Dtto. Mixe, NW slope of Cerro Zemoaltépetl, *Mickel 4637b* (holotype, NY).
- Grammitis andicola* Stolze, *Fieldiana Bot.*, n.s. 32: 103. 1993. Type. Peru. Amazonas: Prov. Chachapoyas, Cerros Callacalla, *Hutchinson & Wright 5826* (holotype, F n.v.; isotypes, GH, UC). Fig. 10C, 13.

**Etymology:** The epithet means “fan-shaped” and undoubtedly refers to the illustration in the Plumier plate which accompanies the diagnosis. However, the plant shown is likely a different species because its habit is not shown by any specimen of *Melpomene flabelliformis*; also, it is said to be from Martinique, which has no records for any species of *Melpomene* save this picture (for further information and discussion see Bishop, 1989b).

*Plants* growing in moss layers, in the Neotropics mainly as epiphyte, in the Paleotropics also often terrestrial or saxicolous. *Rhizomes* moderately to long-creeping, horizontal (Fig. 13A-C), 0.8-1.5 mm diam. *Fronde*s to 270 mm, erect (Fig. 13A-C) to decumbent, inserting into the rhizome in a right angle, distantly placed ((2-)5-15 mm). *Scales* 3.6-4.0 x 0.8-1.5 mm, (14-)20–34 cells wide, dark brown to brown, strongly iridescent, broadly cordate to pseudopeltate,

acute to attenuate at tip (Fig. 13D); apical glands 3-8 cells in nodding clusters (Fig. 13E). *Petioles* 35-95 mm long, 0.6-1.0 mm thick, terete to decurrently marginate from the laminar bases, glabrous to glabrescent, with few short dark brown acicular hairs 0.8-1.2 mm long (Fig. 13F); simple and branched glandular hairs of crosiers and young fronds sometimes persistent in older fronds. *Laminae* to 150-210 x 8-25 mm, linear to narrow-elliptic (broadest in the middle), rounded to widely cuneate at bases, acute to rostrate at tip (Fig. 13A-C). *Rhachises* dark brown to black, planar and slightly sunken adaxially (Fig. 13G), hemispherically protruding abaxially (Fig. 13H), glabrous or with few hairs proximally on both sides, in fertile parts moderately hairy abaxially. *Pinnae* to 7.5-11.5 x (2.8-)3.2-3.5 mm (2-3 times as long as broad), patent, equilateral at base or weakly decurrent towards the bases, fully adnate, linear-oblong, the tips obtuse (Fig. 13G, H); costae not visible, or obscurely so abaxially in dried specimens; pale green below, rarely whitish; proximal 1-3 pinna pairs markedly smaller than the following segments, but not alariform; fertile parts scantily to densely hairy abaxially, margins not hairy, hydathodes present (Fig. 13G). *Sori* 2-4 pairs per segment, with 2-6 dark brown hairs 0.8-1.0(-2.0) mm long (Fig. 13G).

**Distribution and habitat.** From Mexico, Costa Rica, Colombia, Venezuela, Ecuador, Peru, Brazil, Bolivia in the New World (Fig. 10C) to Ethiopia, Cameroon, Kenya, Tanzania, Uganda, Malawi, Mozambique, South Africa, Madagascar, Reunión, Mauritius in the Old World (Fig. 3). In moist montane forests and elfin forests, at 1750-2750 m in Brazil and the Greater Antilles, 2400-3960 m in the Andes, and 2650-3200(-4000) m in Africa.

**Selected specimens examined. MEXICO. Oaxaca:** Dto. Ixtlán, Cerro de Malacate, N of Capulalpan, ca. 8 km E from Ixtlán from 3000 m to 2300 m on NE side of Cerro, esp. 2700 m, 05 Oct 1970, *Mickel & Leonard 5251* (UC); 49 km N of Ixtlán de Juárez on Rte 175, 1-2 km N of Cerro Pelón, 2700 m, 23 Sep 1972, *Mickel & Pardue 6784* (UC).

**COSTA RICA. Cartago:** Paturages au volcan Turrialba, 2600 m, 01 Jan 1899, *Pittier 13260* (P). **Limon:** Cordillera de Talamanca, Atlantic slope, unnamed cordillera between the Río Terbi and the Río Siní, 09°00-12'N, 82°58-59'W, 2400-2750 m, 13 Sep 1984, *Davidse et al. 28986* (UC). **San José:** Tres de Junio-Mire, Panamericana Km 68, 2600 m, Feb. 03, *Kluge 1189* (GOET); Massif of Cerro de La Muerte, 3200 m, 15 Jul 2003, *Kluge 6866, 6874* (GOET); Vueltas along Interamerican Highway, 09°40'N, 83°51'W, 2770 m, 01 Feb 1988, *Hennipman et al. 6992* (UC).

**HAITI. La Grande Anse:** Massif de la Hotte, western group, La Roseaux, Morne La Hotte, 2375 m, 13 Sep 1928, *Ekman H10633* (B); *ibid.*, Port-a-Piment, pine ridge NW of M. Formon, 2275 m, 02 Jan 1927, *Ekman H7550* (B). **L'Ouest:** Massif de la Selle, Croix-des-Bouquets, on Mt. Badeau, 2100-2200 m, 25 Feb 1927, *Ekman H7711* (B).

**DOMINICAN REPUBLIC. La Vega:** Loma Rosilla, 2650 m, 1912, *Fuertes 1777* (P); Cordillera Central, Valle Nuevo, 2400 m, 17 Oct 1929, *Ekman H13752, H13830* (B). **Santiago:** Cordillera Central, Moncion, high ridge between Rio Nagua and Río San Juan, 2200 m, 12 Jun 1929, *Ekman H12839* (NY).

**COLOMBIA. Antioquia:** Belmira, alrededores de la cienaga El Morro, 06°41'09.1"N, 75°40'29.6"W, 3290 m, 28 May 2002, *Rodriguez et al. 3334* (COL). **Boyacá:** Arcabuco, Parque Nacional Igüaque, camino hacia las lagunas, 2900-3200 m, 04 Mar 1985, *Mejia 317* (COL); Cordillera Oriental, Nevado del Cocuy, Chorreón de San Paulino, vertiente S, 3750 m, 10 Sep 1938, Alto de Onzaga, 3400 m, 22 Nov 1967, *Jaramillo Mejia & van der Hammen 4121* (COL); Páramo de Guantiva, entre Santa Rosita y Onzaga, en la quebrada Sietecuaral, 3410 m, 26 Nov 1967, *Jaramillo Mejia & van der Hammen 4299* (COL); La Uvita, Vereda El Hatico, zona de Quebrada Honda, 2600-3190 m, 26 Jul 1996, *Fernandez Alonso et al. 14457* (COL). **Chocó:** Macizo de Tamaná, valle de las Mirlas, 3525 m, 09 Feb 1983, *Torres et al. 1764* (COL). **Cundinamarca:** Guasca, páramo de Guasca, 23 May 1961, *Murillo M. T. & Fayad 147* (COL); Fómeque, Km 20 carretera hacia Chingaza, 3120 m, 10 Jun 1974, *Acosta Arteaga & Rodriguez 477* (COL); Guasca, Vereda Potreritos, a un lado de la carretera Guasca-Cacheta, 2700 m, 03 Aug 1989, *Linares et al. 2872* (COL); Subachoque, El Tablazo, 3400 m, 23 Jun 1998, *Dueñas et al. 2964* (COL). **Meta:** Cubarral, surroundings of laguna de la Guitarra, páramo de Sumapaz, 3420 m, 11 Jul 1981, *Franco et al. 334* (COL); Páramo de Sumapaz, quebrada Sitiales watershed, 0.5 km SW of laguna La Primavera, 3550 m, 26 Jan 1972, *Cleef & Kramer 1045* (COL). **Nariño:** Mun. Pasto, Cordillera Centro-Oriental, microcuenca Las Tiendas, inicio del páramo del Bordoncillo, 01°12'N, 77°08'W, 3150-3450 m, 25-27 Mar 1997, *Ramírez et al. 10554* (UC). **Norte de Santander:** 35 km before Pamplona, quebrada La Sisanta, 3100 m, 08 Nov 1969, *Murillo M. T. & Jaramillo Mejia 1279* (COL). **Santander:** Cucutilla, Vereda Sisavita, Páramo El Romeral, 3498 m, 11 Apr 2001, *Galván Garvajal et al. 117* (COL); Río Susa valley, above old settlement Santa Barbara, on ridge of El Reventón, 3600 m, 30 Nov 1967, *Jaramillo Mejia & van der Hammen 4393* (COL).

**VENEZUELA. Amazonas:** Atabapo, Cerro Marrahuaca-Fhuif, peak, swampy area without trees on the high plain, up the river, 2480-2500 m, 03°35'N, 65°20'W, 02 Feb 1982,

*Steyermark et al. 126043* (NY). **Bolívar:** Kukenan tepui, summit, 05°13'N, 60°18'W, 2550 m, 11 Apr 1988, *Liesner 23141* (UC); Cerro Roraima, cumbre, parte NE de Venezuela inmediata al sur del hito que marca los límites con Guyana, Brasil y Venezuela, 05°12'N, 60°42'W, 2750-2800 m, 26 Aug -02 Sep 1976, *Steyermark et al. 112464* (UC). **Mérida:** Dtto. Libertador, Parque Nacional Simón Bolívar, camino del teleférico (de la Aguada), Laguna La Fría, N slope of Sierra Nevada de Mérida, 2700-3000 m, 21 Dec 1983, *Pipoly et al. 6540* (UC). **Trujillo:** Dtto. Carache, via Páramo Cendé sitio denominado "Las Cruces," 09°33'N, 70°08'W, 27 Nov 1987, *Rivero & Díaz W. 1487* (UC).

**ECUADOR. Azuay:** surroundings of Laguna Toreadora, 02°47.17'S, 79°13.10'W, 3700-3800 m, 14 Nov 2004, *Lehnert 1556* (GOET, UC, QCA). **Carchi:** road Tulcán-Maldonado; Km 32 from Tulcán, base of Volcan Chiles, 06 Jul 2002, *Lehnert 154* (GOET, QCA, UC). **Imbabura:** Lago San Marcos, Cayambe, 3400 m, 29 Nov 1961, *Cazalet & Pennington 5418* (UC). **Loja:** Reserva Huashapamba, 6 km S of Saraguro along Panamericana, 03°39'43"S, 79°16'09"W, 2900 m, 03 Oct 2003, *Lehnert 955* (GOET, UC, QCA). **Morona-Santiago:** road Gualaceo-El Limon, from the pass to El Limon, 3200-3400 m, 08 Feb 1989, *van der Werff & Palacios 10497* (AAU, UC). **Napo:** junction of Río Chalupas and Río Aguas Buenas, cataract at the E end of the upper Chalupas valley, 00°49'S, 78°14'W, 3250 m, 11 Aug 1979, *Holm-Nielsen 19084* (AAU).

**PERU. Amazonas:** Prov. Bagua, third camp, Cordillera Colán SE of La Peca, 2600 m, 25 Sep 1978, *Barbour 3556* (UC); Prov. Chachapoyas, Cerros Calla Calla, E side, 10 km above Leimebamba on the road to Balsas, 2700 m, 29 Mar 1964, *Hutchison & Bennet 4754* (NY, UC, USM); Cerros Calla Calla, W side, 45 km above Balsas, midway on the road to Leimebamba, 3100 m, 22 Jun 1964, *Hutchison & Wright 5826* (UC). **Apurímac:** Abancay region, 01 Oct 1935, *pupils of Prof. Victor Santander C. of Colegio Grau s.n.* (UC). **Cuzco:** Viscochasco, Valle de Lares, 13900 ft, Mar 1933, *Bües 1786* (CUZ); Prov. Calca, Valle del Calca, San Lorenzo, Mar 1932, *Bües 1789* (CUZ); Prov. Achirayac, Distr. Vilcabamba, La Convención, 3000 m, Jul 1934, *Bües 2117* (CUZ). **Junín:** Prov. Satipo/La Convención, Cordillera Vilcabamba, Río Ene slope, near summit of divide, 11°39'36"S, 73°40'02"W, 3350-3400 m, 08 Jun 1997, *Boyle et al. 4234, 4327* (USM). **San Martín:** Prov. Mariscal Caceres, Bajo Laguna Chochos, P.N. Río Abiseo, 3400 m, 20 Jun 1988, *León & Young 2004* (USM); NW corner of Río Abiseo Nat. Park, 07°XX'S, 77°XX'W, 3500-3550 m, 15 Jul 1987, *Young & León 4691, 4700, 4826* (USM).

**BRAZIL. Minas Gerais:** Serra do Itacolomy, 1934, *Badini 78* (RIO); on road to Itacolunyu, 1750 m, 24 Jan 1893, *Schwacke 9096* (RIO); Serra do Caparaó, Serra do Rio



Preto, 2500 m, 13 Sep 1941, *Brade 16928* (RIO). **Rio de Janeiro:** Parque Nacional de Itatiaia, road to Prateleiras, 2400 m, 01 Aug 1973, *Barcia 651, 654* (RIO); Morro Assu, 2400 m, 01 Jul 1915, *von Luetzelburg 846* (UC); Parque Nacional Itatiaia, along road to Agulhas Negras, ca. 22°25'S, ca. 44°40'W, 2000 - 2600 m, 18 Oct 1977, *Landrum 2107* (RIO); Itatiaia, 2300 m, Sep 1913, *Brade & Tamandaré 6467* (RIO); Teresopolis, Pedra Assú, 2200 m, Oct 1929, *Brade 9790* (RIO); Serra dos Orgãos, Pedra Assú, 2200 m, 07 Nov 1929, *Brade 9904* (RIO); Itatiaia, 2400 m, 01 May 1953, *Brade 20299* (RIO). **Sao Paulo:** Campos do Jordão, road to Pindamohangaba, 1900 m, 29 Jun 1998, *Labiak 655* (SP); Serra da Bocaina, 2000 m, 07 May 1951, *Brade 20901* (RIO); Bocaina, alto de Boa Vista, Apr 1896, *Loefgren & Edwall s.n.* (SP 57529).

**BOLIVIA. La Paz:** Prov. Nor Yungas, Coscapa, following the prehispanic trail Sillutinkara, 16°12'S, 67°53'W, 3480 m, 16 Jan 2001, *Jiménez I. & Vidaurre 581* (UC, LPB); Prov. Franz Tamayo, PN-ANMI Madidi, trail Pelechuco-Mojos, Tambo Quemado (campsite), at 45 min. from base of camp, going along the trail to Qalla, 14°41'S, 68°58'W, 3480-3590 m, 30 Apr 2003, *Jiménez I. 1825, 1874* (GOET, UC, LPB).

**ETHIOPIA. Bale:** ca. 50 km N of Dolo Menna (Masslo), on road to Goba, 06°45'N, 39°45'E, 2750 m, *Friis et al. 3609* (B).

**KENYA. Embu:** Mount Kenya, at Kanawetti Forest track, 00°16'05"S, 37°18'10"E, 3200 m, 13 Dec 1966, *Pichi Sermolli 6899* (UC). **Central:** Aberdares National Park, above Karura falls, 00°35'S, 36°42'E, 2850 m, 24 Aug 1999, *Kessler 12549* (UC).

**TANZANIA. Kilimanjaro:** Mt. Kilimanjaro, near waterfall above the "Bismarckhügel", 3000 m, 30 Jan 1914, *Peter 881* (UC); Mt. Kilimanjaro, 26 Jun 1926, *Peter 42001* (GOET, UC); *ibid.*, 3000-4000 m, 1906, *Daubenberger s.n.* (GOET); *ibid.*, 3000-4000 m, 1906, *Daubenberger 54* (GOET); Kilimandjaro-region, environs of Kibosho, climb of Kimawenzi, 3000-4000 m, Dec 1911-Mar 1912, *Daubenberger 1227* (GOET); Kilimanjaro, summer of 1968, *Meisel B-019768* (B). **Morogoro:** S. Uluguru forest reserve, edge of Lukwangule plateau, Uluguru Mts., 2200 m, 17 Mar 1953, *Drummond & Hemsley 1669* (GOET).

**MADAGASCAR. Mahajanga:** Massif du Tsaratanana, montagnes au N de Mangindrano, crête menant de Matsaborimaiky vers Bepia, entre le point culminant, 14°08'39"S, 48°58'24"E, 2490 m, 12 May 2005, *Janssen et al. 2927* (P, GOET). **Prov. unknown:** Haute Monia, Roaullu, Ni-Tsilonduin, 01 May 1920, *de la Bathe 13190* (P).

**REUNION. Prov. unknown:** *Baudouin 1059* (P); *Delavaux s.n.* (P); foret de Bébour, along Ravine Misere along Km post 13 & 14, W side of road, 1525 m, 14 Oct 1992, *Ranker & Adersen 1506* (COLO); Cirque de Cilaos, trail to col de Taibit and Cirque du Mafate, 1300-1800 m, 14 Oct 1992, *Ranker & Adersen 1548* (COLO).

This is the most widespread species of the genus, occurring in the wet mountains of the Neotropics, Africa, Madagascar, and the Mascarenes. Within its range, the species is remarkably constant in its defining characters, which nonetheless show a typical variation. The soral areas usually have some long hairs; additionally there are hairs scattered on rhachises and laminae of fertile frond parts. Sterile fronds have no or only a few hairs on the rhachises and laminae. The only collection seen from Ethiopia has almost glabrous fertile fronds, with hairs in only some of the sori. The terete to weakly marginate petioles are glabrous or glabrescent, only rarely single petioles of a given plant have more hair than the others. A common feature in all these variants is the rather long-creeping rhizomes with pale brown to brown, strongly iridescent rhizome scales. This character combination delimits *M. flabelliformis* from the often confused *M. moniliformis*, which never has hairs between the sori or on the rhachises abaxially; in *M. moniliformis*, the laminae are proximally often truncate (vs. cuneate in *M. flabelliformis*) and the petioles are shorter (1/3 of frond or less in *M. moniliformis* vs. 1/3 of frond or more in *M. flabelliformis*), more decidedly marginate, and hairier (vs. lamina attenuate at both ends, petioles); but aberrant varieties exist of this species, too. *Melpomene moniliformis* var. *adnata* gives a stouter impression, with its rhizomes often shorter-creeping and the laminae on average more coriaceous than in *M. flabelliformis*; however, it may be mistaken for stout plants of *M. flabelliformis* because its large segments can have the same proportions as in *M. flabelliformis*. The var. *minor* and var. *moniliformis* have segments about as long as broad, whereas *M. flabelliformis* has the largest segments twice as long as broad or more. Var. *minor* includes small páramo plants with contracted rhizomes and imbricate pinnae; such dimensions are not known from *M. flabelliformis*. Thus confusion of this almost hairless variety of *M. moniliformis* with glabrous plants of *M. flabelliformis* is unlikely.

*Melpomene moniliformis* var. *paradoxa* from Bolivia and Peru is similar to *M. flabelliformis* in habit and scales. It has long-trailing rhizomes and differs from the other varieties of *M. moniliformis* in its large number of soral hairs (to 10) and its larger scales (24-32 vs. 12-24 cells across the scale base); these features are more like *M. flabelliformis*, but var. *paradoxa* lacks large segments or hairs outside the sori.

I have chosen to separate some Brazilian plants formerly identified as *M. flabelliformis* (Labiak & Prado, 2005a) as *M. moniliformis* var. *subdicarpon*. Features of *M. flabelliformis* and *M. moniliformis* var. *moniliformis* are mixed in that variety, which has the frond cutting and epiphytic life form of the former, but the hairiness (densely hairy on petioles), hair distribution (not on the laminae, confined to sori), and short petioles of the latter. The scales and rhizome characters of var. *subdicarpon* are regarded as typical of *M. moniliformis*, thus its incorporation into that species.

The scales of *Melpomene flabelliformis* have thinner cell walls than those of *M. moniliformis*, which leads to a more obvious iridescence in the former species and a clearer lattice pattern in the latter. Additionally, the tangential cell walls of *M. flabelliformis* are not as clear as those of *M. moniliformis*.

*Melpomene caput-gorgonis* differs from *M. flabelliformis* in its abundant apical scale papillae.

Tryon and Stolze (1993) considered *M. flabelliformis* to include *M. peruviana*, an opinion not in other treatments (de la Sota et al., 2000; Mickel & Smith, 2004). *Melpomene peruviana*, which I believe is distinct from *M. flabelliformis*, evidently served as basis for the description of that species in the *Pteridophyta of Peru* (Tryon & Stolze, 1993). Stolze then described the real *M. flabelliformis* newly as *M. andicola*. With the nomenclatural changes, the descriptions of both species in *Pteridophyta of Peru* may still be used (Tryon & Stolze, 1993). *Melpomene peruviana* can be distinguished by its small size, ascending deltate pinnae, its densely hairy, decurrently marginate to alate, short (rarely more than 12 mm long) petioles, small (8-14 cells across bases), blackish rhizome scales, and mainly saxicolous habit in open areas, whereas *M. flabelliformis* can be rather large (to 40 cm), with patent, obtuse-oblong pinnae, medium to large (14-34 cells across bases), brown rhizome scales, and growing epiphytically or in moss cushions on rocks and soil within forests.

The application of the epithet to this species and its priority over *Polypodium rigescens* Bory has been exhaustively discussed by Bishop (1989b).

**8. *Melpomene flagellata*** Lehnert, sp. nov. Type. Bolivia. La Paz: Prov. Nor Yungas, N side of Cerro Uchumachi above Coroico, 16°12'S, 67°45'W, 2350 m, 14 Jul 1989, *Kessler & Kelschbach 107* (holotype, LPB; isotype, GOET). Figs. 5D, 14.

A *Melpomene moniliforme* in pilis longioribus (1.0-2.0 mm vs. 0.6-1.0 mm) crebrioribus in petiolis sorisque, rhizomatibus ascendentibus (vs. horizontaliter reptantibus) apicibusque segmentorum truncatis (vs. obtusis) differt

Etymology: The name refers to the narrow laminae whose long curved tips are reminiscent of whips (Latin, *flagellum*).

*Plants* predominately epiphytic, growing in moss layers, sometimes saxicolous. *Rhizomes* erect or ascending, short to moderately long (Fig. 14A), 0.8-1.0(-1.5) mm diam. *Fronde*s to 380 mm, erect, inserted onto the rhizome in acute angles, closely placed (1.0-5.0 mm), but not fasciculate (Fig. 14A). *Scales* 3.0-5.0 x 0.5-0.6 mm, 12-16(-20) cells wide, clathrate (Fig. 14B), dark brown to brown, strongly iridescent, cordate to pseudopeltate, acute to attenuate at tips (Fig. 14C); apical glands 3-8 cells, palmately arranged. *Petioles* 15-60(-75) mm long (Fig. 14A), (0.4-)0.5-0.6(-0.8) mm thick, decurrently marginate from the laminar bases, most parts terete (Fig. 14C), with many brown acicular hairs (1.0-2.0 mm) (Fig. 14C), simple and branched glandular hairs of crosiers and young fronds sometimes persistent in older fronds. *Laminae* 150-320 x 4-9 mm, linear to narrow-elliptic (broadest in the middle), long decurrent at base, acute to attenuate at tip. *Rhachises* dark brown to black, planar and slightly sunken adaxially, hemispherically protruding abaxially (Fig. 14D), glabrous or glabrescent with branched glandular hairs abaxially, usually sparsely to densely hairy basally on both sides. *Pinnae* 1.8-3.0(-4.0) x 1.4-3.0 mm (1(-2) times as long as broad), ascending (80-55°), inequilateral at bases, decurrent proximally, fully adnate, rounded to deltate, sometimes oblong, the tips obtuse to truncate (Fig. 14D); costae not visible (Fig. 14D), or obscurely so abaxially, in dried specimens protruding. Proximal pairs markedly smaller than the central segments, often alariform; margins without hairs; hydathodes present. *Sori* 2-4 pairs per segment, with (3-)12-20 hairs (1.2-1.8 mm) (Fig. 14D), rarely without hairs.

**Distribution and habitat.** Elfin forests and moist montane forests at 1950-3300 m in western Peru and Bolivia (Fig. 5C).

**Additional specimens examined. PERU. Cuzco:** Alturas de Siere Convencion, 3000 m, Jun 1924, *Bües 1574* (CUZ).

**BOLIVIA. Cochabamba:** Prov. Carrasco, 132 km old road Cochabamba-Villa Tunari, 17°06'S, 65°35'W, 1950 m, 15 Jul 1996, *Kessler et al. 7318* (LPB, UC), *7320* (GOET, LPB,

UC); 130 km old road Cochabamba-Villa Tunari, 17°07'S, 65°36'W, 2000 m, 10 Jul 1996, *Kessler et al. 7168* (GOET, LPB, UC); road Cochabamba-Villa Tunari, below of Corani, 17°10.51'S, 65°54.02'W, 2750 m, 26 Nov 2002, *Lehnert 517* (GOET, LPB, UC). **La Paz:** Prov. Franz Tamayo, PN-AMNI Madidi, trail Keara-Mojos, about half an hour from Tokuaque, 14°37'S, 68°57'W, 2420 m, 01 Jul 2001, *Jiménez I. & Gallegos 527* (UC); Prov. Larecaja, Sorata, 15°44.04'S, 68°39.28'W, 3300 m, 06 Jan 2003, *Lehnert 555* (GOET, LPB, UC); Prov. Nor Yungas, between Chuspipata and Yolosa, above Sacramento, 2760 m, 01 Jan 1994, *Beck 21310* (LPB, UC); Parque Nacional Cotapata, surroundings of Estación Biológica Tunquini, 16°11'S, 67°52'W, 2300 m, 26 Jul 2000, *Krömer & Acebey 1368* (GOET, LPB, UC); Chuspipata–Sacramento, 16°18'S, 67°49'W, 2900 m, 10 Nov 2002, *Lehnert 491* (GOET, LPB, UC).

The segment shape of *Melpomene flagellata* varies strongly between trapezoid to rounded in small segments to short-deltate in larger ones. *Melpomene flagellata* replaces *M. wolfii* in Bolivia and southern Peru (Fig. 10C), and has thinner rhizomes, thinner petioles with thinner alae, and narrower rhizome scales than *M. wolfii*; also, *M. wolfii* lacks hairs on the petioles. Pubescence of fertile fronds is similar and highly variable in both species (glabrous to densely hairy even on one plant) and distinguishes both from the similar *M. moniliformis*, which is usually glabrous except for hairs in the sori. In *M. flagellata* these hairs reach 1.2–1.8 mm length and can be seen as clustered in the sori of hairy plants; in *M. wolfii*, the hairs are shorter (0.5–0.8 mm) and evenly distributed on the laminae.

Within its small range, *M. flagellata* varies considerably in size and appearance but can nevertheless be readily determined. *Kessler 7320* has very narrow blades; *Kessler 7318* from the same site is equal in size but has broader laminae; *Krömer & Acebey 1368* is generally larger than average but has characteristic short segments, fitting hair distribution, and small scales (16 cells wide across base).

Molecular data show a stronger affinity of *M. flagellata* to *M. moniliformis* than to *M. wolfii* (Lehnert et al., in prep. a).

**9. *Melpomene gracilis*** (Hook.) A. R. Sm., *Novon* 5: 20. 1995. *Polypodium gracile* Hooker, *Bot. Misc.* 2: 239. 1831. *Ctenopteris gracilis* (Hooker) J. Sm., *Hist. Fil.* 185. 1875. Type. Peru. Pasco: Huayllay, [ca. 4500 m], 1830, *Cruckshanks s.n.* (holotype, K; isotype, GH n.v., photo F n.v.). Figs. 7A, 15.

Etymology: The name refers to the delicate appearance of the plants (Latin, *gracilis* = thin, slender).

*Plants saxicolous. Rhizomes* very short-creeping to erect (Fig. 15A), 0.8-1.5 mm diam. *Scales* 1.0-1.5 x 0.4-0.6 mm, (12-)14–20(-24) cells wide, clathrate, dark brown to blackish, weakly iridescent, weakly cordate to truncate, acute to attenuate at tips (Fig. 15B); apical glands with 1 (-3) cells in a linear arrangement, marginal glands unicellular. *Fronde*s to 170-260 mm long, stiff, pendent, subfasciculate (Fig. 15A), subarticulate, inserted into the rhizomes on very short phyllopodia (fide Tryon & Stolze, 1993) hidden in scales. *Petioles* 60 mm long (Fig. 15A), 0.4-0.6 mm diam., terete, densely puberulent when young, glabrescent with age; hairs pluricellular and branched, hyaline to tan, probably glandular. *Laminae* to 130-200 mm long, to 22 mm wide (Fig. 15A), firm chartaceous to subcoriaceous, dark bluish green and glossy adaxially, pale yellowish green abaxially, fully pinnate basally, pinnatifid apically, glabrous except for glandular hairs (Fig. 15C, D). *Pinnae* 5.0-12.5 x 2.0-3.0, strongly ascending (60-30°) at least proximally (Fig. 15C, D), remote (Fig. 15A), weakly intricate (not notable in pressed plants), gibbose with the costae marked as grooves adaxially, linear to long-ovate, the margins entire (Fig. 15C), undulate (Fig. 15A) or pinnatifid less than halfway to the costa (Fig. 15D), the insertion to the rachis contracted; costae not visible or obscurely so abaxially; hydathodes present. *Sori* 2-5 pairs per segment, without hairs (Fig. 15C).

**Distribution and habitat.** On rocks in páramos and punas, often in sheltered spots like gullies and *Polylepis* patches, in Ecuador, Peru, and Bolivia at 3300-4500 m (Fig. 7A).

**Specimens examined. ECUADOR. Chimborazo/Morona Santiago:** Cerro Yanaurcu, N ridge of the mountain, 4200-4300 m, 02°14'S, 78°30', 29 Oct 1995, *Sklenar & Kosteckova 1511* (UC). **Azuay:** Surroundings of Laguna Toreadora, 02°47.17'S, 79°13.10'W, 3700-3800 m, 14 Nov 2004, *Lehnert 1554* (GOET, QCA, UC); sector Maylas, near the pass on Gualaceo-Limon road, 03°00.08'S, 78°39.70'W, 3300 m, 15 Nov 2004, *Lehnert 1569* (GOET, QCA, UC).

**BOLIVIA. La Paz:** Prov. Franz Tamayo, Pelechuco, 11000 ft, ca. 14° 48' S, ca. 69° 04' W, 3350 m, 04 Mar 1902, *Williams 2622* (NY)

The supposed epiphytic life form of the species (Tryon & Stolze, 1993) cannot be confirmed. The type locality known for its stone desert with eroded rocks at an elevation of ca. 4000 m. The only trees forming forests at this elevation are *Polylepis* species, which are not known from this locality (Kessler, 1995). It is more likely that the type grew in a sheltered spot in rock crevices, like the other plants recently collected in Ecuador; these were found in *Polylepis* forests but not as epiphytes.

This species is generally larger than *Melpomene allosuroides*, with which a strong affinity exists. The differences are the longer, less revolute segments of *M. gracilis*, and the sometimes undulate to incised margins (vs. always entire in *M. allosuroides*).

The weakly intricate pinnae resemble those of *Ceradenia intricata* (C. V. Morton) L.E. Bishop ex A. R. Sm., but that species has more closely arranged pinnae and the typical *Ceradenia* wax-like deposits in the sori.

The paucity of collections of *Melpomene gracilis* specimens can be explained by the poor growth of that species. The plants have often just one or two green fronds and appear not worthy collecting. The species is probably not as rare as the number of collections may suggest.

**10. *Melpomene huancabambensis*** Lehnert, sp. nov. Type. Peru. San Martin: Prov. Rioja, Buenos Aires, along road Pedro Ruiz-Rioja, 2000 m, 05°42'09"S, 77°53'06"W, *van der Werff et al.* 15352 (holotype, UC; isotypes, MO). Figs. 16, 17A.

*A Melpomene pilosissima* absentia hydathodorum, a *M. michaele*, *M. xiphopteroide* et *M. jimenezii* pilis in lamina abaxiale aequaliter distributis (vs. in soris confertis) differt.

**Etymology:** The name refers to the geographic restriction of the species to the Amotape-Huancabamba region in northern Peru.

*Plants* epiphytic in moss layers. *Rhizomes* stout, very short creeping to erect, 1.0 mm diam. *Fronds* pendent (Fig. 16A), inserted onto the rhizome in narrow angles, fasciculate (0.2-1.0 mm apart). *Scales* 2.0-3.2 x 0.3-0.5 mm, (10-)12-14(-16) cells wide, the cells weakly prosenchymatic, clathrate (Fig. 16B), dark brown, strongly iridescent, narrowly cordate, long-acute to attenuate at tips; apical glands 3-5 cells, in a nodding cluster or linear arrangement. *Petioles* (12-)45-55 mm long, 0.6-1.0 mm thick, terete, densely hairy, acicular hairs lax, dark

brown and (1.8-)2.0-3.5 mm long (Fig. 16C); simple and branched glandular hairs absent or very sparse. *Laminae* to 140-290 x 29-36 mm, narrowly elliptic (broadest at or beyond the middle), cuneate to shortly decurrent at bases, acute at tips (Fig. 16A). *Rhachises* very dark brown to black, planar adaxially (Fig. 16D), strongly hemispherically protruding abaxially (Fig. 16E), strongly hairy abaxially, moderately hairy adaxially, proximally stronger; hairs castaneous, 1.5-3.0 mm long. *Pinnae* 22.0-28.0 x 8.0 mm (3-4 times as long as wide), central pinnae patent or nearly so (inserting at an angle of 90-80°), distal pinnae weakly ascending (75-65°), equilateral at bases, fully adnate, oblong, the tips obtuse; costae obscurely visible in dried specimens (Fig. 16D, E); proximal pinna pairs markedly smaller than the following pinnae (1/2 to 1/3 of longest pinnae) (Fig. 16A), sometimes the lowermost 2-5 pinna pairs alariform; hairs like those on rhachises clustered in sori and along costa, but also evenly distributed on laminae abaxially, present adaxially mainly along the costae, always some hairs on the margins (Fig. 16E); hydathodes lacking (Fig. 16D) or very small. *Sori* 3-9 pairs per segment, (0)1-3 setae to 1.5 mm long in them, more hairs around them on the lamina, often covering the sori (Fig. 16E).

**Distribution and habitat.** Montane forests at 1900-2200 m in northern Peru and southern Ecuador (Fig. 17A).

**Additional specimens examined. ECUADOR. Zamora-Chinchi:** P.N. Podocarpus, park entrance “San Francisco,” on new Loja-Zamora rd., 03°59.349’S, 79°05.713’W, 2151 m, 14 Dec 2006, *Sundue 1123* (NY, UC). **PERU. San Martin:** Prov. Rioja, along road Rioja-Pedro Ruiz, El Mirador, 1900 m, 26 Mar 1998, *van der Werff et al. 15749* (MO, NY, UC); along road Pedro Ruiz-Rioja, 05°42'09"S, 77°53'06"W, 2000 m, 21 Mar 1998, *van der Werff et al. 15353* (MO, UC).

*Melpomene huancabambensis* is an ally of *M. pilosissima*, with which it matches in the densely hairy, terete petioles and the hairy laminae, which may have hairs along the pinna margins, and the adaxial laminae. It is characterized by patent pinnae, hairs on the laminae adaxially, and a lack of hydathodes. *Melpomene pilosissima* var. *tsatchelae* has sometimes partially visible costae (vs. always obscured in *M. huancabambensis*), ascending pinnae (vs. patent), and always well-developed hydathodes (vs. lacking hydathodes). *Melpomene xiphopteroides* differs in having hairs clustered in the sori (vs. not clustered in sori in *M. huancabambensis*). *Melpomene vernicosa* differs in having the hairs clustered along costae



and in sori (vs. evenly distributed in *M. huancabambensis*), glabrous pinna margins (vs. hairy), and more coriaceous laminae (vs. papyraceous). Other species with absent or weakly developed hydathodes (*M. jimenezii*, *M. michaelis*) have ascending pinnae, more coriaceous laminae, and hairs clustered in the sori.

**11. *Melpomene jimenezii*** Lehnert, sp. nov. Type. Bolivia. La Paz: Prov. Franz Tamayo, Parque Nacional Madidi, trail Pelechuco-Mojos, locality Tambo Quemado (camping area), on the trail towards Qalla, crossing the fourth river and going up the trail which leads through the *Polylepis* forest, 14°41'S, 68°58'W, 3490 m, *Jiménez I. 1859* (holotype, LPB; isotypes, GOET, UC). Figs. 17A, 18A-C.

*A Melpomene pilosissima* absentia hydathorum, a *M. michaelis* statura majore, pilis inter soris sparse distributis vel carentibus (vs. pilis crebris inter soris) praestans.

Etymology: The name honors Ivan Jiménez, Bolivian botanist and colleague, who collected the type specimen.

*Plants* epiphytic, growing in moss layers. *Rhizomes* shortly erect (Fig. 18A), 1.2-1.8 mm diam. *Fronds* to 350 mm, pendent, inserted onto rhizomes at acute angles, closely placed (1-4 mm) (Fig. 18A). *Scales* 5.5-7.5 x 0.4-0.6 mm, (8-)14-18(-20) cells wide, clathrate (but usually many lumina occluded) (Fig. 18B), dark brown to brown, weakly iridescent, subcordate to cordate at bases, long attenuate at tips (Fig. 18B); apical glands 5-12 cells, palmately arranged. *Petioles* 40-80 mm long, 0.8-1.0 mm diam., terete, with many long (1.2-3.0 mm) dark brown acicular hairs (Fig. 18A), simple and branched glandular hairs of crosiers and young fronds persistent on older fronds. *Laminae* 205-285 x 30-64 mm, lanceolate or broadly elliptic (broadest at or above the middle), acute to attenuate at tips; bases rounded to cuneate, proximal pinnae often remote (Fig. 18A). *Rhachises* dark brown to black, planar to weakly protruding adaxially, hemispherical protruding abaxially (Fig. 18C), some to many brown acicular hairs on both sides (1.0-1.5 mm), usually hairier abaxially than adaxially; abaxially also with many simple and branched glandular hairs. *Pinnae* 18-35 x 2.8-3.0 mm (6-12 times as long as broad), patent to weakly ascending (80-60°) (Fig. 18A), fully adnate, equilateral at bases, or weakly decurrent towards the blade apices, tips obtuse; proximal pinna pairs smaller than the following segments, but not alariform, oblong; margins entire or dentate

basally in large segments (Fig. 18C), fertile pinnae often conduplicate; costae not visible on both laminar sides, or obscurely so abaxially in dried specimens; stomata usually visible as dark brown to reddish dots (Fig. 18C); hairs to 2 mm long, clustered in sori, lacking or sparse along costae or on laminae abaxially, margins without hairs (Fig. 18C); hydathodes usually absent, some fronds with the hydathodes patchily developed. *Sori* 3-10 pairs per segment, each with 4-10 hairs (0.8-1.5 mm).

**Distribution and habitat.** Elfín forest and moist montane forests at 2400-3490 m in Peru and Bolivia (Fig. 17A).

**Additional specimen examined. PERU. Amazonas:** Leimebamba, 2400 m, 30 Dec 1962, *Woytkowski 7839* (UC). **Pasco:** Prov. Oxapampa, Huancabamba district, locality Lanturachi, sector Santa Barbara, 10°21'S, 75°39'W, 3800 m, 10 Oct 2003, *Perera et al. 531* (MO, USM).

**BOLIVIA. La Paz:** Bolivia, La Paz, Franz Tamayo, PN-ANMI Madidi, senda Pelechuco-Mojos, localidad Tambo Quemado (lugar para campar), 3250 m, 14°39'S, 68°57'W, 04 May 2003, *Jiménez I. 1891* (LPB, UC); *ibid.*, por el sendero que va hacia Qalla, cruzando el 4° río y subiendo por el sendero que atravieza el bosque de *Polylepis*, 14°41'S, 68°58'W, 3360 m, 03 May 2003, *Jiménez I. 1842A* (LPB, UC).

This species is remarkable because it lacks conspicuous hydathodes in most fronds. Occasionally, some pinnae have hydathodes, while hydathodes are otherwise absent on the same frond. According to Parris (1997), absence and presence of hydathodes may change in many grammitid taxa in the Paleotropics, but until now it has been considered a reliably constant feature for the neotropical genera.

The lack of hydathodes separates *M. jimenezii* from similar species such as *M. firma*, which always has well developed hydathodes, and also differs in conspicuous black costae (vs. costae invisible or obscure) and fewer hairs on the petioles (vs. densely long-hairy). From *M. pilosissima*, *M. jimenezii* furthermore differs in longer segments, hairs clustered in sori (vs. evenly distributed on laminae) and lacking hairs along the margins and the adaxial laminae (vs. regularly hairy along the margins and the adaxial laminae). The smaller *M. michaelis* is very similar, but differs from *M. jimenezii* by having hairs on the laminae between the sori (vs. restricted to the sori), lacking red stomata (vs. stomata often red), and having rhizome

scales only half the size of those of *M. jimenezii*, with thicker cell walls and often occluded cell lumina.

**12. *Melpomene leptostoma*** (Fée) A. R. Sm. & R. C. Moran, *Novon* 2: 430. 1992. *Polypodium leptostomum* Fée, *Mém. Foug.* 7: 58. 1857. *Ctenopteris leptostoma* (Fée) Copel., *Philipp. J. Sci.* 84: 421. 1955 (1956). *Grammitis leptostoma* (Fée) F. Seymour, *Phytologia* 31: 179. 1975. Type. Mexico. Veracruz: near Orizaba, *Schaffner 210* (holotype, P).  
*Polypodium productum* Maxon, *Contr. U.S. Natl. Herb.* 13: 11. 1909. Type. Guatemala. Alta Verapaz, near Cobán, *von Türckheim II.1347*, pro parte (holotype, US). Figs. 10B, 19.

**Etymology:** Greek *lepto* means thin or peeled, thus the epithet may refer to the hydathodes which are quite indistinct.

*Plants* epiphytic in moss layers. *Rhizomes* very short (Fig. 19A), erect to ascending, 1.0 mm diam. *Fronds* pendent, fasciculate, inserted onto the rhizomes at acute angles, closely placed (1 mm or less) (Fig. 19A). *Scales* to 2.2 x 0.4-0.5 mm, 8-10(-12) cells wide, clathrate (Fig. 19B), dark brown to brown, strongly iridescent, cordate to pseudopeltate, acute to attenuate at tips; apical glands 1-4 cells, linearly arranged (Fig. 19C). *Petioles* 5-20(-30) mm long, 0.4-0.5 mm thick, terete, with many short, dark brown to brown acicular hairs 0.75-1.50 mm long (Fig. 19D), rarely glabrescent; simple and branched glandular hairs of crossiers and young fronds may persist in older fronds. *Laminae* to 135-240(-350) x 15-20(-30) mm, narrowly elliptic (broadest in the middle), cuneate to decurrent at bases, acute to attenuate at tips (Fig. 20A). *Rhachises* dark brown to black, hemispherically protruding abaxially (Fig. 20E), flat to protruding adaxially (Fig. 19F); hairy on both sides (Fig. 19E, F), hairs like those on petioles. *Pinnae* 5.5-9.0 x 1.2-1.8 mm (4-5 times as long as broad), strongly ascending (60-45°), fully adnate, inequilateral and decurrent towards the bases, linear-oblong, the tips acute (Fig. 19E, F); margins entire or broadly dentate in large fronds, without acicular hairs, glandular cells present (Fig. 19E); costae at least weakly visible on both sides (Fig. 19E, F); basal 1-3 pairs markedly smaller than the following segments, but not alariform, sometimes remote (Fig. 19A). *Sori* 1-6 pairs per segment, without hairs (Fig. 19E).

**Distribution and habitat.** Cloud forests at 1400-2400 m in Mexico and Guatemala (Fig. 10B).

**Additional specimens examined. MEXICO. Chiapas:** La Trinitaria, along Comitan river at its sumidero, Lagos de Montebello, 42 km NE of La Trinitaria, 1300 m, 13 Nov 1971, *Breedlove & Smith 22381* (NY); E of laguna Tzikaw, Monte Bello NP, 1300 m, 16 Nov 1972, *Breedlove & Dressler 29625A* (Ny); E of Comitan Dominguez, along dirt road 1.8 mi E of turnoff to Ejido Tzisco, 07 Jan 1984, *Hardison et al. 92A* (UC); Parque Nacional Lagunas de Montebello, cerca de la Laguna Tzisco, 3 km al E, Mpio. La Trinitaria, 15 Nov 1984, *Téllez et al. 7972* (UC). **Hidalgo:** Tlanchinol, 4 km to the E of Tlanchinol, trail to Apantlasol, 03 Sep 1997, *Martínez-S. 28473* (NY). **Oaxaca:** Oaxaca, 4700 m, 1840, *Galeotti 6380* (P); Oaxaca, 1000 m, 1842, *Galeotti 6380bis* (P); Sierra de Juárez, Km 80 road 175 Tuxtepec-Oaxaca, 1500 m, 19 Nov 2005, *Kessler 13498* (GOET); Sierra de Juárez, Km 85 road 175 Tuxtepec-Oaxaca, 1800 m, 19 Nov 2005, *Kessler 13500* (GOET); Sierra de Juárez, Km 102 road 175 Tuxtepec-Oaxaca, 2400 m, 19 Nov 2005, *Kessler 13518* (GOET); Sierra de Juárez, Km 95 road 175 Tuxtepec-Oaxaca, 2200 m, 19 Nov 2005, *Kessler 13528* (GOET); Dto. Ixtlán, 79 km N of Ixtlán de Juárez on Rte 175, 1 km S of Campamento Vista Hermosa, ca. 1 h along trail toward Tarabundí, 4600-3850 ft, 27 Jul 1971, *Mickel 5737* (UC); 58 km N of Ixtlán, 11 km N of high point at Cerro Pelón, 6600 ft, 27 Oct 1969, *Mickel & Hellwig 4268* (UC); 23 km S of Valle Nacional, 5 km N of Vista Hermosa, 3800-4200 m, 23 Sep 1972, *Mickel & Pardue 6740* (UC). **Puebla:** 9 km from Teziutlan to Tlapocoyan, 1480 m, 26 Jul 1974, *Ramos & J. M. Fernández R-123* (NY). **Veracruz-Llave:** Orizaba, region of Orizaba, Monte Azul, 02 Oct 1866, *Bourgeau 3155* (P); mountain ridge of Santa Cruz (second label: Forêt de la Houertas las Animas, 2 heures de Jalapa, L. Hahn sept. 66), Aug 1853, *Hahn 27* (P).

**GUATEMALA. Alta Verapaz:** Coban, Mai 1908, *von Türckheim II.1347 A* (P); Tactic, 5000 ft, Dec 1881, *von Türckheim 479* (P).

The laxly pendent fronds and the hairs restricted to the rachises make this species readily recognizable. Most other sympatric species have stiffer fronds, and also have some to many hairs on the laminae or in the sori, e.g., *M. xiphopteroides*, *M. firma*, and *M. pilosissima*. The only other species with glabrous sori (*M. moniliformis*, *M. deltata*) have much shorter, weaker ascending to patent pinnae.

The species appears to be remote from others in *Melpomene*. An early isolation and divergence in southern Mexico during the evolution of the genus is suspected. *Melpomene*

*leptostoma* appears as sister to the rest of the genus with a strong statistical support in the phylogenetic analysis (Lehnert et al., in prep. a).

**13. *Melpomene melanosticta*** (Kunze) A. R. Sm. & R. C. Moran, *Novon* 2: 430. 1992.

*Polypodium melanostictum* Kunze, *Linnaea* 9: 44. 1834. *Ctenopteris melanosticta* (Kunze) Copel., *Philipp. J. Sci.* 84: 385. 1955 (1956). *Grammitis melanosticta* (Kunze) F. Seymour, *Phytologia* 31: 179. 1975. Type. Peru. Huanuco. “In flor. Peruv. rupibus aridis ad Cuesta de Carpish” (Carpish), 1829, *Poeppig s.n.* (holotype, LZ destroyed; isotype, B?, W?).

*Polypodium calvum* Maxon, *J. Wash. Acad. Sci.* 12: 440. 1922. *Ctenopteris calva* (Maxon) Copel., *Philipp. J. Sci.* 84: 386. 1955 (1956). Type. Cuba. Oriente, *León 11131* (holotype, US). Figs. 17B, 20.

**Etymology:** The epithet means “dark spotted” and refers to the often dark reddish or brown stomata, mentioned in the diagnosis as *subtus punctulatis* (Kunze, 1834).

*Plants* predominately epiphytic, sometimes epilithic. *Rhizomes* compact to short erect (Fig. 20A), 0.8-1.0(-1.2) mm diam. *Fronds* (40-)60-210(-300) mm, patent (Fig. 20A), stiff, inserted onto the rhizomes at acute angles, closely placed to fasciculate (1 mm or less) (Fig. 20A). *Scales* 1.5-3.6 x 0.5-0.6 mm, (8-)10–12(-14) cells wide, clathrate (Fig. 20B, C), dark brown to black, weakly iridescent, broadly lanceolate, cordate at base, acute at tip; apical glands 3-8, in a nodding cluster (Fig. 20D); scales sometimes with small gland-bearing lobes along the margins (Fig. 20B), structurally similar to the apices. *Petioles* (2-)5-15(-30) mm long, (0.3-)0.6-0.8 mm thick, alate throughout, glabrous; simple and branched glandular hairs of crosiers and young fronds sometimes persistent on older fronds. *Laminae* to 110-190 x 6-12(-15) mm, linear to narrow-elliptic, broadest in the middle, cuneate-decurrent at bases, short to long acute at tips (Fig. 20A). *Rhachises* dark brown to black, planar and slightly sunken adaxially, weakly hemispherically protruding abaxially. *Pinnae* (1.5-)2.0-6.0(-7.0) x (1.5-)1.8-3.0 mm (1.5-2.0 times as long as broad), patent or weakly ascending (90-75°) equilateral at base or weakly decurrent towards the bases, fully adnate, rounded to oblong with obtuse tips; costae not visible; pinnae planar to subgibbose, glabrous except for sori, which are weakly immersed in laminar tissue; pinna pairs weakly to strongly reduced towards the bases, the lowermost

pair sometimes alariform; stomata often brown to red. *Sori* (1-)2-4 pairs per segment, without hairs, or rarely some sori of a frond with 1-2 short hairs 0.5 mm long.

**Distribution and habitat.** Moist montane and submontane forests at 600-1550(-1900) m in Mexico, Guatemala, Costa Rica, Cuba, Dominican Republic, Guadeloupe, Venezuela, British Guyana, Surinam, Colombia, Ecuador, Peru, Brazil, and Bolivia (Fig. 17B).

**Selected specimens examined. GUATEMALA. Alta Verapaz:** Coban, 1349 m, Nov 1906, *von Türckheim II.1347 p.p.* (P).

**COSTA RICA. Cartago:** 22 km E of Turrialba; high ridge above Platanillo, 1200-1450 m, 22 Aug 1967, *Bishop 888* (UC); ca. 22 km E of Turrialba, high ridge above Platanillo, 1200-1450 m, 22 Aug 1967, *Mickel 3394* (NY). **Prov. unknown:** 1903, *Wercklé 178* (P); Navarro, 19 Mar 1905, *Wercklé s.n.* (P).

**CUBA. Santiago de Cuba:** Loma del Gato, 1100 m, Aug 1923, *Clement 1008* (P); Sierra Maestra, top of Punta de Palmamocha, S of Yara, 1400 m, 05 Apr 1915, *Ekman 5213* (B). **Prov. unknown:** "In Cuba Orientali," Sep 1859-Jan. 1860, *Wright C. 1050* (P, UC).

**DOMINICAN REPUBLIC. Santo Domingo:** Monte Cristi, Cordillera Central, Moncion, 1200 m, 04 Jun 1929, *Ekman 12730* (NY).

**GUADELOUPE. Basse Terre:** Comm. Basse Terre, La Souffrière, Col de l'Echelle, around la Lache Fendue, and near Savane à Mulets, 1264 m, 16°03'N, 61°40'W, 06 Mar 2005, *Christenhuusz & Katzer 3910* (NY, TUR).

**COLOMBIA. Boyacá:** road from Pauna to Otro Mundo, 1350 m, 16 Oct 1967, *Jaramillo Mejia 3651, 3670* (COL). **Caqueta:** surroundings of the camp to SE, 00°56'15"N, 72°42'00.6"W, 635 m, 27 Nov 1992, *Velayos et al. 6411* (COL). **Chocó:** Nóvita, ladera N del cerro Torrá Filo al W del Río Surama, camino al Alto del Oso, 600-900 m, Feb 1977, *Forero E. et al. 3159* (COL); San José del Palmar, hoya del Río Torito (afluente del Río Hábita), declive oriental, finca Laos Guadales, 730-830 m, 14 Mar 1980, *Forero E. et al. 7316* (COL). **Meta:** Acacias, Cordillera Oriental, Colonia Penal y Agrícola de Oriente, Cuhilla de La Meseta, 1130 m, 09 Aug 1981, *Jaramillo Mejia 7540* (COL). **Santander:** Río Mogoticos valley, road between Mogotes and San Joaquin, 1800 m, 02 Dec 1967, *Jaramillo Mejia 4512* (COL). **Valle:** Calima, on Río Calima, 14-15 Sep 1922, *Killip 11230* (NY).

**VENEZUELA. Amazonas:** Dpto. Atabapo, Cerro Huachamacari, Río Cunucunuma, vicinity summit camp, 1900 m, 14 Dec 1950, *Maguire et al. 30202* (UC); Cerro Huachamacari, E slope, 03°49'N, 65°42'W, 600-700 m, 03 Nov 1988, *Liesner 25716* (UC);

Dpto. Río Negro, Cerro Aracamuni, summit, Popa camp, 01°26'N, 65°47'W, 1550 m, 16 Aug 1987, *Liesner & Delascio 21981* (UC); Camp XI, Cerro de la Neblina, 6.2 km NNE Pico Phelps (= Neblina), along trail into Cañon Grande down ridge NW of camp, 00°51'45"N, 65°58'52"W, 1300-1390 m, 27 Feb 1985, *Beitel 85300* (UC); Cerro de La Neblina Camp IV, 15 km NNE of Pico Phelps, N branch of river in canyon, 00°51'N, 65°57'W, 780 m, 15-18 Mar 1984, *Liesner 16693* (UC). **Bolívar:** Dpto. Piar, Guayaraca, between escarpment and Río Guayaraca, S base of Auyan Tepui, 05°44'N, 62°32'W, 950 m, 25-27 Nov 1982, *Davidse & Huber 22756* (UC); Dpto. Piar, Amaruay tepui, ridge S of SW corner of tepui going up to wall, 05°54'N, 62°15'W, 750-950 m, 24 Apr 1986, *Liesner & Holst 20285* (UC). **Táchira:** Dpto. Uribante, Empresa Las Cuevas near La Fundación, 08°50'N, 71°47'W, 900 m, 07 Jul 1983, *van der Werff & Gonzáles 5007* (UC). **Yaracuy:** Dpto. Nirgua, Serranía Santa Maria-Cerro La Chapa, 6 km al N de Nirgua, 10°12.5'N, 68°33.5'W, 1200-1350 m, 18-19 Dec 1991, *Meier W. & Roeser 926* (UC).

**GUYANA. Prov. unknown:** *Schomburgk 1214* (B).

**SURINAME. Prov. unknown:** Sipaliwini, Lisa Kreek Savanah, Tafelberg Mountain, low forest savanah on top of Tafelberg Mountain, located 1/2 km SW of Lisa Kreek camp, 03°54'32"N, 56°12'44"W, 600 m, 26 Jun 1998, *Hawkins 1792* (UC).

**ECUADOR. Imbabura:** forest of La Magdalena (Mandurial), on S-facing slopes just N of Río Guayllabamba, opposite Hda. Conquista, E of Saguangal, 00°15'N, 78°47'W, 975 m, 29 Nov 1996, *Øllgaard et al. 2165* (AAU). **Morona-Santiago:** Gualaquiza. Hills around town of Gualaquiza, 03°24'S, 78°34'W, 1100 m, 29 Jul 1993, *Fay & Fay 4180* (AAU, UC); Misión Bomboiza, 03°29'S, 78°34'W, 800 m, 23 Apr 1973, *Holm-Nielsen et al. 4287* (AAU). **Pichincha:** Reserva Maquipucuna, ca. 5 km (airline) ESE of Nanegal, Hda. El Carmen, trail along Río Umachaca, just W of research station, 00°07'N, 78°38'W, 1250-1350 m, 28 Feb -04 Mar 1995, *Øllgaard 979* (AAU); a. 5 km (airline) ESE of Nanegal, Hda. El Carmen, trail along Río Umachaca, just W of research station, 00°07'N, 78°38'W, 1250-1350 m, 28 Feb -04 Mar 1995, *Øllgaard et al. 1074* (AAU). **Zamora-Chinchipec:** Campamento Shaimé (Shaimi) along Río Nangaritzá, trail to the ridge N of the village, trail starting from behind the visitor cabañas, 04°19'S, 78°40'W, 930-1100 m, 07 Nov 2004, *Lehnert 1533* (GOET, QCA, UC); Miazí, at junction of Río Chumbiriatza with Río Nangaritzá, 04°19'S, 78°40'W, 950-1250 m, 21-23 Oct 1991, *Øllgaard et al. 99270* (AAU).

**PERU. Puno:** Prov. Sandía, Chunchusmayo, 900 m, 28 Jun 1902, *Weberbauer 1230* (B). **San Martín:** Prov. Mariscal Cáceres, Palo Blanco, W of the bridge, Tocache Nuevo,

600-700 m, 02.12.1972, *Schunke 5723* (NY); Prov. San Martin, “in monte Campana, prope Tarapoto,” Aug 1856, *Spruce 4642* (P).

**BRAZIL. Amazonas:** Plato da Serra Aracá, SE part of Serra Norte, 00°51'N, 63°22'W, 1150-1250 m, 08 Feb 1984, *Tavares et al. 84* (NY). **Bahia:** 14° S, 700 m, 18 Dec 1892, *Gonnelle 1888* (P); Espiritu Santo: Santa Tereza, 15 Aug 1976, *Barcia 944, 948* (RIO); Espiritu Santo, Vargem Alta, 600 m, 03 Jun 1949, *Brade 19975* (RIO). **Minas Gerais:** Serra do Casaca, *Damazio 18368* (UC); Morro São Sebastião, 04 Feb 1894, *Gomes 2431* (RIO); Mun. Sta. Barbara, Serra do Caraca, 17 Dec 1982, *Pirani et al. 342* (P); Cerro do Cipo, 30 May 1996, *Salino 2757* (BHCB); Serra das Camarinhas, ca. 1250 m, 28 Aug 1896, *Schwacke 12451* (P); Serra do Fracão, 1000 m, 05 Nov 1903, *Schwacke 15031* (P, RIO); Caraca, atras da gruta de Lourdes, 28 Feb 1976, *WelsWindisch & Ghillány 470* (RIO). **Rio de Janeiro:** Serra dos Orgaos, 1856, *Begrade s.n.* (GOET); Theresopolis, Serra dos Orgaos, 24 Feb 1887, *Schenck s.n.* (B). **Roraima:** vicinity of Auaris, 760-800 m, 04°03'N, 64°22'W, 05 Feb 1969, *Prance et al. 9593* (NY); Serra dos Surucucs, NW of mission station, 02°42-47'N, 63°33-36'W, 21 Feb 1969, *Prance et al. 10153* (COL, RIO). **Sao Paulo:** Mun. Salesópolis, Serra do Mar, ca. 2 km a estrada de manutencao do oleoducto Salesópolis-São Sebastião, Dec 1973, *Windisch 570* (RIO).

**BOLIVIA. Beni:** Ballivian, 16 km por el camino maderero, 12 km de Yucumo a Rurrenabaque, 15°05'S, 67°07'W, 800 m, 03 Aug 1997, *Kessler et al. 10994* (LPB, UC). **La Paz:** Prov. Abel Iturralde, Parque Nacional Madidi, campamento de guardaparques Sadiri, camino Sadiri-Tumupasa, por la senda a las antenas de Entel, 14°10'S, 67°53'W, 990 m, 07 Jul 2004, *Jiménez I. & Huaylla 2651* (GOET, LPB, UC); Prov. Bautista Saavedra, Paujeyuyo, 15°02'12"S, 68°27'26"W, 940 m, 14 Nov 2003, *Fuentes A et al. 6065* (GOET, LPB); 3 km Pauji-Yuyo, entre Apolo y Charazani, 15°02'S, 68°29'W, 1450 m, 05 Jun 1997, *Kessler et al. 9754* (LPB, UC); Prov. Caranavi, Serrania Bellavista, entre Carrasco y Km 52, 15° 39.99'S, 67° 27.76'W, 1300 m, 12 Apr 2003, *Lehnert 765* (GOET, LPB, UC); Prov. Sud Yungas, Alto Beni, Sapecho, Colonia Tupiza B, 15°31'S, 67°18'W, 850 m, 29 Jul 1999, *Krömer & Acebey 655* (LPB, UC); *ibid.*, 26 Jun 2000, *Krömer & Acebey 1210* (LPB, UC).

The dark stomata that gave this species its name do not occur in all fronds and not even in all specimens seen. The dark color seems to be dependent on the provenance and the drying condition, and has been observed in other species as well (*M. xiphopteroides*, *M. vernicosa*). *Melpomene melanosticta* may be confused with *M. xiphopteroides* because both often grow together and have similar leaf cutting, but that species has few to many, rather long hairs



clustered in the sori and abundant on the petioles (vs. glabrous with occasional short hairs in sori).

Although no authentic specimen of the type collection has been found during this study, the rightful application of the epithet is not doubted. In the discussion, Kunze compares *Melpomene melanosticta* with *M. flabelliformis* (as *Polypodium rigescens* Bory ex Willd.) and *M. peruviana* (as *Polypodium peruvianum* Desv.), and mentions the hairs in sori and the creeping rhizomes of these species as differences from *M. melanosticta*. Thus we can conclude that the specimen upon which the description is based had no hairs in the sori and a compact or at least very short-creeping rhizomes. This is in concordance with the general concept of this species (see Mickel & Smith, 2005; Tryon & Stolze, 1993). However, my efforts to recollect the species at the type locality yielded only in erroneously taken plants of *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A. R. Sm., in which the characteristic black fungal fruiting bodies (Smith, 1993) were scarce or lacking on most fronds, but dark stomata were present. In this case, *Terpsichore anfractuosa* can still be distinguished from *M. melanosticta* by its proliferous roots (vs. not proliferous in *M. melanosticta*) and the scattered hairs on the rhachises (vs. rhachises always glabrous).

**14. *Melpomene michaelis*** Lehnert, sp. nov. Type. Bolivia. Cochabamba: Prov. Carrasco, carretera Cochabamba-Villa Tunari, debajo de Corani, 2750 m, 17° 10.51'S, 65° 54.02'W, *Lehnert 519* (holotype, GOET; isotypes, LPB, UC). Figs. 17A, 18D-F.

*A Melpomene pilosissima* pilis in soris confertis, hydathodis partim reductis differt.

Etymology: The name honours both Michael Kessler, my mentor at Göttingen University, and Michael Sundue, a colleague from New York Botanic Garden, who first recognized this species as being distinct.

*Plants* predominately saxicolous, also epiphytic. *Rhizomes* very shortly creeping (Fig. 18D), ascending to erect, 0.8-1.4 mm diam., rarely branched. *Fronde*s 230-340 mm, rather laxly pendent, inserted onto the rhizomes at acute angles, caespitose, closely placed (0.2-1.0 mm) (Fig. 18D). *Scales* to 2.0-3.0 x 0.4-0.6 mm, (8-)10–12(-16) cells wide, clathrate (Fig. 18E), dark brown to brown, weakly iridescent, narrowly lanceolate, narrowly cordate basally, attenuate at tips; apical glands 1-3 cells, in linearly arranged; sometimes cells of scales

unexpanded, then scales blackish and not iridescent (Fig. 18F). *Petioles* 26-55 mm long, 0.4-0.6 mm diam., terete, with many long (1-3 mm) dark brown hairs; simple and branched glandular hairs of crossiers and young fronds sometimes persistent on older fronds. *Laminae* to 115-125 x 11-20 mm (2/3 of frond length), narrowly elliptic (widest at and/or below the middle), rounded to broadly cuneate at bases, short-attenuate to acute at tips (Fig. 18D). *Rhachises* dark brown to black, planar and slightly sunken adaxially, hemispherically protruding abaxially, densely hairy as on petioles abaxially and in the proximal half adaxially. *Pinnae* 4.5-7.2 x 1.4-2.2 mm (2.5-3 times as long as broad), weakly ascending (80-75°), inequilateral at bases, fully adnate, long-deltate to oblong, the tips obtuse; costae not visible, or partly so abaxially; proximal 1-3 pinna pairs markedly smaller than the following pinnae, but not alariform; hairs few to many on the abaxial laminae, clustered in and around sori, always some along the margins, at least one at the tips, rarely some adaxially; hydathodes small, inconspicuous and regularly lacking in some parts of the fronds. *Sori* 1-6 pairs per segment, with 1-3 long hairs (1.5-2.0 mm) within sori and several around them.

**Distribution and habitat.** Wet montane forests at 2250-3450 m in Peru and Bolivia (Fig. 17A).

**Additional specimens examined. PERU. Cuzco:** Prov. Urubamba, Machu Picchu, along trail from Machu Picchu ruins to Wiñay Waina, 2300 m, 21 Jan 1976, *Bishop 2513* (UC); entre San Luis y Abra Malaga, 13° 06.22'S, 72°22.42'W, 3450 m, 16 Oct 2002, *Lehnert 443* (GOET, UC, USM). **BOLIVIA. Cochabamba:** Prov. Ayopaya, San Cristobal, subiendo por el sendero que va a San Miguel, 16°39'S, 66°43'W, 3250 m, 06 Jun 2002, *Jiménez I. 1149* (LPB, UC); Prov. Carrasco, Sehuencas, encima cabañas del Country Club, 17°30'S, 65°17'W, 2250 m, 15 Dec 1993, *Ibisch 93-1894* (LPB), 3 km de Siberia hacia Karahuasi, 17°48'S, 64°41'W, 2400 m, 18 Oct 1996, *Kessler et al. 9141* (LPB, UC); Carretera Cochabamba-Villa Tunari, debajo de Corani, 17° 10, 51'S, 65° 54, 02'W, 2750 m, 26 Nov 2002, *Lehnert 519* (GOET, LPB, UC). **Santa Cruz:** Prov. Caballero, 7.5 km (by air) N of Comarapa, vicinity of Tinqu Laguna, 17°51'S, 64°32'W, 2625 m, 25 Nov 1999, *Nee 50639* (LPB, NY, UC).

This new species is habitally identical to *M. pilosissima* var. *pilosissima* and var. *tsatchlae*, but there are several small morphological differences, which coincide with its clearly restricted distribution. The main differences of *M. michaelis* are the lacking or

inconspicuous hydathodes and the clustered hairs in the sori; both varieties of *M. pilosissima* have well developed hydathodes and the laminae evenly distributed hairs on the abaxial laminae (hairs present also in sori, but not clustered). *Melpomene michaelis* is found in Peru and Bolivia, separated by the Huancabamba-depression from *M. pilosissima* var. *tsatchelae* in Ecuador, Colombia, Venezuela, and Costa Rica. Both taxa are known only as saxicolous plants. In contrast, *M. pilosissima* var. *pilosissima*.

*Melpomene michaelis* co-occurs with *M. jimenezii*, which at first looks like a large version of *M. michaelis*. Apart from the size, it generally differs in lacking hydathodes (vs. occasional small hydathodes in some pinnae in *M. michaelis*) and in lacking hairs on the lamina tissue between the sori. It also has glabrous pinnae margins and adaxial laminae (vs. sometimes with scattered hairs in *M. michaelis*).

A peculiar trend is observed in the rhizome scales of *M. michaelis*: Already having scales with their cells smaller than in most *Melpomene* species in average, the cells in the southern populations are even smaller. Their cell lumina are often occluded or sometimes not discernable.

**15. *Melpomene moniliformis*** (Lagasca ex Sw.) A. R. Sm. & R. C. Moran, Novon 2: 430. 1992. Figs. 21-23.

Etymology: The epithet means “chain-like” and refers to the shape of the fronds.

*Plants* predominantly terrestrial or epilithic in the Andes and Brazil, often epiphytic in Mesoamerica and the Caribbean, growing in moss layers, rock crevices or on open soil. *Rhizomes* moderately to short-creeping (Figs. 21A, B, 22C, G, H), some extremes very short- (páramo) (Fig. 22A) or very long-creeping (shaded epiphytes) (Fig. 22E), 0.5-1.0(-1.5) mm diam. *Fronds* 20 to 270 mm, erect, inserted onto the rhizomes at right angles, closely to remotely placed (1-5 mm). *Scales* 4.0-5.0 x 0.8-1.5 mm, (10-)16–24(-28) cells wide, clathrate (Fig. 21C), dark brown to brown, strongly iridescent, broadly cordate to pseudopeltate, acute to attenuate at tip; apical glands ca. 3-8 cells, palmately arranged (Fig. 21D). *Petioles* 5-65(-90) mm long, (0.4-)0.6-0.8(-1.0) mm diam., marginate to narrowly alate from the laminar bases, throughout in small plants, with few to many hyaline to brown acicular hairs (0.75- 1.2 mm), these usually ephemeral, but especially in large epiphytic plants sometimes persistent; simple and branched glandular hairs of crosiers and young frond sometimes persistent in older

fronds. *Laminae* to 190 x 14 mm, linear to narrow elliptic (broadest in the middle), rounded to truncate at bases, short-acute at tips. *Rhachises* dark brown to black, planar and slightly sunken adaxially, hemispherically protruding abaxially, glabrous or glabrescent with branched hairs abaxially, sometimes sparsely to densely hairy adaxially in proximal parts. *Pinnae* 1.8-4.5(-7.5) x 1.4-3.5 mm (ca. 1-2 times as long as broad) (Figs. 21F, 22B, D, F), firm chartaceous to coriaceous, flat to subgibbose, patent, equilateral at bases or weakly decurrent towards the bases, fully adnate, rounded to deltate, sometimes oblong, the tips obtuse; costae not visible, or obscurely so abaxially in dried specimens (Fig. 22F); 1-3 proximal pinna pairs markedly smaller than more distal segments, rarely alariform; hydathodes well developed, often notable as small pits (Fig. 22D). *Sori* 2-4 pairs per segment, without (Fig. 22F) or with 1-10 hairs 0.5-1.0 mm long (Fig. 22D).

**Distribution and habitat.** Páramos, punas (jalca), elfin forests, and wet montane forests at 1800-4550 m in Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Cuba, Jamaica, Haiti, Dominican Republic, Puerto Rico, Venezuela, Colombia, Ecuador, Peru, Brazil, and Bolivia (Fig. 23).

*Melpomene moniliformis* is often confused with *M. flabelliformis*. In fact, both species are more similar than older species concepts may suggest (Tryon & Stolze, 1993; see *M. flabelliformis*). Petioles of *M. moniliformis* are hairy in youth but often (but not always) glabrescent with age and, comprise ca. 1/4 or less of frond length; the rhachises are proximally as hairy on both sides as the petioles (i.e., it may also vary greatly with age), and there are no or only 1-3 (rarely to 10) setae in the sori and none on the laminae between them; in *M. flabelliformis*, the petioles are glabrous or sparsely hairy and then persistently so, measure up to 1/3 of the frond length, the abaxial laminae have several hairs in and around the sori, and usually also on rhachises and fertile laminar portions. The pinnae are usually shorter in *M. moniliformis* than in *M. flabelliformis*, but there is a certain overlap; especially Costa Rican specimens of *M. moniliformis* have exceptionally long pinnae.

*Melpomene wolfii* is best distinguished from *M. moniliformis* by the obtuse to emarginate tips of the weakly ascending pinnae; in *M. moniliformis*, the pinnae are always patent with obtuse to rounded tips. Furthermore, *M. wolfii* is variably hairy on the laminae (glabrous to densely short hairy in fertile portions) and constantly glabrous on the petioles; in *M. moniliformis* the situation is the other way round (glabrous to glabrescent on petioles and

always glabrous on laminae except for hairs in sori). Other similar species are *M. melanosticta*, *M. flagellata*, and *M. caput-gorgonis*, which see for general differences.

Smaller forms of *M. moniliformis* are more easily separated from *M. flabelliformis* than larger ones, which can be confusingly similar. Hence I have chosen to distinguish several varieties of *M. moniliformis* to stimulate further studies on this complex. A key to the varieties is omitted here because they are included in the general key.

**15a. *Melpomene moniliformis*** (Lagasca ex Sw.) A. R. Sm. & R. C. Moran var. *moniliformis*.

*Polypodium moniliforme* Lagasca ex Sw., Syn. Fil. 33. 1806. *Ctenopteris moniliformis* (Lagasca ex Sw.) J. Sm., Hist. Fil. 184. 1875. *Grammitis moniliformis* (Lagasca ex Sw.) Proctor, Brit. Fern Gaz. 9: 219. 1965. *Xiphopteris moniliformis* (Lagasca ex Sw.) Crabbe, Brit. Fern Gaz. 9: 319. 1967. Type. Peru. Collector not stated (holotype, S).

*Polypodium subcrenatum* Hook., Icon. Pl. 8: pl. 719. 1848. Type. Ecuador. Pichincha, *Jameson 215* (holotype, K).

*Polypodium angustissimum* Fée, Crypt. Vasc. Brésil 2: 5, t. 96, fig. 3. 1873. Type. Brazil. *Glaziou 5297, 5298* (holotype, P). Figs. 21, 23A.

*Plants* small to medium sized, terrestrial, rarely epiphytic. *Rhizomes* 1.5 mm diam., moderately creeping with the fronds clearly apart (Figs. 21A, B). *Scales* 2.0-2.5 x 0.6 mm, 14-18(-20) cells across their bases. *Fronde*s 10-20 cm, stiffly erect (Fig. 21A, B); dried fronds with imbricate pinnae. *Petioles* decurrently alate to weakly marginate (Fig. 21D). *Laminae* 80-145 x 5-11 mm, glabrescent with many brown hairs which may persist if plants grow in cushions, then laminar bases not truncate but weakly cuneate with the lower pinna pairs gradually smaller; rachises proximally short-hairy on both sides, but glabrous in fertile parts. *Pinnae* (= segments) 2.0-5.0 x 2.5-3.0 mm, as long as broad (Fig. 21E) or 1.5 times longer, with hyaline margins two cell rows wide. *Sori* always with 1-5 hairs 1.0(-1.5) mm long.

**Distribution and habitat.** Sheltered rocky habitats in páramos and punas, in *Polylepis*- and elfin forests at 2000-4500 m; whole range of the species save the tepui - region of Venezuela (Fig. 23A).

**Selected specimens examined. MEXICO. Morelos:** Umbria, barranco behind Cuernavaca, [ca. 18°55'N, ca. 99°15'W,] *Bourgeau s.n.* (P). **Oaxaca:** Zempoaltépetl, middle

to upper slopes, 19-27 Feb 1937, *Camp 2656* (UC); Dtto. Ixtlán, Cerro Pelón, 47 km N of Ixtlán on Rte 175 at crest just as road starts down toward Valle Nacional, [ca. 16° 59'N, ca. 96°06'W,] 3000 m, 23 Jul 1971, *Mickel 5505* (UC); trail from San Pedro Nolasco N to the Llano Verde, [ca. 17°15'N, ca. 96°24'W,] 6000-7200 ft, 05 Oct 1969, *Mickel & Hellwig 3823* (UC). **Veracruz:** base of Orizaba, [ca. 18°51'N, ca. 97°05'W,] 1840, *Galeotti 6253* (P).

**COSTA RICA. Limon:** Cordillera de Talamanca, Atlantic slope, Kámuk massif, páramo NE of the main Kámuk peak, 19°16-17'N, 83°00-02'W, 3000-3300 m, 17-18 Sep 1984, *Davidse & Herrera-Ch. 29313* (UC). **San José:** National Park Braulio Carrillo, transect trail between OTS-Station La Selva and Volcan Barva, 2700 m, 28 Apr 2003, *Kluge 6257* (GOET).

**PANAMA. Chiriqui:** Loma Larga to summit, Volcán de Chiriqui, 2500-3000 m, 04-06 Jul 1938, *Woodson jr. et al 1090* (NY).

**DOMINICAN REPUBLIC. Peravia:** La Nevera, from Valle Nuevo to San José de Ocoa, [ca. 18°55'N, ca. 70°05'W,] 2100 m, 18 Oct 1968, *Liogier 13125* (P).

**JAMAICA.** Summit of Blue Mountain Peak, 2100-2200 m, 07-09 Jul 1926, *Maxon 9857, 9887* (NY).

**COLOMBIA. Antioquia:** between Río Negro and Sta. Helena, 2650 m, Jul 1944, *Garcia-Barriga 11097* (COL). **Arauca:** Sierra Nevada del Cocuy, headwaters of the quebrada El Playón, Patio Bolos, hoya San José, 2 km to ENE from Alto Cusiri, 4285 m, 10 Mar 1973, *Cleef 9040* (COL). **Boyacá:** Chinavita, Cerro Mamapacha, above W ridge of lagoon on SE part of W plate of cerro, 2950 m, 11 Dec 1998, *Stancik 1603* (COL); Toquilla-Labranzagrande, Páramo Franco, ca. 8 km from Toquilla, 3150 m, 09 Feb 1999, *Stancik 2212* (COL). **Caldas:** Carrtera Manizales-Nevado del Ruiz, 13 km from Manizales, 2500 m, 05 Aug 1958, *Bishler 1471* (COL); road from Termales to Refugio, 4500 m, 22 Oct 1961, *Murillo M. T. 477* (COL). **Caldas/Tolima:** Cordillera Central, Nevado del Ruiz, paramos between Termales and Nevado and Libano, W-facing slope above second campsite, sta. 12, on road to Libano, 4050 m, 20 Dec 1958, *Barclay & Juajibioy 6442-A* (COL). **Cundinamarca:** Cordillera Oriental, E slope, Páramo de Guasca, 3200-3300 m, 02 Jun 1940, *Cuatrecasas 9495* (COL); Parque Nacional Natural Chingaza, headwaters of Quebrada Piedras Gordas, 3600 m, 25 Apr 2001, *Zuluaga-R. 5028* (COL). **Meta:** Páramo de Sumapaz, Hoya Sitiales, laguna La Primavera and surroundings, Pedregal 300 m NW of the laguna, 3580 m, 25 Jan 1972, *Cleef 993* (COL); Macizo de Sumapaz, vertiente oriental de la cordillera. Hoya de la quebrada El Buque, 3400 m, 11-12 Jul 1981, *Díaz-P. 2767* (COL). **Nariño:** Guachual-Cumbal, Páramo del Infernillo, the ridge in direction to Volcán Cumbal, 3700 m,

09 Mar 1999, *Stancik 2698* (COL). **Norte de Santander:** Cordillera Oriental, páramo de Tama, arriba de la Cueva, 3100-3200 m, 27 Oct 1941, *Cuatrecasas et al. 12635* (COL). **Santander:** Coromoro, Laguna de La Jiquera or Fiquera, Quebrada Coromoro, 3750 m, 29 Nov 1967, *Jaramillo Mejía et al. 4378* (COL).

**VENEZUELA. Mérida:** Dtto. Campo Elias, E slope of peak El Campanario, páramo of Los Conejos, Sierra de la Culata, 4000-4250 m, 22 Mar 1972, *Ruiz-Teran 6957* (UC); Dtto. Rangel, Páramo de Mucuchis, 29.1 mi W of La Soledad (Edo. Barinas) along road to Santo Domingo (near Km 10 road marker, i.e., ca. 10 km E of Apartaderos), 08°49'N, 70°47'W, 3050 m, 19 Nov 1982, *Smith A. R. et al. 1421* (UC); Mucubaji, Km 14 road Apartaderos-Barinas, 13 Aug 1980, *Stergios & Taphorn 2113* (UC). **Táchira:** NNE slopes of Pata de Judío, 3100-3500 m, 19 Oct 1978, *Luteyn et al. 5961* (AAU). **Trujillo:** road to peak above Bocono Municipal Park, 3000 m, 25 Dec 1986, *Fay A. 1600* (UC); Dtto. Boconó, 14-17 km SE of Boconó, on road to Guaramacál, near summit of road, 09°12'N, 70°12'W, 2700-2800 m, 25-26 Nov 1982, *Smith A. R. et al. 1574* (UC).

**ECUADOR. Azuay:** Páramo de las Cajas, W slope ca. 1 km above Mihuir, 2700-2900 m, 26 Apr 1985, *Harling & Anderson 24627* (QCA); Cajas, N of Laguna Toreadora, 02°47.17'S, 79°13.10'W, 3850 m, 17 Nov 2003, *Lehnert 1114* (GOET, UC, QCA). **Bolivar/Chimborazo:** at the pass on the road Riobamba-Guaranda, 01°39'S, 78°50'W, 4000 m, 27 Nov 1981, *Filskov et al. 37500* (AAU). **Carchi:** summit on the road El Angel-Tulcán, Km 17 from El Angel, 00°40'N, 77°52'W, 3700 m, 28 May 1980, *Balslev & Quintana 23914* (AAU); Páramo El Angel, in the pass on road El Angel-Tulcán, 00°41'N, 78°54'W, 3750-3800 m, 15 May 1973, *Holm-Nielsen et al. 5481* (AAU, UC). **Cotopaxi:** Cotopaxi National Park, Limpiopungo, flat plain NW of Cotopaxicone, 00°37'S, 78°28'W, 3800 m, 21 May 1988, *Balslev et al. 69099* (AAU); Parque Nacional Cotopaxi, 00°40'S, 78°30'W, 3500 m, 15 Apr 1982, *Bosco Nowak 1* (QCA); San Francisco, forest Huahuaucó, parroquia Toacazo, Cantón Latacunga, 00°45'S, 78°40'W, 3370-4550 m, 10 Oct 1995, *Jaramillo & Tapia 17642B* (QCA). **Loja:** Fierro Urco, Saraguro-Loja, Km 12.4 turnoff towards Fierro Urco, Km 23.8, 03°43'10"S, 79°19'18"W, 3840 m, 06 Dec 1994, *Jørgensen et al. 1243* (AAU, UC); ca. 8 km S of Saraguro on road to Loja, 03°37'S, 79°11'W, 3100 m, 13 Feb 1991, *Kessler 2473* (QCA); pass „El Tiro“ between Loja and Zamora, trail from province border sign up to the cerro, 03°59'S, 79°08'W, 2750 m, 11 Nov 2003, *Lehnert 1105* (GOET, UC, QCA); Cerro Villnaco 7-12 km W of Loja, 2700-3000 m, 09 Oct 1944, *Wiggins 10967* (UC). **Morona-Santiago:** along road Gualaceo-El Limón, 2800-3500 m, 15 Aug 1989, *van der Werff & Gudiño 11088* (UC). **Napo:** Camino Quito-Baeza, Laguna Papallacta, 3400 m, 16 May 1987,

*Heredia* 7 (QCA); Laguna Yuragcocha, 3 km E of Cerro Quilindaña, 00°47'S, 78°21'W, 4050 m, 31 Mar 1979, *Holm-Nielsen 16340A* (AAU). **Pichincha:** Nevado Cayambe, N slope, near Olmedo, 00°06.08'N, 77°58.82'W, 3800 m, 30 Jun 2002, *Lehnert 122* (GOET, UC, QCA); Cerro Atacazo, pendiente norte cumbre, 00°20-23'S, 78°36-38'W, 4250 m, 17 Jun 1983, *Treiber de Espinosa 108* (QCA).

**PERU. Amazonas:** Chachapoyas, road Leymebamba-Balsas, Km 14-25, 06° 43'S, 77° 50'W, 3100 m, 07 Aug 2002, *Lehnert 249, 258, 262* (GOET, UC, USM); upper slopes of Puna-Urcu SE of Chachapoyas, 2700-3000 m, 01 Jun 1962, *Wurdack 701* (USM). **Ancash:** Huaraz, Quebrada de Llaca, 09° 28.83'S, 77°27.96'W, 4500 m, 15 Aug 2002, *Lehnert 276* (GOET, UC, USM); Huari, Huascaran National Park, Quebrada Pucaraju (Pucaragra, fide map), a lateral valley of Quebrada Rurinchay, 09°21'S, 77°17'W, 3900-4200 m, 15 Jun 1986, *Smith D.N. et al. 12702* (USM). **Apurimac:** Soccllaccasa pass, 3900 m, 10 Nov 1935, *West 3822* (UC). **Cajamarca:** Cajamarca, Cumbre El Gavilan, road to Cajamarca, 3200 m, 31 Mar 1948, *Ferreyra 3301* (USM); Hualgayoc, above La Tahoma, between Bambamarca and Hualgayoc, 3300 m, 16 Aug 1952, *Ferreyra 8538* (USM); Cajamarca-Bambacara road, 55 km N of Cajamarca, 06°55'S, 78°35'W, 3750 m, 02 Jun 1984, *Smith D. N. & Sánchez-Vega 7451* (UC). **Cuzco:** Paucartambo, road between Paucartambo and Shintuyo (to Puerto Maldonado), 12-13 km N of park entrance to Manú National Park, 14°30'S, 71°17'W, 2900 m, 05 Oct 1995, *Croat 78202* (UC); Quispicanchi, Marcapata, trail passing public toilets, 13° 35.28'S, 70°58.30'W, 3000 m, 22 Oct 2002, *Lehnert 450, 452* (GOET, UC, USM). **Huancavelica:** Tayacaja, above the hacienda Tocas, between Colcabamba and Paucarbamba, ca. 12°24'S, ca. 74°42'W, 3400-3500 m, 20 Apr 1954, *Tovar 1971* (USM). **Huanuco:** Prov. Huanuco, Carpish, 2600-2700 m, 23 Jun 1953, *Ferreyra 9425* (USM), Huanuco-Tingo Maria, 09°44.02'S, 76°05.55'W, 23 Aug 2002, *Lehnert 288* (GOET, UC, USM). **La Libertad:** Prov. Santiago de Chuco, Shoreyo-Trujillo road, ca. 5 km from Shoreyo, 07°59'S, 78°23'W, 3600 m, 26 Aug 1982, *Smith D. N. 2343* (AAU); Prov. Sánchez Carrión, Al pié del Nevado de Huaylillas, 07°52.8'S, 78°01'W, 3840 m, 21 May 2001, *Sagástegui & Zapata 16501* (UC). **Pasco:** Oxapampa, Cordillera Yanachaga, Cerro Pajonal "chacos," 12 km SE of Oxapampa, 2700-2800 m, 07 Oct 1982, *Foster 9036, 9063* (USM); San Alberto, Cordillera de Yanachaga, 2300-2500 m, 06 Mar 1986, *van der Werff et al. 8494* (USM). **San Martín:** Mariscal Caceres, Pampa de Cuy, 29 Feb 1988, *León & Young 1139* (USM); Puerta del Monte, NW corner of Río Abiseo National Park, 07°XX'S [sic], 77°XX'W [sic], 3450 m, 10 Jul 1987, *Young & León 4364* (USM).



**BRAZIL. Espírito Santo:** Nova Lombardia, [ca. 19°55'S, ca. 40°34'W,] Aug 1976, *Barcia 1146* (RIO). **Minas Gerais:** Alto Caparaó, Parque Nacional do Caparaó, on the way to Pico da Bandeira, ca. 20°31'S, 41°53'W, 2600 m, 21 Mar 1999, *Salino & Morais 4538* (UC), Passa Quatro, Itaguasé, [ca. 22°22'S, ca. 44°58',] 2000 m, 09 May 1948, *Brade 19025* (RIO). **Rio de Janeiro:** Itatiaya, 2400 m, 01 May 1950, *Brade 20298* (RIO); Serra dos Orgãos, 2200 m, 11 Aug 1940, *Brade 16559A* (RIO); Itatiaya, Serra da Mantiqueira, S slope under rocks, 2700 m, 02 Mar 1931, *Kaempfe 397* (RIO); Serra do Itatiaya, 2400 m, Jun 1913, *Brade 1899* (RIO); Municipio de Nova Friburgo, Pico da Caledônia, [ca. 22°16'S, ca. 42°31'W,] 2000 m, 30 Mar 1989, *Sylvestre et al. 204* (RIO); Campo Itatiaya, Aguas Negras, 01 May 1906, *Luederwald s.n.* (P, SP 22086). **Sao Paulo:** Campos de Jordão, Apr 1937, *Lanstyack s.n.* (RIO 33139); Campos de Jordão, 05-10 Feb 1937, *Cassipos Porto 3088* (RIO).

**BOLIVIA. Cochabamba:** Prov. Ayopaya, 2 km to the SE of Saila Pata, 16°54'S, 66°55'W, 3750 m, 15 Nov 1997, *Kessler et al. 12451* (UC, LPB); Prov. Carrasco, 108 km on old road Cochabamba-Villa Tunari, 17°09'S, 65°38'W, 2950 m, 22 Jun 1996, *Kessler et al. 6591* (GOET, UC, LPB); Prov. Chapare, Abra de Colomi, 3500 m, 20 Jun 1929, *Steinbach 9867* (UC). **La Paz:** Prov. Inquisivi, some 8 km from Quime to Inquisivi, Camillaya above the village, 16°58'S, 67°12'W, 3000 m, 29 Dec 1997, *Beck et al. 24368* (LPB); Prov. Murillo, Zongo Valley, 5 km above Cuticucho, 2.7 km below Botijlaca, 16°10'40"S, 68°08'24"W, 3170 m, 06 Aug 1990, *Fay & Fay 2940* (US, LPB); Prov. Bautista Saavedra, 15 km de Charazani hacia Apolo, 15°11'S, 68°46'W, 2400 m, 30 Jun 1997, *Kessler et al. 10436* (UC, LPB); 15 km de Charazani a Chullina, 15°10'S, 68°53'W, 3400 m, 28 Jun 1998, *Kessler et al. 10581* (GOET, LPB); Prov. Larecaja, Sorata, 15°44.04'S, 68°39.28'W, 3300 m, 06 Jan 2003, *Lehnert 560* (GOET, LP, UC); Prov. Murillo, 20.8 km N of pass to Río Zongo valley, 16°09'S, 68°07'W, 3200 m, 20 Feb 1987, *Solomon 16140* (US, LPB); Prov. Sud Yungas, Mururata, bajo la mina Bolsa Negra, pasando por el pueblo de Tres Ríos, 16°35'S, 67°45'W, 3900 m, 18 Nov 1995, *Gonzales J. 1422* (UC, LPB). **Santa Cruz:** Prov. Caballero, Comarapa, ca. 1 km de Siberia hacia Torecillos, 2650 m, 18 Mar 2003, *Lehnert 712, 713* (GOET, LPB, UC).

This variety is transient in all its characters with the var. minor. It may be found in open habitats exposed to the sun where it most resembles var. minor. Plants from the shade may be similar to var. *paradoxa* in segment shape (Fig. 23F), but differ from that variety in having fewer hairs in the sori and in smaller scales.

**15b. *Melpomene moniliformis* var. *minor*** (H. Christ) Lehnert, comb. nov. *Polypodium moniliforme* var. *minus* H. Christ, Bull. Soc. Genève sér. 2, 1: 217. 1909. Syntypes: Costa Rica. Cartago, crater of Volcán Irazú, *Pittier 179* (P; isosytype, US). Brazil. Rio de Janeiro, *Ule 3785* (P).

*Polypodium moniliforme* var. *major* Liebm., Kongel. Danske Videnks. Selsk. Skr. Naturvidensk. Math. Afd., ser. 5, 1: 196. 1849. Type. Mexico. Pico de Orizaba, 9000-10000 ft, *Liebmann s.n.* (Lectotype chosen by Smith, Fl. Chiapas 2: 123. 1981, C n.v.; isolectotype, P). Fig. 21E, F.

*Plants* terrestrial, very small (Fig. 21E). *Rhizomes* contracted but clearly horizontally creeping. *Scales* 1.6-2.5 x 0.5-0.6 mm, (8-)12-16 cells wide across their bases. *Fronde*s to 5 cm, erect (Fig. 21E), glabrous, often with the distal lobes and tips of the pinnae conduplicate, covering their lower parts and parts of the proximally subsequent pinnae (Fig. 23B), especially when dried. *Petioles* short (10-20 mm, 0.4-0.6 mm diam.), alate throughout, glabrescent with few hyaline to brown, often flaccid hairs or glabrous (except for glandular hairs). *Pinnae* (= segments) as long as broad, or nearly so, glabrous, often imbricate (Fig. 21F). *Sori* glabrous or rarely some sori each with one short hair 0.5-0.8 mm long, hidden among sporangia.

**Distribution and habitat.** In open páramos or comparable vegetation, directly on soil or rocks, at 2400-4550 m in Mexico, Costa Rica, Jamaica, Venezuela, Colombia, Ecuador, Peru, SE Brazil (Mt. Itatiaya), and Bolivia; nearly matching the distribution of *M. moniliformis* var. *moniliformis* (Fig. 23A).

**Selected specimens examined. MEXICO. Oaxaca:** Sierra de San Felipe, 10500 ft, 13 Dec 1895, *Pringle 6194* (B, GOET, UC). Veracruz: Pico de Orizaba, Sep, *Liebmann s.n.* (P).

**COSTA RICA. San José:** direct line from Hotel La Georgina to Cerro Frío of the Cerro Buena Vista complex (Cerro de la Muerte), area with television and radio towers, 09°33-34'N, 83°43-46'W, 3100-3400 m, 20 Sep 1983, *Davidse G. 25039* (UC).

**JAMAICA.** Blue Mountain Peak, 7429 ft, 11-12 Feb 1913, *Underwood 1470* (P).

**VENEZUELA. Trujillo:** Dtto. Carache, Via Páramo Cendé sitio denominado "Las Cruces," 09°33'N, 70°08'W, 27 Nov 1987, *Rivero & Diaz 1497* (UC). **Amazonas:** Dept.

Atabapo, Cerro Marahuaca, summit of SE corner, 03°37'N, 65°21'W, 2700 m, 12 Oct 1988, *Liesner 24698* (UC).

**COLOMBIA. Boyacá:** Cordillera Oriental, vertiente oriental, carretera Sogamoso a Pajarito, valle del Río Cusiana, 3100 m, 20 Oct 1967, *Jaramillo Mejia et al. 3730* (COL); Sierra Nevada de Cocuy, lado S, valle de Lagunillas, lado S del campamento la Plaza, 4500 m, 25 Jan 1959, *van der Hammen 1343* (COL). **Caldas:** Nevado del Ruiz, Arenales 2 km al SW del refugio con muchos afloramientos de roca volcanica, 4520 m, 18 Mar 1972, *Cleef 2446* (COL). **Cauca:** Cordillera Central, Parque Nacional Puracé, camino de Pilimbalá al volcán del Puracé, 3700 m, 19 Jul 1976, *Jaramillo Mejia & van der Hammen, 5217* (COL); Puracé, Volcán Puracé, 3850-4500 m, 05 Oct 1984, *Lozano G. et al. 4587* (COL). **Cundinamarca,** Chingaza, Páramo Chiongaza, Telecom, 04°40'46"N, 72°12'14"W, 3650 m, 07 Jan 2000, *Acosta 22* (COL). Cundinamarca, La Galera, Páramo de Palacio, , 3000-3500 m, 11 Oct 1961, *Murillo M.T. 378* (COL.). **Huila-Cauca:** Macizo Colombiano, páramo Las papas, cerros y alrededores de la laguna La Magdalena, 3530 m, 16 Oct 1958, Idrobo, Pinto & Bishler, 3288 (COL); Macizo Colombiano, páramo Las papas, cerros y alrededores de la laguna La Magdalena., 3530 m, 16 Oct 1958, Idrobo et al. 3343 (COL). **Magdalena:** Sierra Nevada de Santa Marta. 0.5 km N of Laguna Chubdula near a small lake, [ca. 10 °55'N, ca. 73°53'W,] 3600 m, 01 Aug 1972, *Kirkbride jr. & Forero 1821* (COL). **Meta:** Páramo de Sumapaz, hoyo de la quebrada Sitiales. Filo Sitiales entre las Lagunas La Guitarra y la Primavera., 4040 m, 26 Jan 1972, *Cleef 1168-A* (COL). Risaralda, Pereira, Alrededores de la Laguna Otun, 4000-4300 m, 04 Feb 1980, *Díaz-P. et al. 1771* (COL). **Santander:** Santa Barbara, 3300 m, 04 Nov 1997, *Bustos-P. 141* (COL.). **Valle del Cauca:** Laguna, alto de Farallones, 3600-3800 m, 25 Feb 1979, *Downey 101* (COL).

**PERU. Amazonas:** Chachapoyas, Carretera Leymebamba-Balsas, Km 14-18, 06°43.1'S, 77°51.1'W, 07 Aug 2002, *Lehnert 250, 256* (GOET, UC, USM). **Apurimac:** Abancay, Cerro Ampay; señal "Ruta Laguna Uspaq'ocha/R Ccorhuani", 13°35.48'S, 72°52.82'W, 3300 m, 02 Sep 2002, *Lehnert 348* (GOET, UC, USM). **Cajamarca:** ca. Km 35 camino de Cajamarca hacia Hualgayóc (Bambamarca), 06°57'S, 78°35'W, 3540 m, 12 Feb 1984, *Cowan & Canne 4463* (USM); Cumbre El Gavilan, entre Cajamarca y San Juan, 3200 m, 17 Aug 1952, *Ferreyra 8585* (USM). **Cuzco:** Urubamba, Abra Malaga, 4300 m, 16 Oct 2002, *Lehnert 418* (GOET, UC, USM). **Huanuco:** Huanuco, Huanuco-Tingo Maria, 09°44.02'S, 76°05.55'W, 23 Aug 2002, *Lehnert 289* (GOET, UC, USM). **La Libertad:** Pataz, Parcela en area no quemada en Manachaqui, Parque Nacional Río Abiseo, 3650 m , 23 Mar 1988, *León & Young 1711* (USM). **Pasco:** Oxapampa, Trail to summit of Cordillera

Yanachaga via Río San Daniel, 10°23'S, 75°27'W, 12 Jul 1984, *Smith D. N. 7750* (USM).

**Puno:** Sandia, Entre Sandia y Cuyocuyo, 3100-3300 m, 17 May 1966, *Ferreyra 16812* (USM). **San Martín:** Mariscal Caceres, Río Abiseo National Park, 3650 m, 14 Mar 1988, *León & Young 1682* (USM); Mariscal Caceres, Chochos. NW corner of Río Abiseo Nat. Park, 07°XX'S, 77°XX'W, 3400 m, 13 Jul 1987, *Young & León 4542* (USM).

**BRAZIL. Rio de Janeiro:** Serra do Itatiaia, 2400 m, July 1913, *Brade & Tamandaré 6468* (AAU); Serra Itatiaia, Dec 1896, *Ule 675* (US).

**BOLIVIA. La Paz:** Prov. Nor Yungas, trench to Valle Coscapa, Parque Nacional Cotapata, 16°12'S, 67°53'W, 3450 m, 09 Sep 1997, *Kessler et al. 11730* (UC, LPB); Unduavi, Valle de Coscapa, 16° 17'S, 67° 51'W, 3500 m, 02 Oct 2002, *Lehnert 407* (GOET, UC, LPB); Prov. Murillo, Valle de Zongo, hydroelectric plant Zongo, 16°06'S, 68°07'W, 3600 m, 07 May 1995, *González & Meneses 814* (UC, LPB).

Easily confused with Andean *Melpomene peruviana* (scales of the same size but darker, sori and fertile portions always with some hairs 1-2 mm long, petioles persistently hairy). The var. *minor* occurs throughout the range of the var. *moniliformis* and is formed by small terrestrial plants from open places; there are many transitions between the two varieties.

**15c. *Melpomene moniliformis* var. *adnata*** (Kunze) Lehnert, comb. et stat. nov. *Jamesonia adnata* Kunze, *Farrnkräuter* 2: 80, t. 133, fig. 1. 1851. Type. Colombia. Dept. Tolima, Prov. Mariquita, Tolima, 13200 ft, Feb 1843, *Linden 1006* (holotype, LZ destroyed; isotypes, B, FI n.v., P). Figs. 22C, D, 23B,

Etymology: Refers to the adnate pinnae contrary to those of *Jamesonia* species, to which genus it was first erroneously assigned.

*Plants* medium sized, terrestrial or epiphytic. *Rhizomes* horizontal (Fig. 22A), moderately creeping, (1.2-)1.5-2.0 mm diam. *Fronde*s to 25 cm, stiffly erect (Fig. 22A), moderately spaced. *Scales* to 5.0 x 1.5 mm, 20-28 cell wide across their bases (Fig. 22C), dark brown, weakly iridescent, with palmately arranged apical glandular hairs (Fig. 22D). *Petioles* 45-60 mm, 0.8 mm diam., alate or marginate throughout, glabrous, young ones with ephemeral hairs. *Laminae* to 160 x 15 mm (Fig. 23A), pinnae to 5.0-6.0(-7.0) x 2.5-3.0(-3.5) mm (1.5-2.0 times longer than wide) (Fig. 23B), in dried specimens longitudinally folded or revolute.

*Sori* 4-6 pairs per pinna, glabrous (Fig. 23B) or rarely with 1-2 short (max. 1 mm long) hairs hidden in sori.

**Distribution and habitat.** In páramos, elfin forests, and montane forests at 1900-4400 m in Mexico, Guatemala, Costa Rica, Venezuela, Colombia, Ecuador, and Peru.

**Selected specimens examined. MEXICO. Oaxaca:** Sierra Madre Oriental, ca. 2 mi N of Cerro Pelón, 3000 m, 30 Aug 1975, *Webster et al.* 20285 (UC); Dtto. Central, N slope of Cerro San Felipe, 2400-2600 m, 13 Oct 1969, *Mickel & Hellwig* 4041 (UC).

**GUATEMALA. Sololá/Totonicapán:** 5-10 km W of Los Encuentros, Cerro María Tecum, Sierra Madre Mountains, 2900-3100 m, 24 Dec 1972, *Williams et al.* 41754 (UC).

**COSTA RICA. Cartago:** Km 89 Rt. 2 to páramo de la Muerte and San Isidro, 09°35'N, 83°42'W, 3300 m, 30 Oct 1993, *Rivero R.* 2487, 2489, 2501 (UC). **Limón:** Cordillera de Talamanca, SE foot of Cerro Kámuk, 09°16'N, 83°02'30"W, 3200-3350 m, 24 Mar 1984, *Davidse et al.* 25940 (AAU, UC). **Puntarenas/Bocas del Toro,** Cordillera de Talamanca, Cerro Echandi, on the international border, 09°02'N, 82°49'W, 3050-3160 m, 22 Aug 1983, *Davidse et al.* 23917 (UC). **San José:** Canton de Dota, Cordillera de Talamanca, Jaboncillo de Dota, camino a San Gerardo de Dota, 09°36'15"N, 83°47'20"W, 2400-3000 m, 15 Jul 1996, *Rojas A. et al.* 2692 (UC); Cerro de la Muerte, páramo Buena Vista; 1-3 km S of Interamerican Highway, 3350 m, 09 Aug 1967, *Bishop* 871 (UC); road from Cartago to San Isidro del General (Pan American Highway, Rt. 2), Km 72-73, or 21-22 km SE of Empalme, 2800 m, 30 Jan 1986, *Smith A. R. & Béliz* 2072 (UC).

**PANAMA. Chiriquí:** Volcán Baru, on road to towers at top, near towers at summit, 08°47'N, 82°32'W, 3300-3400 m, 13 May 1990, *McPherson* 15058 (UC).

**VENEZUELA. Mérida:** Dtto. Rangel, Laguna de Mucubají, Km 3 on road from Apartaderos to Santo Domingo, property of the Universidad de Los Andes, Parque Nacional Sierra Nevada, 08°48'N, 70°49'W, 3600 m, 22 Nov 1982, *Smith A. R. et al.* 1503 (UC); Parque Nacional Sierra Nevada, mostly along the trail Laguna Mucubají-Laguna Negra-Laguna Los Patos, 3500-4000 m, 04 Nov 1992, *Meier W. et al.* 3016 (UC); Laguna Negra (S of Eagle Peak), 3400 m, 28 Dec 1986, *Fay A.* 1622 (UC). **Trujillo:** mountains and páramo of Guaramacal, 09°12'N, 70°09'W, 2500-3000 m, 01 May 1985, *Ortega F.* 2661 (UC); Páramo de Guaramacal, 2500-3000 m, 03 Feb 1987, *van der Werff et al.* 8825 (UC).

**COLOMBIA. Caldas:** Cordillera Central, vertiente occidental, páramos del Nevado del Ruiz, 3900-4200 m, 05 May 1940, *Cuatrecasas* 9278 (COL). **Huila:** Cordillera Central,

Cordillera del Buey (west slope). From Finca Loyola above Valencia to páramo de Las Papas, 13 Dec 1975, *Bishop 1958* (UC). **Huila-Cauca:** Macizo Colombiano, páramo Las papas, cerros y alrededores de la laguna La Magdalena, 3530 m, 16 Oct 1958, *Idrobo et al. 13154* (COL); Macizo Colombiano, páramo Las Papas, cerros y alrededores de la laguna La Magdalena, 3530 m, 16 Oct 1958, *Idrobo et al. 3151* (COL).

**ECUADOR. Azuay:** Road Cuenca-Sayausí-Molleturo, hosteria Dos Chorreras 22.2 km, 02°46'46"S, 79°10'30"W, 3400-3420 m, 06 Jan 2000, *Jørgensen et al. 1652* (UC). **Bolivar/Chimborazo:** Volcan Chimborazo, W side of mountain, gully which crosses the road to the refuge in a hair-pin bend ca. 4 km from the road Ambato-Guaranda, 01°28'S, 78°48'W, 4400-4600 m, 14 Sep 1995, *Sklenar & Kostecokvar 1316* (QCA). **Carchi:** Carretera Tulcán-Maldonado, km 50 de Tulcán, 00° 49, 90'N, 77° 59, 00'W, 3800 m, 06 Jul 2002, *Lehnert 159* (GOET, UC, QCA); Páramo El Angel, in the pass on road El Angel-Tulcán, 00°41'N, 77°54'W, 3750-3850 m, 15 May 1973, *Holm-Nielsen et al. 5474* (AAU). **Chimborazo:** El Altar, N side of the volcano, on the ridge below the Canonigo peak, 01°41'S, 78°24'W, 4400 m, 19 Aug 1995, *Sklenar & Kostecokvar 92-3* (QCA). **Cotopaxi:** along Quevedo-Latacunga road, between Pilaló and Pujili, 00°59'S, 78°58'W, 3401 m, 26 Nov 2004, *Lehnert 1576* (GOET, UC, QCA); Parque Nacional Cotopaxi, quebrada un km antes de la entrada, 00°40'S, 78°30'W, 3500 m, 15 May 1982, *Quintana & Bastidas 103* (QCA). **Imbabura:** SW slopes of the volcano Cotacachi, 00°22'N, 78°21'W, 4100-4320 m, 09 Nov 1983, *Boysen et al. 45629* (AAU). **Napo:** Valle Vicioso E of Volcán Cotopaxi and N of Mt. Quilindaña, 00°45'S, 78°20'W, 3650 m, 22 May 1988, *Balslev et al. 69163* (AAU). **Pichincha:** Bosque Protector Pasococha, 30 km SE de Quito, 00°27'S, 78°28'W, 2850-3900 m, 23 Oct 1988, *Paz 92* (QCA); Canton Quito, 00°14'S, 78°48'W, 1900 m, 15 Jun 1991, *Fay & Fay 3120* (AAU, UC); Nevado Cayambe, ladera N, cerca Olmedo, 00°06.12'N, 77°59.95'W, 3800 m, 30 Jun 2002, *Lehnert 116* (GOET, UC, QCA); Páramo de Guamani., 00°15'S, 78°12'W, 3700 m, 07 Oct 1987, *Ramsey & Merrow-Smith 1154* (AAU). **Tungurahua:** Santiago de Pillaro, Parque Nacional Llanganetes, SW ridge of Cerro Hermoso, 01°13'50"S, 78°17'25"W, 4050 m, 14 Nov 1999, *Neill et al. 12091* (UC); Tungurahua volcano, 01°26'S, 78°27'W, 4000 m, 18-19 Nov 1983, *Korning & Thomsen 47345* (AAU).

**PERU. La Libertad:** Bolivar, Las Quinuas, 3350 m, 02 Jun 1960, *López & Sagástegui-A. 3347* (UC). **Lima:** near Antaicocha, Cerro Colorado, E of Canta, 4000-4100 m, 20 Jun 1925, *Pennell 14692* (NY). **Piura:** Huancabamba, above Canchaque on road to Huancabamba, below summit, [ca. 05°20'S, ca. 79°20'W,] 3000 m, 10 Oct 1957, *Hutchison 1638* (UC).

This variety appears like a stout *Melpomene flabelliformis* but is different in its glabrous sori and fertile portions (*vs.* usually with hairs to 1.5-2 mm long in fertile parts in sori and on rhachises in *M. flabelliformis*); it also differs by its more coriaceous laminae with truncate bases (*vs.* firm chartaceous laminae with cunetae bases in *M. flabelliformis*) and the continuous alae or margins on the petioles (*vs.* weakly decurrently marginate).

This variety may have derived from populations of var. *minor*, which tend to be equally glabrous but have much smaller pinnae and scales.

**15d. *Melpomene moniliformis* var. *tepuiensis*** Lehnert, var. nov. Type. Venezuela. Bolívar: Ilu-tepui, lower plateau, 2500 m, 05°25'36"N, 60°29'W, 16 Apr 1988, *Liesner 23404* (holotype, UC; isotype, MO). Figs. 22 H, 23 B.

A *Melpomene moniliforme* var. *moniliforme* frondibus longioribus segmentis parum ascendentibus squamibusque amplioribus (supra basin 24-26 celulis *vs.* 14-18(-20) celulis), a var. *paradoxa* rhizomatibus crassioribus (1.5 mm *vs.* 0.8-1.2 mm diametro) pinnis longioribus (4.0-8.0 x 3.0-4.2 mm *vs.* 4.5 x 4.0 mm) praestans.

Etymology: The name refers to the tepuis of Venezuela.

*Plants* medium to large, epiphytic. *Rhizomes* horizontal, short- to moderately long-creeping (Fig. 22H), to 1.5 mm diam. *Fronde*s to 200-300 mm, erect to ascending, straight (Fig. 22H), placed 3-10 mm apart (Fig. 22H). *Scales* dark brown, strongly iridescent, relatively large with 4.0-5.0 x 1.0-1.2 mm and 24-26 cells across their bases. *Petioles* to 40-80 mm, 0.8 mm diam., marginate to almost terete, sparsely hairy to glabrescent, hairs 0.5-0.8 mm long. *Laminae* 180-200 x 5-15 mm, proximally cuneate to weakly decurrent; pinnae 4.0-8.0 x 3.0-4.2 mm, 1-2 times as long as broad, patent to weakly ascending (80-70°), obtuse to weakly truncate, glabrous except for 4-8 hairs clustered in sori (0.6-1.0 mm long).

**Distribution and habitat.** In shrubs and low forest in boggy areas of tepui plateaus at 2500-2550 m. Endemic to tepuis (Ilu-tepui and Kukenan Tepui) in Venezuela (Fig. 23B).

**Additional specimens examined. VENEZUELA. Bolívar:** Kukenan tepui, summit, 2550 m, 05°13'N, 60°18'W, 12 Apr 1988, *Liesner 23170* (UC, MO).

This variety is similar to var. *paradoxa*, but sometimes has longer segments and fewer hairs in the sori. The var. *tepuiensis* is restricted to Venezuelan tepuis while var. *paradoxa* occurs in the central Andes.

*Melpomene moniliformis* var. *tepuiensis* resembles *Melpomene deltata* in habit (Fig. 9A) and segment shape (Fig. 9B); however, *M. deltata* is completely glabrous (vs. some hairs in sori and on the petioles in *M. moniliformis* var. *tepuiensis*) and never has truncate segment tips (vs. segments tips sometimes truncate). Contrary to other varieties of *M. moniliformis*, *M. flabelliformis* grows together with *M. moniliformis* var. *tepuiensis* and may be mistaken for it because both are equal in size of fronds and scales. In general, the differences from this variety are the same as from *M. moniliformis*, i.e., presence of hairs between the sori and on rhachises of fertile parts, with the hairs longer than in *M. moniliformis*. In direct comparison, var. *tepuiensis* has also stronger ascending pinnae, shorter petioles and more closely placed fronds than *M. flabelliformis*.

**15e. *Melpomene moniliformis* var. *paradoxa*** Lehnert, var. nov. Type. Bolivia. La Paz: Prov. Nor Yungas, trocha al Valle Coscapa, Parque Nacional Cotapata, 16°12'S, 67°53'W, 3450 m, 09 Sep 1997, *Kessler et al. 11717* (holotype, LPB; isotypes, GOET, UC). Figs. 22E, F, 23B.

A *Melpomene moniliforme* var. *moniliforme* squamis maioribus (supra basin cum 14-20 celulas vs. 20-32 celulas), a var. *adnata* pilis in soris creberioribus segmentisque parce longioribus quam amplis (vs. segmentis usque bis longioribus quam amplis) differt.

Etymology: Named for its puzzling morphology, which is intermediate between *M. flabelliformis* and *M. moniliformis* (see discussion).

*Plants* large, epiphytic in moss cushions. *Rhizomes* horizontal, long creeping (Fig. 22E), (0.6-)0.8-1.2 mm diam. *Fronde*s to 270-320 mm, spaced well apart (5-10 mm), generally arching (Fig. 22E). *Scales* dark brown to brown, iridescent, medium sized with 3.5-4.0(-8.0) x 1.0-1.6 mm and (20-)22-28(-32) cells across their bases (Fig. 22C). *Petioles* 20-60 mm long, 0.5-0.8



mm diam., weakly marginate to rarely alate, sparsely hairy with hairs to 1.2 mm long. *Laminae* narrow, glabrous except for the sori. *Pinnae* 4.5 x 4.0 mm (only as long as broad), patent, obtuse to rounded, the costae not visible or obscurely so (Fig. 22F); proximal pinna pairs often gradually reduced to alae. *Sori* single or 2(-3) pairs per pinna, with 5-10 hairs 0.8-1.2 mm long (Fig. 22F).

**Distribution and habitat.** Elfin forests and wet montane forests at 2800-3700 m in Peru and Bolivia (Fig. 23B).

**Selected specimens examined. PERU. Ayacucho:** Codorconca, 12 Oct 1964, *Barrón s.n.* (USM). **Cuzco:** Prov. Urubamba, between San Luis and Abra Malaga, Km 154, 13°05.4'S, 72°22.2'W, 3300 m, 16 Oct 2002, *Lehnert 439* (GOET, UC, USM); Machu Picchu, 4 km from the Runucuray-Sayacmarca pass in the Inca trail, above the lake between Sayacmarca and the pass (vegetation plot 166), 3665 m, 23 Aug 1982, *Peyton & Tilney Peyton 1570* (UC).

**BOLIVIA. Cochabamba:** Prov. Carrasco, Colomi, along road, 62.2 km from Cochabamba (Río Rocha), 17.1284°S, 65.5321°W, 3100 m, 30 Dec 1998, *de Boer 1156* (LPB); 108 km antigua carretera Cochabamba-Villa Tunari, 17°09'S, 65°38'W, 2950 m, 22 Jun 1996, *Kessler 6569* (LPB, UC); 94 km on old road Cochabamba-Villa Tunari, 17°12'S, 65°41'W, 3500 m, 28 Jun 1996, *Kessler et al. 6773* (GOET, LPB); road Cochabamba-Villa Tunari; below Corani, near Km 71+00, trail up the mountain, 17°10.59'S, 65°53.67'W, 2800 m, 27 Nov 2002, *Lehnert 525* (LPB), **La Paz:** Prov. Nor Yungas, Unduavi, 3300 m, Nov 1910, *Buchtien 70* (P); roadside bank between Cotapata and Chuspipata, S-facing, La Paz-Caranavi road, 16°17'S, 67°50'W, 3200 m, 15 Aug 1990, *Fay & Fay 3034* (LPB, MO); trench to the Valle Coscapa, Parque Nacional Cotapata, 16°12'S, 67°53'W, 3450 m, 09 Sep 1997, *Kessler et al. 11717* (LPB, UC); Unduavi, trench to the Valle de Coscapa, 3400 m, 17 Dec 2002, *Lehnert 536, 539, 542* (GOET, LPB, UC); 1 km W of Chuspipata., 16°17'S, 67°49'W, 3140 m, 24 Mar 1982, *Solomon 7260* (LPB, UC); Prov. Bautista Saavedra, Charazani, E of Chullina, 3500 m, 22 Dec 1993, *Herzog H87* (LPB).

This variety matches *M. flabelliformis* in the rhizome and scale size, but is closer to *M. moniliformis* regarding the scale color, laminar shape, and hair distribution. It could be of hybrid origin, but apart from the intermediate morphology there is no evidence for this. *Melpomene flagellata* differs in having longer hairs (1.2-1.8 mm) and densely hairy petioles;

it also has most of the pinna tips truncate (vs. always obtuse or rounded in *M. moniliformis* var. *paradoxa*). *Melpomene caput-gorgonis* has shorter petioles, often wider, elliptical laminae (vs. laminae linear in *M. moniliformis* var. *paradoxa*), and conspicuously multiple glands at the scale tips (vs. only a single branched glandular hair). It is possible that all of these species represent different recombinations of a hybrid swarm but until now we lack evidence for this hypothesis. However, it is noteworthy that a putative hybrid between *M. personata* and *M. erecta* (which see) was found in the same area where all of these questionably species and varieties occur.

**15f. *Melpomene moniliformis* var. *subdicarpon*** (Fée) Lehnert, comb. et stat. nov.  
*Polypodium subdicarpon* Fée, Crypt. Vasc. Brésil 2: 55, t. 96, fig. 4. 1874. Type. Brazil.  
*Glaziou 4410* (holotype, P; isotype, B). Figs. 22G, 23B.

*Plants* epiphytic, growing in moss layers, rock crevices or open soil. *Rhizomes* moderately to short-creeping (Fig. 22G), 0.8-1.2 mm diam. *Fronds* erect, inserted onto the rhizomes at right angles, closely placed (2-4 mm). *Scales* 4.0-4.5 x 0.8-1.0 mm, (10-)14-18(-20) cells wide at their bases, clathrate, dark brown to brown, weakly iridescent, cordate to pseudopeltate, acute to attenuate at tips; apical glands 3-8 cells, in nodding clusters or palmately arranged. *Petioles* 20-45 mm long, 0.6 mm thick, decurrently alate to marginate throughout, densely hairy to glabrescent, with short, dark brown, acicular hairs 0.5-1.0 mm long; simple and branched glandular hairs of crosiers and young fronds may persist in older fronds. *Laminae* 120-210 x 8-12 mm, linear to narrow elliptic (widest in the middle), decurrent at bases, long-acute at tips. *Rhachises* dark brown to black, planar and slightly sunken adaxially, hemispherically protruding abaxially, with some scattered hairs near the base. *Pinnae* 6.0 x 3.4-4.0 mm (1.5-2.0 times as long as broad), weakly ascending, equilateral at base or weakly decurrent towards the base, fully adnate, oblong to broadly deltate, the tips obtuse to rounded; costae not visible; hairs absent except in the sori, rarely single hairs on the abaxial laminae; 1-3 proximal pinna pairs markedly smaller than the subsequent segments, sometimes alariform; hydathodes present, slightly sunken in tissue. *Sori* 2-4 pairs per segment, without or with 1-5(-10) short hairs 0.5-1.0 mm long.

**Distribution and habitat.** In Mata Atlântica at 1800-2460 m, endemic to Brazil (Fig. 24B).

**Selected specimens examined. BRAZIL. Espírito Santo:** SE slope of Serra da Caparaó, 1550-2460 m, 30 Nov 1929, *Mexia* 4061 (UC). **Minas Gerais:** Serra do Papagai, Nov 1897, *Atihuria* 2614 (P). **Paraná:** Itataia, subida ao Planalto, E rio, 2000 m, 26 Jan 1975, *Hatschbach et al.* 35844 (UC). **Rio de Janeiro:** Serra do Itatiaya, 2200 m, Oct 1903, *Dusén* 2131 (P). **Santa Catarina:** 2000 m, *Ule s.n.* (P). **São Paulo:** Campos do Jordão, estrada por Pindamoangaba, 1800 m, 28 Jun 1998, *Labiak* 659 (SP); estação Campo Grande, Sep 1896, *Loefgren s.n.* (SP 21926).

This Brazilian variety of *Melpomene moniliformis* differs from the nominate variety in longer, slightly ascending pinnae and usually hairier petioles. The general distribution of hairs and scale size, however, are the same and separates var. *subdicarpon* from *M. flabelliformis*: hairs are absent between the sori and the scales are 14-18 cells wide across their bases in var. *subdicarpon*, whereas hairs may be present between the sori in *M. flabelliformis*, whose scales are 20-30 cells wide across their bases. Brazilian *M. flabelliformis* tend to have rather few hairs on petioles and laminae, and may appear glabrous at first sight; var. *subdicarpon* is usually quite hairy on petioles what can often be seen with the unaided eye. The hairy petioles are reminiscent of *M. flagellata* from Bolivia; this species has longer hairs in the sori (1.2-1.8 mm vs. 0.5-1.0 mm in var. *subdicarpon*) and at least some of the generally shorter pinnae with a truncate tips (vs. always rounded to obtuse tips).

**16. *Melpomene occidentalis*** Lehnert, sp. nov. Type. Ecuador. Zamora-Chinchipe: New road Loja-Zamora, ca. 4 km E of pass "El Tiro," ridge from white cross on left road side (towards the valley), 03°59'S, 79°08'W, 2550 m, 25 Sep 2004, *Lehnert* 1343 (holotype, QCA; isotypes, GOET, UC). Figs. 7C, 24.

A *Melpomene firma* in petiolis teretibus glabribus vel glabrescentibus (vs. valde marginatis adaxialiter pilosis), pinnis numquam deflexis (vs. basalibus deflexis), squamis latioribusque (0.8-1.6 vs. 0.4-0.6 mm) differt.

Etymology: The name refers to the western centered distribution of the species in South America compared to the similar *M. firma*, which extends E to the Guyana Highlands and central Bolivia.

*Plants* predominately epiphytic, rarely saxicolous or terrestrial; growing in moss layers. *Rhizomes* moderately to short-creeping, ascending to erect (Fig. 24A, B), (0.8-)1.2-1.8(-2.2) mm diam. *Fronds* to 220-280 mm long, erect (Fig. 24A), planar or weakly arching, inserted onto the rhizomes at an acute angle, closely placed (1-3(-5) mm apart) (Fig. 24A). *Scales* 6.0-9.0 x 0.8-1.6 mm, (18-)20-26 cells wide, clathrate, dark brown to brown, iridescent, cordate at bases, acute to attenuate at tips; margins with small hyaline retrorse papillae 1-3 cells long; apical glands 3-8 cells, in a linear arrangement or nodding cluster. *Petioles* (25-)30-95(-140) mm long, 0.8-1.0 mm thick, terete (Fig. 24C) to weakly marginate throughout, glabrous; simple and branched glandular hairs of crosiers and young fronds sometimes persistent in older fronds. *Laminae* (110-)145-220(-330) x (22-)30-45(-80) mm, lanceolate or broadly elliptic (broadest in the middle), acute to attenuate at tip; bases rounded to cuneate (Fig. 24A, B). *Rhachises* dark brown to black, planar to weakly protruding adaxially, hemispherically protruding abaxially, with few to many short, brown, acicular hairs to 0.2-0.8 mm long on both sides, usually adaxially hairier than abaxially (Fig. 24D, E). *Pinnae* (8-)16-20(-42) x (1.5-)1.8-2.2(-4.4) mm (5-8 times as long as wide) (Fig. 24D), patent or weakly ascending (90-75°) (Fig. 24A, B), fully adnate, inequilateral at bases, weakly surcurrent towards the blade apices (Fig. 24D, E), linear-oblong to long deltate, tips obtuse; margins entire (Fig. 24D) or dentate proximally in large segments; costae visible on both sides of the segments (Fig. 24D, E); proximal pinnae pairs smaller than the central segments, but not alariform, not remote, or if remote then connected by a thin strand of laminar tissue; stomata sometimes visible as dark brown to reddish dots; margins sometimes with ephemeral glandular hairs or cells; hydathodes conspicuous (Fig. 24D, E). *Sori* 5-12(-15) pairs per segment, with 4-10 stiff, short, dark castaneous hairs 0.4-0.8 mm long mostly around them.

**Distribution and habitat.** Moist montane forests at 2100-3400 m in Venezuela, Colombia and Ecuador (Fig. 7C).

**Specimens examined. VENEZUELA. Tachirá:** Páramo Tarmá, near the Colombian-Venezuelan border, 2475-2550 m, 20-23 May 1967, *Steyermark et al.* 98600 (NY). **Prov. unknown:** [Mérida?] Manzanos, 2800 m, *Lindig* 300 (B, P).

**COLOMBIA. Antioquia:** San José de la Montaña, Alto El Cristo, 06°46'53"N, 75°41'45"W, 3420 m, 23 Jul 2002, *Rodriguez W. et al.* 3513 (COL). **Huila:** Cordillera Central, Cordillera del Buey, hike from Finca Loyola over the páramo down to San Antonio,

2100 m, 14 Dec 1975, *Bishop 1993* (UC). **Nariño:** La Botana (Pasto region), 2900 m, 29 Oct 1972, *Hagemann & Leist 1306* (COL).

**ECUADOR. Cotopaxi:** Quevedo-Latacunga road, above Pilaló, 00°58'S, 78°58'W, 2850 m, 08 Apr 1973, *Holm-Nielsen et al. 3251* (UC); along Quevedo-Latacunga road, between Pilaló and Pujili, 00°59'S, 78°58'W, 3400 m, 26 Nov 2004, *Lehnert 1575* (GOET, QCA, UC). **Loja:** E of Nudo de Cajanuma, just N of "Centro de Información," sample plot site, 04°05'S, 79°10'W, 2900 m, 20 Sep 1989, *Bøgh 47959* (AAU); Parque Nacional Podocarpus, above Nudo de Cajanuma around "Centro de Información," 04°05'S, 79°10'W, 2800-3000 m, 16 Nov 1989, *Bøgh 86609* (AAU); Cajanuma, SE of Loja, 04°07'S, 79°10'W, 2750 m, 03 Nov 2004, *Lehnert 1507* (GOET, QCA, UC); Cerro Toledo, E of Yangana, between Loja and Valladolid, 04°23'S, 79°07'W, 3000-3100 m, 26 Oct 2004, *Lehnert 1464a* (GOET, QCA, UC), **Loja/Zamora-Chinchipe:** limit of Parque Nacional Podocarpus, around pass on road Loja-Zamora, 03°58'S, 79°07'W, 2900 m, 08 Jan 1989, *Madsen 85474* (AAU). **Morona-Santiago:** E of pass on Gualaceo-Limon road, 03°00.27'S, 78°39.10'W, 3000-3200 m, 16 Nov 2004, *Lehnert 1558a* (GOET, QCA, UC). **Napo:** Cartagena, km 25 from El Carmelo on road towards La Bonita, 00°37'N, 77°30'W, 2800 m, 13 Apr 1979, *Løjtnant et al. 12334* (AAU); outskirts of Pifo, 2500 m, 08 May 1935, *Mexia 7353a* (UC). **Pichincha:** carretera Quito-Santo Domingo, 2500 m, 24 May 1987, *van der Werff & Palacios 9600* (MO, UC). **Zamora-Chinchipe:** new road Loja - Zamora, ca. 4 km E of pass "El Tiro," 03°59'S, 79°08'W, 2650 m, 23 Sep 2004, *Lehnert 1332* (GOET, QCA, UC); Estación Científica San Francisco, above refuge, along trail "Antennenbergweg," just below junction with trail T1, study plot A 5, 03°59'36.4"S, 79°04'03.2"W, 2660 m, 26 Sep 2003, *Lehnert 909a* (GOET, QCA, UC).

The main differences of this species to *Melpomene firma* are the completely glabrous petioles (vs. persistently hairy adaxially, or rarely glabrescent, in *M. firma*), and the patent to ascending pinnae (vs. patent to deflexed). Colombian plants may have sinuses wider than the pinna width (*Hagemann 1306*, COL), but contrary to the remote pinnae of *M. firma* they are still connected by thin strands of laminar tissue. Plants from northern Ecuador have more deltate pinnae and may be confused with species of the *M. pilosissima* or *M. personata* complexes. Those species differ in lacking marginal glands on the scales and having the costae partly to completely hidden in the laminar tissue. The *M. pilosissima* alliance is also hairier, with the hairs longer (to 3 mm) and often occurring on the pinnae margins or the

adaxial laminar surfaces. The species allied to *M. personata* differ in their generally prostrate rhizomes and the adaxially not visible costae.

**17. *Melpomene personata*** Lehnert, sp. nov. Type. Bolivia. La Paz: Prov. Bautista Saavedra, 15 km de Charazani hacia Chullina, 15°10'S, 68°53'W, 3400 m, 05 Jul 1996, *Kessler 10606* (holotype, UC; isotypes, GOET, LPB). Figs. 25, 26B.

A *Melpomene pilosissima* rhizomatibus longioribus horizontaliter reptantibus pilisque in soris confertis (vs. rhizomatibus brevibus erectis, pilis aequaliter distributis in pagina abaxiale), a *M. youngii* et *M. albicante* in absentia cera alba in lamina abaxiale (vs. pagina abaxiale albe vel albicante) differt.

Etymology: The name alludes to the fact that the species has often been mistaken for *M. pilosissima* (lat. *personata* = masked, disguised), and also alludes to the genus name: Greek actors wore masks (lat. *persona*) to symbolize the different characters of the plays, including tragedies (*Melpomene* is the muse of tragedy).

*Plants* predominately epiphytic, rarely saxicolous, growing in moss layers. *Rhizomes* horizontal, moderately to long-creeping, 0.8-1.2(-1.5) mm diam. (Fig. 25A). *Fronds* stiffly pendent, inserted onto the rhizome at right angles, moderately to widely spaced (3-10 mm) (Fig. 25A). *Scales* (2.0-)3.0-4.5(-6.0) x (0.3-)0.4-1.0 mm, (8-)10-14(-22) cells wide across their bases, clathrate (Fig. 25B), dark brown to brown, iridescent, narrowly cordate, long acute to attenuate at tip; apical glands 1-3 cells linearly arranged (Andes) or 2-5 cells palmately arranged (Costa Rica, Guatemala). *Petioles* 20-150 mm long, 0.6(-0.8) mm thick, terete or weakly marginate near the lamina bases, with few to many (0.9-2.0 mm) dark brown acicular hairs (Fig. 25C); simple and branched glandular hairs of crosiers and young fronds sometimes persistent on older fronds. *Laminae* to 155-180(-220) x 26 (-40) mm (2/3 to 3/4 of frond length, rarely in single fronds less), broadly linear to narrow elliptic (broadest in the middle), bases cuneate to short tapering, apices long acute (Fig. 25A). *Rhachises* dark brown to black, planar and slightly sunken adaxially (Fig. 25E), hemispherically protruding abaxially (Fig. 25D, F); sparsely hairy on both sides (Fig. 25E), usually more hairs abaxially; hairs to 1.2 mm long, brown. *Pinnae* 8.0-15.0(-22.0) x 1.2-2.5(-3.5) mm (6-8 times as long as broad), ascending (70-60°) (Fig. 25A), equilateral at base or weakly decurrent towards the bases, fully

adnate, linear-oblong, the tip acute to obtuse; costae visible abaxially (e.g.; *Jiménez I. 1773*) (Fig. 25D), at least obscurely so (Fig. 25F); proximal 2-6 pinna pairs markedly smaller than the subsequent segments (Fig. 25A), lowest ones usually alariform; hairs few (Fig. 25F) to many on the costae, absent on margins and adaxial laminae; hydathodes present (Fig. 25E). *Sori* 2-10 pairs per segment, with 6-10 long setae (0.8-1.0 mm) (Fig. 25F).

**Distribution and habitat.** Shrubby páramos, elfin forests, and wet montane forests at 2700-4050 m in Mexico, Guatemala, Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, and Bolivia (Fig. 26B).

**Selected specimens examined. MEXICO. Chiapas:** San Cristobal Las Casas, E side of Zontehuitz near summit, 2800 m, 30 Nov 1971, *Breedlove 22928* (NY); Union Juárez, SE side of the summit of Volcán Tacaná, 3600 m, 03.03.1972, *Breedlove 24310* (NY); *ibid.*, 10 Nov 1972, *Breedlove 29353* (NY); Mount Tacana, 2000-4038 m, Aug 38, *Matuda 2379A* (NY); N of San Cristobal las Casas on top of Cerro Zontehuitz, 3100 m, 27 Jul 1963, *Mickel 1247B* (NY).

**GUATEMALA. Chimaltenango:** Cerro de Tecpám, region of Santa Elena, 2400-2700 m, 26.12.1938, *Standley 61075* (NY). **Guatemala:** Hyw. No. 1, 2900 m, 21 Feb 1947, *Brenckle 47-61* (UC). **Huehuetenango:** Limestone region 3-15 km N of Chemal, Sierra de los Cuchumatanes, 3400 m, 02 Dec 1962, *Molina-R. et al. 22138* (NY); Sierra Cuchumatanes between Km 136 to 150 to San Juan Ixcoy, 3000-3500 m, 12-23 Jan 1966, *Molina-R. et al. 16541* (NY). **Totonicapán:** Maria Tecún, 3000-3600 m, 12-23 Jan 1966, *Molina-R. et al. 16357* (NY).

**COSTA RICA. Cartago:** Cerro de la Muerte, 1 km NW of Villa Mills on Interamerican Highway, behind Hotel La Georgina, 2900 m, 08 Aug 1967, *Mickel 3203* (NY); Km 89 Rt. 2 to páramo de la Muerte and San Isidro, 09°35'N, 83°42'W, 3300 m, 30 Oct 1993, *Rivero 2488, 2494, 2495, 2497* (UC); Cantón de Paraíso, R.F. Río Macho, cuenca del Reventazón, carretera interamericana, road Cartago-San Isidro, cerro de la Muerte, 3150-3300 m, 09°34'30"N, 83°45'W, 21 Apr 1999, *Rojas A. 5082* (NY). **San José:** Cerro de la Muerte; 1 km NW of Villa Mills on the Interamerican Highway, cross from Hotel La Georgina, 2900 m, 08 Aug 1967, *Bishop 869* (UC); along Inter-American Highway, Cerro de la Muerte, 09°35'N, 83°45'W, 3220 m, 18 Nov 1986, *Hennipman et al. 7010* (UC); Cerro Sákira-páramo, 3300 m, Feb 2003, *Kluge 1182* (GOET); Massiv of Cerro de La Muerte, 3200 m, 15 Jul 2003, *Kluge 6841* (GOET); *ibid.*, 3300 m, 16 Jul 2003, *Kluge 6909, 6910* (GOET);

ibid., 3400 m, 17 Jul 2003, *Kluge 6946* (GOET); road from Cartago to San Isidro del General (Pan American Highway, Rt. 2), Km 96-97, ca. 1.5 km S of Villa Mills (near Siberia), 2900 m, 29 Jan 1986, *Smith A. R. & Béliz 2061* (UC).

**PANAMA. Chiriqui:** between Itamut and Bine Peaks, Fabrega massif, Bocas del Toro, 3200 m, 05-09 Mar 1984, *Gómez L. D. et al. 22539* (UC); Volcán Baru, on road to towers at top; near towers at summit, 08°47'N, 82°32'W, 3300-3400 m, 13 May 1990, *McPherson 15054* (UC).

**COLOMBIA. Antioquia:** Guatapé, Vereda Santa Rita, finca Montepinae, 1850 m, 06°15'N, 75°10'W, 06 Mar 1990, *Contreras & Echeverri 217* (NY). **Boyacá:** Sierra Nevada de Cocuy, on steep S side of the Valle del Corallitos, at lower edge of this near river, 4000 m, 09 Jun 1957, *Grubb & Guymer P102* (AAU); between Arcabuco and Villa de Leyva, trail Las Coloradas, above El Charizal, 3420 m, 31 Aug 1967, *Jaramillo Mejía et al. 3166* (AAU). **Cauca:** Cordillera Central, Parque Nacional de Puracé, trail from Pilimbalá to the volcano of Purace, 3700 m, 10 Jul 1976, *Jaramillo Mejía & van der Hammen 5219* (AAU). **Cundinamarca:** Laguna de Chisacá and surroundings, 3900-4200 m, 19 Oct 1958, *Bishler 1517* (COL); Fómeque, Parque Nacional Natural Chingaza, surroundings of laguna de Chingaza, E shore of Río Chuza, 2990 m, 05 Oct 1981, *Franco P. et al. 495* (AAU); Cogua, Vereda Quebrada Hóna, Reserva Forestal Protectora, 3200-3300 m, Aug-Oct. 2003, *Trujillo 13* (COL). **Santander:** Coromoro, laguna La Fiquera, quebrada de Coromoro, 3750 m, 29 Nov 1967, *Jaramillo Mejía & van der Hammen 4380* (AAU); road between Bucaramanga and Pamplona, W slope of Páramo de Berlin, El Picacho, 3300 m, 11 Nov 1969, *Murillo M. T. & Jaramillo Mejía 1342* (AAU). **Prov. unknown:** Excursion to the Llanos de San Martín, Toquiza area, *Stübel 704* (B).

**VENEZUELA. Mérida:** Dtto. Justo Briceño, Páramo Piedras Blancas, Laguna la Fea, SE de la Carretera Vía Piñago, 3950-4500 m, 09 Jul 1982, *Briceño et al. 635* (AAU); Dtto. Libertador, Parque Nacional Simón Bolívar, camino del teleférico (de la Aguada); Laguna La Fría; vertiente septentrional de la Sierra Nevada de Mérida, 2700-3000 m, 21 Dec 1984, *Pipoly et al. 6542* (UC); Dtto. Rangel, Las Escaleras-Laguna El Boquerón, páramo de Minugú, unos 10 km al SE de San Rafael de Mucuchíes, 3150-3400 m, 21 May 1972, *Ruiz-Teran 7314* (UC). **Trujillo:** Dtto. Carache, via Páramo Cendé sitio denominado "Las Cruces", 09°33'N, 70°08'W, 27 Nov 1987, *Rivero & Diaz W. 1495* (UC).

**ECUADOR. Azuay:** Recreation Park Cajas, 4000-4100 m, 02 Sep 1984, *Jaramillo J. 7198* (AAU); Cajas, N of Laguna Toreadora, 02°47.17'S, 79°13.10'W, 3850 m, 17 Nov 2003, *Lehnert 1116* (GOET, QCA, UC). **Carchi:** Montufar, within 3 km of pueblo of Colonia



Huaqueña, 00°35.5'N, 77°42'W, 3500 m, 30 Jun 1994, *Fay & Fay 4342* (AAU); base of Volcán Chiles, km 34-36 on road Tulcán-Maldonado, 3900-4050 m, 00°47'N, 77°57'W, 19 May 1973, *Holm-Nielsen et al. 5922* (AAU, UC); El Angel-Tulcán main road, Km 1, turnoff towards W, ca. 8 km, 00°34'N, 77°54'W, 3460 m, 08 Aug 1990, *Jørgensen et al. 92264* (AAU); road Tulcán-Maldonado, Km 32 de Tulcán, base del Volcan Chiles, *Lehnert 145, 146* (GOET, QCA, UC). **Chimborazo/Cañar:** W escarpment between Santa Rosa and Joyagshi, 2500-2700 m, 06-09 Jul 1945, *Camp 4076* (NY). **Imbabura:** Laguna Grande de Mojanda, 15 km S of Otavalo, 3750 m, 00°08'N, 78°16'W, 14 May 1985, *Eriksen 59365* (AAU); road Ibarra-Mariano Acosta, E of the pass, 00°20'N, 78°00'W, 3500-3600 m, 09 Aug 1976, *Øllgaard & Balslev 8585, 8579* (AAU).

**PERU. Cuzco:** Prov. Paucartambo, Pillahuata, near Tres Cruces, + 130 km from Cuzco to Pilcopata, 13°05'S, 71°30'W, 2000 m, 13 Dec 1986, *Núñez 7798* (CUZ, LPB); Achirani, Marcacocha, 3000 m, 30 Jul 1939, *Vargas C. 1573* (CUZ); Dtto. Marcacocha; near Achirani, 2600 m, 30 Jul 1939, *Vargas C. 11141* (CUZ, UC); Prov. Urubamba, Abra Malaga, 4330 m, 16 Oct 2002, *Lehnert 423* (GOET, UC, USM); Machupicchu, at 88 km and 112 km from Cuzco, Santuario Historico de Machupicchu and along Inca trail, in Qorihuayrachina, llulluchayoc, Ronkuraky, Phuqupatamarca, Wiñayhuayna and Intipunco, 13°09'10"S, 72°31'W, 4150 m, 14-22 Oct 1987, *Núñez & Arque 8339* (UC); Altura Colca, Valle de Lares, 9000 ft, Mar 1932, *Bües 1807* (CUZ). **Junin:** Prov. Satipo/La Convención, Cordillera Vilcabamba, Río Ene slope, near summit of divide, 3350-3400 m, 11°39'36'S, 73°40'02"W, *Boyle et al. 4326* (UC, USM); Prov. Tarma, high region of second Cordillera, valley of Marañoch near Tarma, 1840, *Philippi s.n.* (B, isosyntype of *Polypodium firmum* Klotzsch). **San Martin:** Mariscal Caceres, Chochos, NW corner of Río Abiseo National Park, 3500 m, 15 Jul 1987, *Young & León 4716* (USM).

**BOLIVIA. Cochabamba:** Prov. Ayopaya, 2 km al SE de Saila Pata, 16°55'S, 66°55'W, 3550 m, 15 Nov 1997, *Kessler et al. 12475* (GOET, LPB, UC); Prov. Carrasco, 100 km [on] old road Cochabamba-Villa Tunari, 17°12'S, 65°42'W, 3250 m, 26 Jun 1996, *Kessler 6728* (GOET, LPB, UC); 68 km old road Cochabamba-Villa Tunari, 17°14'S, 65°13'W, 3600 m, 11 Jul 1996, *Kessler et al. 7234* (GOET, LPB, UC); 63 km old road Cochabamba-Villa Tunari, 17°15'S, 65°43'W, 3750 m, 02 Jun 1996, *Kessler et al. 6887* (GOET, LPB); 115 km [on] old road Cochabamba-Villa Tunari, 17°07'S, 65°38'W, 2700 m, 01 Jul 1996, *Kessler et al. 6862* (GOET, LPB, UC); Prov. Chapare, ca. 8 km N Maycamayu, ca. 70 km from Sacaba, 17°12'S, 65°57'W, 3350 m, 12 Aug 1991, *Kessler 2919* (AAU, LPB). **La Paz:** Prov. Bautista Saavedra, 15 km de Charazani hacia Chullina, 15°10'S, 68°53'W, 3400 m, 05 Jul 1996,

*Kessler et al. 10606* (GOET, LPB, UC); Prov. Franz Tamayo, PN-ANMI Madidi, trail Pelechuco-Mojos, locality Tambo Quemado (camping site), going down along the trail, a little past the second river, 14°41'S, 68°58'W, 3470 m, 29 Apr 2003, *Jiménez I. 1773* (GOET, LPB, UC); Prov. Inquisivi, some 8 km from Quime towards Inquisivi, Camillaya arriba del pueblo, 16°58'S, 67°12'W, 3000 m, 29 Dec 1997, *Beck 24364* (LPB); Prov. Murillo, Arriba de la laguna de Viscachani al valle de Zongo, 16°13'S, 68°07'W, 4050 m, 10 Oct 1995, *Kessler et al. 5885* (AAU, LPB); Prov. Nor Yungas, Estación Biológica Tunquini, senda del Pantanón a Hornuni, 16°11'S, 67°53'W, 3350 m, 19 Sep 2000, *Bach et al. 1080* (GOET, LPB, UC); pasando Unduavi antes de llegar a Cotapata, subiendo la senda antigua hacia Coroico, 3500 m, 22 Oct 1994, *Beck & Ruthsatz 21492* (GOET, LPB, UC); Valle de Coscapa, 16°17'S, 67°51'W, 3400 m, 02 Oct 2002, *Lehnert 396, 398, 404, 405* (GOET, LPB, UC); *ibid.*, 17 Dec 2002, *Lehnert 535, 537, 538, 541* (GOET, LPB, UC); Prov. Sud Yungas, Unduavi, near the mine Lourdes, 16°18'S, 67°52'W, 3450 m, 25 Nov 1995, *Gonzales et al. 1557* (LPB, UC).

*Melpomene personata* is a common species in the Andes. Many Central American plants differ from the Andean ones slightly in having more but smaller, isodiametric cells in the scales, more apical glands, and not visible or weakly visible costae. Apart from that, the characters are similar. Many specimens of *M. personata* have been erroneously determined as *M. pilosissima*, which has added greatly to the confusion within that species complex. Molecular data, however, indicate that *M. personata* is not closely related to *M. pilosissima* and allies, but in fact belongs to the *M. moniliformis* clade (Lehnert et al., in prep. a). Morphologically, *M. personata* is characterized by horizontally creeping rhizomes (vs. usually erect in *M. pilosissima*); rhizome length can vary greatly, but usually is longer than in *M. pilosissima* and allies, with the fronds also placed further apart (3-10 mm vs. 0.5-2.0 mm in *M. pilosissima*). From *M. pilosissima* and *M. huancabambensis*, *M. personata* differs in having the hairs abaxially clustered in the sori and along the costae (vs. hairs evenly distributed); from *M. xiphopteroides* and *M. pilosissima* var. *tsatchelae*, it differs in the terete petioles (vs. petioles marginate to alate); from *M. huancabambensis*, *M. jimenezii*, and *M. michaelis* in having shorter hairs (to 2 mm in *M. personata* vs. to 3 mm) and conspicuous hydathodes (vs. hydathodes reduced or lacking); from *M. vernicosa* and *M. jimenezii* in the thinner (0.4-0.8 mm vs. 0.8-1.5 mm), glabrous or glabrescent petioles (vs. petioles persistently hairy).

Other species with which *M. personata* may be mistaken include *M. sodiroi*, *M. albicans*, and *M. youngii*. All differ from *M. personata* in hidden costae and white wax-like

deposit on the abaxial laminae (vs. costae at least obscurely visible and lamina without wax). *Melpomene sodiroi* has also larger scales and normally gibbose segments; *M. youngii* is completely glabrous and lacks hair in the sori (vs. hairy petioles, hairs clustered in sori in *M. personata*).

The Peruvian collection *Philippi s.n.* (B) belongs to *Melpomene personata* and was annotated as paralectotype of *Polypodium firmum* Klotzsch (= *Melpomene firma*). These two species can be easily distinguished, as the lectotype of *M. firma* (*Schomburgk 1170*, B) has an erect rhizomes, patent pinnae, truncate laminar bases and small glands along the scale margins, while *M. personata* has horizontally creeping rhizomes, ascending pinnae, rounded to cuneate laminar bases and lacks marginal glands on the scales.

**18. *Melpomene peruviana*** (Desv.) A. R. Sm. & R. C. Moran, *Novon* 2: 430. 1992. *Polypodium peruvianum* Desv., *Mém. Soc. Linn. Paris* 6: 231. 1827. *Ctenopteris peruviana* (Desv.) J. Sm., *Hist. Fil.* 184. 1875. *Grammitis peruviana* (Desv.) C. V. Morton, *Contr. U.S. Natl. Herb.* 38. 115. 1967. *Xiphopteris peruviana* (Desv.) Crabbe, *Brit. Fern Gaz.* 9: 319. 1967. Type. Peru. Collector unknown (holotype, P).

*Polypodium peruvianum* var. *subgibbosum* Rosenst., *Meded. Rijks-Herb.* 19: 16. 1913. Type. Bolivia. [Cochabamba?] Valle Lagodos, *Herzog 2373a* (holotype, S; isotype, UC).

*Polypodium orbygnianum* Fée, nom. nud.

*Melpomene zempoaltepetlensis* (Mickel & Beitel) A. R. Sm., *Novon* 5: 21. 1995. *Grammitis zempoaltepetlensis* Mickel & Beitel, *Mem. New York Bot. Gard.* 46: 205. 1988. Type. Mexico. Oaxaca, Dist. Mixe, NW slope of Cerro Zempoaltépetl, trail from Yacoche to Totontepec, *Mickel 4638* (holotype, NY). Figs. 26A, 27.

*Plants* predominantly terrestrial or saxicolous, growing in moss layers, rock crevices or open soil; in Argentina, southern Bolivia and Brazil rarely epiphytic. *Rhizomes* moderately to shortly creeping, horizontal, strongly branching, 0.8-1.0 mm diam. (Fig. 27A). *Fronde*s stiffly held downward, inserted onto the rhizome at acute to right angles, closely to moderately spaced (0.8-3.0 mm). *Scales* 2.0-3.6(-4.0) x 0.5-1.0 mm, (8-)10-14(-18) cells wide, clathrate (Fig. 27B, C), dark brown to brown, rarely blackish, iridescent, narrowly cordate to pseudopeltate at base, acute to short-attenuate at tips; apical glands 3-8 cells, in nodding clusters or palmately arranged. *Petioles* 10-35(-90) mm long, 0.5 mm thick, decurrently alate from the laminae to marginate if short (<35 mm) (Fig. 27D), terete if long (>35 mm), always

with few to many dark brown hairs 0.5-1.5(-1.8) mm long; simple and branched glandular hairs of crosiers and young fronds sometimes persistent in older fronds; petiolar bases with some scales attached. *Laminae* 15-85(-90) x 4-10 mm, linear to narrowly lanceolate (broadest below the middle), base rounded to cuneate, tips short acute (Fig. 27A). *Rhachises* dark brown to black, planar and slightly sunken adaxially (Fig. 27E), hemispherically protruding abaxially (Fig. 27F); moderately hairy abaxially, in the lower half also adaxially (Fig. 27E). *Pinnae* 3.5-5.0 x 1.4-2.2 mm (2-3 times as long as wide), fully adnate, deltate to oblong, the tip obtuse or short-acute (Fig. 27E, F), weakly ascending at base and tip of fronds, almost patent in the centre of the fronds (Fig. 27A), proximal and distal ones inequilateral, decidedly decurrent basally, central ones nearly equilateral, but at least weakly decurrent towards their bases (Fig. 27A); costae not visible (Fig. 27E, F), or obscurely so abaxially in dried specimens; 1-3 proximal pinna pairs usually markedly smaller than subsequent segments, the lowermost often alariform (Fig. 27A); no hairs on margins (Fig. 17E, F); stomata usually visible as clearer green spots; hydathodes present (Fig. 27E). *Sori* 2-4 pairs per segment, with hairs 0.6 mm long (Fig. 27F).

**Distribution and habitat.** Páramos, punas (jalca), Bolivian-Tucuman forests, dry steppes and grass lands at 1400-5000 m in Mexico, Colombia, Ecuador, Peru, Bolivia, Argentina, and Brazil (Fig. 26A); common in the south of its range, rare in the north.

**Selected specimens examined. MEXICO. Mexico:** Sierra de las Cruces, 11 Sep 1892, *Pringle 4288* (B, P, UC); Cerro Cabeza, 01 Apr 1937, *Lyonnet 1480* (UC); Tezcoco, Cerro Tlálóc, Sierra Nevada, 19°24'N, 98°43'W, 4000 m, 22 Aug 1982, *Wendt & Atkinson 3948* (NY). **Oaxaca:** Mixes, W slope of Cerro Zempoaltépetl to Yacoche, 1000-8000 ft, 18 Sep 1970, *Mickel & Leonard 4597* (UC), *4598B* (NY). **Veracruz:** Cofre de Perote, E side of mountain, 3930 m, 06 Aug 1958, *Beaman 2173* (US).

**VENEZUELA. Mérida:** trail Quebrada del Chama-Caserio Mucumpis, Páramo Piedra Blanca, Mifafi, 14 Aug 1980, *Stergios & Taphorn 2168* (UC); Dtto. Rangel, Páramo Piedras Blanca, ca. 1 km N of Apartaderos-Tímotos road along road leading to Piñango, 08°50'N, 70°52'W, 4100 m, 22 Nov 1982, *Smith A. R. et al. 1478* (UC).

**COLOMBIA. Boyacá:** Cordillera Oriental, Sierra Nevada de Cocuy, Alto Ritacuva, SW facing slope, E of campsite, 4400 m, 16 Apr 1959, *Barclay & Juajibioy 7408-A* (COL); Nevado del Cocuy, Ritacuba, Las Playitas, 3950 m, 07 Jun 1959, *Bishler 2770* (COL); Monguí, páramo to the E of the village Alto de Osetá, 3715 m, 23 Oct 1967, *Jaramillo Mejia*

4029 (COL). **Cundinamarca:** "Alto del Páramo," ca. 15 km NW of Zipaguirá, Cordillera Oriental, 06 Aug 1950, *Smith S. G. 1383* (UC). **Magdalena:** Sierra Nevada de Santa Marta, valley descending SW from Picos Reina and Ojeda, 4200-4300 m, 05 Oct 1959, *Cuatrecasas & Romero Castaneda 24612* (NY); near small lake which is source of Río Donachui, 4500 m, 21 May 1977, *White & Alverson 520* (NY). **Risaralda:** Santa Rosa, Cordillera Central, Volcán Santa Rosa, Aldo W., 4125-4500 m, 21-22 Jan 1980, *Jaramillo Mejía et al. 5750, 5778* (COL). **Santander:** Páramo de Santurban, near Vetas, [ca. 07° 19'N, ca. 72° 52'W,] 3950-4160 m, 17 Jan 1927, *Killip & Smith A. C. 17477* (COL).

**ECUADOR. Azuay:** Laguna Azuay, Las Cajas., 02°43'S, 79°12'W, 3900 m, 9-10 Sep 1983, *Boysen Larsen & Eriksen 45005* (AAU); **Imbabura:** "Crescit in monte Imbabura," 04 Jul 1871, *Sodiro s.n.* (P). **Napo:** Volcán Antisana, rocky slopes on the W side of the mountain, 00°30'S, 78°10'W, 4500-4550 m, 20 Jul 1997, *Sklenar & Sklenarova 2803* (UC). **Napo-Pastaza:** surroundings of the cordillera de los Llanganati, Chichuila Sacha or Ainchilibi, lower NW grassy slope of Ainchilibi, above ciénaga (Chihuilasacha), 3700-3725 m, 25-29 Apr 1959, *Barclay & Juajibioy 9019* (COL). **Pichincha:** Río Saloya valley, opposite the W slope of Atacazo, road Quito-Santo Domingo, 3000 m, 19 Dec 1947, *de la Rue s.n.* (P); Guagrayalina, WNW slope of the Antisana, 4600 m, 01 Feb 1980, *Halloy B-49* (AAU); Nevado Cayambe, SW side, 00°01'N, 78°01'W, 4400-4500 m, 02 Jul 1995, *Sklenar & Kosteckovar 751* (UC); Nevado Cayambe, 00°01'N, 78°01'W, 4500 m, 02 Jul 1996, *Sklenar & Kosteckovar 52\_2* (UC). **Tungurahua:** "Andes Quitenses, Tunguragua," *Spruce 5414* (P).

**PERU. Ancash:** Prov. Huaraz, road to Llanganuco, rocky dike below the Laguna Llanganuco, 09°03.82'S, 77°37.0'W, 4200 m, 14 Aug 2002, *Lehnert 269* (GOET, UC, USM); Laguna Llaca, 09°27.6'S, 77°27.3'W, 5000 m, 15 Aug 2002, *Lehnert 277* (GOET, UC, USM); Huáscaran National Park, Quebrada Llaca, N side of lake, 09°27'S, 77°27'W, 4500 m, 05 Jan 1985, *Smith D. N. et al. 8993* (AAU); Huascarán National Park, Parón valley E of lake, 08°59'S, 77°38'W, 4250 m, 27 Sep 1985, *Smith D. N. et al. 11470* (AAU); Prov. Yungay, Huascarán National Park, Llanganuco Sector, Quebrada Ancosh at Portachuelo, 09°03'S, 77°35'W, 4770-4870 m, 31 Dec 1984, *Smith D. N. & Goodwin 8897* (USM); Huascarán National Park, Morococha at largest lake, 08°55'S, 77°35'W, 4550 m, 15 Jul 1985, *Smith D. N. et al. 9228* (AAU); Prov. Huari, Huascarán National Park, Quebrada Pachachaca, a lateral valley of Quebrada Ruricincha, 09°28'S, 77°15'W, 4000-4200 m, *Smith D. N. et al. 12244* (USM); Prov. Carhuaz, Huáscaran National Park, Quebrada Ishinca, N side of valley, 09°22'S, 77°25'W, 4400 m, 13 Feb 1985, *Smith D. N. et al. 9515* (AAU); Prov. Recuay, Huascarán National Park, lateral valley of Quebrada Queshque, toward Río Pacahcoto

drainage, 09°50'S, 77°18'W, 4550-4600 m, 19 Mar 1986, *Smith D. N. et al. 11880* (AAU). **Ayacucho:** Prov. Huamanga, Ayacucho–Andahuaylas, passing detour to Vilcas Huamán, 13°20'S, 74°13'W, 4200 m, 31 Aug 2002, *Lehnert 334* (GOET, UC, USM); *ibid.*, Km 200, above Ocro, 13°23.53'S, 73°57.30'W, 4200 m, 31 Aug 2002, *Lehnert 339* (GOET, UC, USM). **Cuzco:** Prov. Calca, Ampares, center of the town, around the bridge, SW of Cuzco and S of town, 3330-3340 m, 13 Dec 1986, *Núñez 6737* (CUZ, LPB); between Lares and Hierbabuena, 2800-3200 m, 30 Jan 1958, *Bües 11990* (CUZ); Prov. Quispicanchi, Marcapata, trail passing the public toilets, 13°35.28'S, 70°58.30'W, 3000 m, 22 Oct 2002, *Lehnert 449, 451* (GOET, UC, USM); Prov. Urubamba, Machu Picchu, under overhanging rock near summit of Waina Picchu, 2600 m, 20 Jan 1976, *Bishop 2501* (UC), environs of Tinke, between Ocongate and the Cordillera de Auzangate, 3650-3800 m, 25-31 May 1958, *Humbert 30744* (B); Abra Malaga, 4230 m, 16 Oct 2002, *Lehnert 421* (GOET, UC, USM); Huayocari to Yanacocha, Urubamba, NW from Cuzco, 13°16'S, 72°04'W, 14 Feb 1987, *Núñez et al. 6985* (USM). **Huancavelica:** Tayacaja, Huacracocha, at 20 km from Huancayo, 4100 m, 02 May 1954, *Tovar 2184* (USM). **Huanuco:** Chavenillo, 3600 m, 14 Jan 1954, *Coronado & Woytkowski 177* (UC); Pachita, Pano, 2500 m, 03 Mar 1947, *Ferreyra 1781* (USM). **Junin:** Huancayo, Huaytapallana, 4450 m, 12 Jan 1972, *Cerrate & Chanco 5459* (USM); Huancayo, 3500 m, 15 May 1960, *Kunkel 350* (B); 4700 m, 15 May 1960, *Kunkel 350a* (B); Huancayo, alrededores, 3600-3800 m, 15 Mar 1943, *Soukup 1915* (USM), above Capillacocha, near Carhuamayo, 4300 m, 01 Jul 1954, *Tovar 2415* (USM). **La Libertad:** Santiago de Chuco, surroundings of laguna Coipín, 4100 m, 11 Jun 2001, *Sagástegui-A. et al. 16715* (UC); Santiago de Chuco, Huillilas NE of Cachicadan, 4000 m, 26 Dec 1938, *Stork & Horton 10008* (UC); Huamachuco, 5 km S of El Portachuelo Pass, 3800 m, 29 Nov 1936, *West 8147* (UC). **Lambayeque:** Prov. Ferrenafe, ca. 7 km NW of Incahuasi, near Cerro Punamachay on trail to Laguna Hualtaco, 3300-3500 m, 16 Nov 1984, *Dillon & Skillman 4117* (USM). **Puno:** Prov. Sandia, entre Sandia y Cuyocuyo, 3100-3300 m, 16 May 1966, *Ferreyra & Vera 16753* (USM). **Dept. unknown:** *Pavon s.n.* (P); *Dombey s.n.* (P); 1839–1840, *Gay 1877* (P).

**BRAZIL. Minas Gerais:** mountain locally called Serra do Papagaio, 1816-1821, *de Sainte-Hilaire 538* (P). **Rio de Janeiro:** Serra di Itatiaya, 2400 m, 04-10 Jun 1913, *Brade & Tamandaré 6469* (RIO, UC); Serra di Itatiaya, Monte Serrat, 800 m, 04-10 Jun 1913, *Brade & Tamandaré 6470* (RIO); Serra do Itatiaya, 2200 m, 17 May 1902, *Dusén 156* (P, RIO); Itatiaya, 01 Jun 1902, *Dusén 13987* (UC); Haut des Orgues, 08 Aug 1869, *Glaziou 3575* (P); Itatiaya, 17 Mar 1905, v. *Goebel s.n.* (UC); Itatiaya, Jun 1906, *Luederwald s.n.* (SP-24181); Morro Assu, 2200 m, 01 Mar 1916, v. *Luetzelburg 6014a* (UC); Itatiaya, Agulhas Negras, 22

Jul 1967, *Strang 1051 & Castellanos (26638)* (BHCB, RIO). **Santa Catarina:** Am Rande der Serra Goral, Mar 1891, *Ule 2338* (P).

**BOLIVIA. Chuquisaca:** Chuquisaca (= Sucre?), *D'Orbigny 423* (P); Prov. Sud Cinti, Cerro Bufete, parte superior del farallon norte, 20°49'55"S, 64°22'39"W, 2200-2280 m, 16 May 1995, *Holst et al. 4698* (UC); Prov. Belisario Boëto, 5 km pasando Nuevo Mundo, 19°00'S, 64°46'W, 2300 m, 16 Jul 1998, *Kessler et al. 44* (LPB, UC); Tomista, Dec 1845-Jan 1846, *Weddell 3745* (P); between Tipoyo and Cerro Obispo, 2900 m, 03 Apr 1994, *Wood 8202* (US). **Cochabamba:** Prov. Carrasco, 61 km [on] old road Cochabamba-Villa Tunari, 17°15'S, 65°43'W, 3950 m, 02 Jul 1996, *Kessler 6869* (GOET, LPB, UC); 8 km from Empalme to Siberia, 17°46'S, 64°48'W, 2900 m, 22 Oct 1996, *Kessler et al. 9194* (LPB, UC); Cochabamba, Carrasco, Carretera Cochabamba-Villa Tunari, debajo de Corani, 17°10.51'S, 65°54.02'W, 2750 m, 26 Nov 2002, *Lehnert 518* (GOET, LPB, UC); Prov. Chapare, La Abra de Colomi, 3400 m, 19 Jun 1929, *Steinbach 9859* (UC); Prov. Campero Leyes, camino de Sucre a Aiquiule, despues de la cuesta del Meadero, 21 Nov 1993, *Kiesling & Metzling 8467* (LPB). **La Paz:** Cordillera de la Paz, *D'Orbigny 143* (P); Prov. Bautista Saavedera, Charazani, 15°11.15'S, 68°54.90'W, 2700 m, 15 Sep 2002, *Lehnert 361* (GOET, LPB, UC); Prov. Inquisivi, pass road Quime-Caxata SW Huana Khota, 17°03'S, 67°17'W, 4150-4250 m, 01 Oct 1997, *Müller & Heinrichs J. 6503* (GOET); Prov. Larecaja, 40 km de Sorata a Quiabaya, 3500 m, 29 Jul 1995, *Kessler et al. 4331* (AAU, LPB); Prov. Murillo, 8 km beyond the summit of La Cumbre on the road to Chulumani, 4175 m, 10 Mar 1980, *Hickey & Eshbaugh 761* (AAU); Prov. Sud Yungas, Mururata, bajo la mina Bolsa Negra, pasando por el pueblo de Tres Ríos, 16°35'S, 67°45'W, 3900 m, 18 Nov 1995, *Gonzales J. 1291* (GOET, LPB, UC); Mururata bajo la Mina Bolsa Negra y Laguna Arteza Kota, 16°35'S, 67°45'W, 4000 m, 04 Nov 1995, *Gonzales J. 1326* (LPB, UC); Mina San Francisco, arriba de Choquekhota, 16°29'33"S, 67°53'45"W, 4250 m, 17 Apr 2003, *Lehnert 773* (GOET, LPB, UC). **Santa Cruz:** Prov. Caballero, Comarapa, entre Torecillos y Siberia, 17°49.65'S, 64°40.14'W, 2600 m, 18 Mar 2003, *Lehnert 698* (GOET, LPB, UC); Prov. Valle Grande, Valle Grande, *D'Orbigny 375* (P); between Pinaru and Valle Grande, *D'Orbigny 375* (P). **Tarija:** Prov. Aniceto Arce Ruíz, Cerro Pabellón, arriba del pueblo Cañas, 21°52'S, 64°52'W, 2600 m, 15 Mar 1998, *Beck 26048* (LPB); Reserva Natural de Flora y Fauna Tariquia, campamento Alisos; subiendo por el sendero que va a la cumbre, 22°00'S, 64°34'W, 2130 m, 13 Jun 2004, *Jiménez I. 2416* (GOET, LPB, UC); al W de Abra Blanca, cerca de Rejará, 2940 m, 17 Dec 1987, *Beck & Liberman 16019* (LPB); Prov. Cercado, Cordillera de Sama, heading down to Tarija, along the road, 21°28.88'S, 64°53.52'W, 3480 m,

01 Apr 2003, *Lehnert 750* (GOET, LPB, UC); Abra del Condor; ledge WSW of the white stone hill, near the road to Entre Rios, 21°29.91'S, 64°31.06'W, 2450 m, 04 Apr 2003, *Lehnert 755* (GOET, LPB, UC); Prov. Méndez, Sama, 3450 m, 07 Feb 1987, *Ehrlich 336* (LPB, UC).

This species can be regarded as the one of the ecologically toughest within the genus as it ranges into regions that are climatically too extreme for other species of *Melpomene*. Its adaptation can be seen in drought tolerance, either against hot climate, e.g., in Argentina and Mexico, or against strong cold winds, e.g., in the punas of Peru and Bolivia.

*Melpomene peruviana* has been often confused with *M. flabelliformis*, based on a misunderstanding of R. Stolze of the species (Stolze & Tryon, 1993). *Melpomene flabelliformis* is a generally larger plant with wider scales, and longer, less hairy petioles (usually glabrous) (see *M. flabelliformis* for further discussion).

Most similar is *Melpomene sklenarii* from Ecuador and Colombia but that species has a different habit with the fronds well-spaced and held erect. The segments of *M. sklenarii* are more obtuse to round at the tips (vs. more or less acute in *M. peruviana*); the fertile parts of the laminae may be densely hairy to almost glabrous, with the hairs evenly distributed and not clustered in the sori (vs. clustered in the sori and sparse otherwise in *M. peruviana*).

Affinities are seen to *Melpomene personata*, which is similar in the habit (fronds pointing downwards, rhizomes horizontally creeping, fronds not fasciculate) and the hair distribution (mainly in sori, variable on laminae and petioles). The differences are clearly in the size and life form: *Melpomene peruviana* is usually small and saxicolous or terrestrial plant, often growing in large colonies; *Melpomene personata* is always epiphytic and reaches larger dimensions. In the rare occasions when *M. peruviana* grows epiphytically (southern Bolivia, Argentina, Brazil) it remains smaller than *M. personata*, suggesting that they are not simply ecotypes of the same species.

The epiphytic form of *M. peruviana* is characterized by shorter-creeping rhizomes and larger segments compared to the terrestrial plants; the segment shape (except for sometimes weakly undulate margins) and the number of sori per segment (2-4 pairs) do not change. These characters distinguish it from *M. xiphopteroides* in Brazil, with which it often been confused: the latter species has oblong, usually obtuse segments with up to 8 pairs of sori; it sometimes also has red stomata, a condition not observed in *M. peruviana*.

The geographic separation of the Mexican population of *Melpomene peruviana* from the continuous Andean-Brazilian population is uncomparable within the genus, but similar patterns are known from other plant genera (e.g., *Fosterella*; Ibsch et al., 1999). A separation on the



taxonomical level of the Mexican plants as *M. zempoaltepetlensis* does not seem justified because they differ only in having glandular hairs on the scale apices more frequently in a palmate arrangement. Andean plants have the apical glandular cells mostly arranged linearly, but Argentinian plants have them more frequently palmately arranged again (pers. obs.; de la Sota et al. 2000). De la Sota et al. (2000) report a high variability in stomata size and density, and spore size and viability in the Argentinian population of *M. peruviana*. With its population in the Argentinian Serra de los Ventanas (Cabrera, 1968), it is also the species with the southernmost distribution in the genus.

**19. *Melpomene pilosissima*** (M. Martens & Galeotti) A. R. Sm. & R. C. Moran, Novon 2: 431. 1992. Figs. 18A, 28.

*Rhizomes* very short-creeping, ascending to erect, 0.8-1.2 mm diam. (Fig. 28A). *Fronde*s to 18-25 cm long, patent to stiffly pendent, inserted onto the rhizomes at acute angles, caespitose, closely placed (0.5-3.0 mm) (Fig. 28 A). *Scales* to 5.5 x 0.6 mm, (8-)10-12(-16) cells wide across bases, clathrate (Fig. 28B), dark brown to brown, strongly iridescent, lanceolate, narrowly cordate proximally, acute to attenuate at tip; apical glands 1-8 cells, linearly (Fig. 28C) or palmately arranged. *Petioles* 26-80(-100) mm long, 0.5-0.8 mm diam., terete to weakly alate from the lamina base, with many long dark brown hairs 0.8-3.0 mm long; simple and branched glandular hairs of crosiers and young fronds sometimes persistent on older fronds. *Laminae* to 100-125 x 8-22 mm (2/3 of frond length), narrowly elliptic to lanceolate (broadest at and/or below the middle), rounded to broadly cuneate at bases, shortly acute at tips (Fig. 28A). *Rhachises* dark brown to black, planar and slightly sunken adaxially (Fig. 28D), hemispherically protruding abaxially (Fig. 28E), scatteredly to densely hairy (as on the petiole) abaxially and in the proximal half adaxially. *Pinnae* 5.0-12.0 x 1.0-2.6 mm (4-5 times as long as broad), weakly ascending (80-60°), inequilateral at bases, fully adnate, long-deltate to oblong, the tips obtuse to acute (Fig. 28D, E); costae not visible to usually partially visible abaxially (Fig. 28E); 1-3 proximal pinna pairs markedly smaller than the following pinnae (Fig. 28A), sometimes remote, but not alariform; hairs few to many, evenly distributed on the abaxial laminae, always some along the margins, at least one at the tips; hairs not clustered in sori (Fig. 28E), hydathodes well developed (Fig. 28D). *Sori* 1-6 pairs per segment, with setae 1.5-2.0 mm long, scattered in and around them (Fig. 28E).

Two varieties are recognized:

**19a. *Melpomene pilosissima*** (M. Martens & Galeotti) A. R. Sm. & R. C. Moran var. *pilosissima*. *Polypodium pilosissimum* M. Martens & Galeotti, Nouv. Mém. Acad. Roy. Sci. Bruxelles 15(5): 39, t. 9, fig. 2. 1842. *Ctenopteris pilosissima* (M. Martens & Galeotti) Copel., Philipp. J. Sci. 84: 390. 1955 (1956). *Grammitis pilosissima* (M. Martens & Galeotti) C. V. Morton, Contr. U.S. Natl. Herb. 38: 114. 1967. *Xiphopteris pilosissima* (M. Martens & Galeotti) Crabbe, Brit. Fern Gaz. 9: 319. 1967. Type. Mexico. Oaxaca, Galeotti 6397 (lectotype, designated by Smith, Fl. Chiapas 2: 124. 1981, BR; isolectotype, K). Figs. 18A, 28A-C.

*Plants* predominately epiphytic, rarely epilithic or terrestrial. *Rhizomes* very short-creeping, ascending to erect, 0.8-1.2 mm diam (Fig. 28A). *Fronds* patent to stiffly pendent, inserted onto the rhizomes at acute angles, caespitose, closely placed (0.5-2.0 mm) (Fig. 28A). *Scales* to 5.5 x 0.6 mm, (8)10–12(16) cells wide at base, clathrate (Fig. 28B), dark brown to brown, strongly iridescent, lanceolate, narrowly cordate basally, acute to attenuate at tips; apical glands 1-3 cells, linearly or palmately arranged (Fig. 28C). *Petioles* 26-55 mm long, 0.6 mm diam., terete or weakly marginate from the laminar bases, with many dark brown hairs 0.8-2.2 mm long; simple and branched glandular hairs of crosiers and young fronds sometimes persisting in older fronds. *Laminae* to 115-125 x 8-21 mm (2/3 of frond length), narrowly elliptic (broadest at and/or below the middle), rounded to broadly cuneate at bases, short-acute at tips (Fig 28A). *Rhachises* dark brown to black, planar and slightly sunken adaxially, hemispherically protruding abaxially, densely hairy abaxially and in the proximal half adaxially. *Pinnae* 5.0-12.0 x 1.4-2.6 mm (4-5 times as long as wide), weakly ascending (80-75°), inequilateral at base, fully adnate, long deltate to oblong, the tip obtuse; costae not apparent, or obscurely so abaxially in dried specimens; proximal 1-3 pinna pairs markedly smaller than the following segments, but not alariform; hairs few to many, evenly distributed on the abaxial laminae, always some along the margins, at least one at the pinna tips; hairs not clustered in sori; hydathodes well developed. *Sori* 1-6 pairs per segment, with 1-3 hairs 1.5-2.0 mm long in them and several around them.

**Distribution and habitat.** Cloud forests at 2800-3500 m in Mexico, Guatemala, Honduras, Costa Rica, Venezuela, and Colombia.

**Selected specimens examined. MEXICO. Chiapas:** 1902, *Münch s.n.* (P). **Guerrero:** Tlacotepec, Puerto Gallo, on S slope of Cerro Teotepec, 2450 m, 11 Aug 1964, *Rzedowski 18602* (NY). **Oaxaca:** Sierra de Juárez, Km 106 ruta 175 Tuxtepec-Oaxaca, 2700 m, 19 Nov 2005, *Kessler 13513, 13514* (GOET); Dto. Ixtlán, 2 km E of Ixtlán, 1-2 km N of Vivero Rancho Teja, 7200-800 m, 27 Sep 1970, *Mickel & Leonard 4966* (UC); Dto. Central, N slope of Cerro San Felipe, 7800-8400 ft, 13 Oct 1969, *Mickel & Hellwig 4043* (UC); Dto. Ixtlán, trail from San Pedro Nolasco N to the Llano Verde, 6000-7200 ft, 05 Oct 1969, *Mickel & Hellwig 3775* (UC), Dto. Mixes, SE shoulder of Cerro Zempoaltépetl, 8200 ft, 22 Sep 1970, *Mickel & Leonard 4886* (UC); about 15 km E of Ixtlán, near Natividad, along trail leading to Llano Verde, 6000-7000 ft, 01 Nov 1969, *Smith A. R. 478* (UC). **Veracruz:** near Jalapa, Aug 1828, *Schiede & Deppe 749 (728)* (B).

**GUATEMALA. San Marcos:** on volcán Tacaná, on the road to Talquián (Mex.) on top of the volcano, on the borderline México-Guatemala, 2750 m, 06 Feb 1987, *Martínez-S. et al. 19583* (UC).

**HONDURAS. Francisco Morazan:** Tegucigalpa, montaña La Tigra, 2333 m, 03 May 1980, *Cruz 176* (AAU).

**COSTA RICA. Cartago:** 2 mi SW of Agua Caliente and S of Cartago, 1600 m, 01 Apr 1928, *Stork 1334* (UC). **San José:** Cerro de la Muerte, páramo Buena Vista, 1-3 km S of Interamerican: Highway, 3350 m, 09 Aug 1967, *Bishop 872* (UC).

**VENEZUELA. Mérida:** Sierra de la Culata, N of Mérida, N of Monterrey, headwaters of Río Mucujún, height between Qubrada El Arado and Quebrada El Robo, 08°41'30"N, 71°07'W, 2700-2880 m, 02 Jul 2000, *Meier W. & Moreno 7301* (UC). **Trujillo:** Carache, passing Páramo Cendé, shores of Río Cendé, 3000 m, 09°32'N, 70°08'W, 15 Apr 1988, *Rivero-R. & Rondón 1593, 1626* (UC).

**COLOMBIA. Boyacá:** from Mongui to the E, in village named Alto de Osetá, 3620 m, 23 Oct 1967, *Jaramillo Mejía et al. 4039* (COL); Monguí, páramo to the E of village Alto de Osetá, 3715 m, 23 Oct 1967, *Jaramillo Mejía et al., 4027* (COL); Tunja, Cordillera de Sosa, Los Pulpitos, 3500 m, 31 Aug 1967, *Hagemann 217* (COL). **Cundinamarca:** road Guasca to Gachetá, Km 60-61, 2720 m, 22 Jan 1974, *Acosta-Arteaga 105* (COL); Pasca, Vereda Cajita, forest along Laguna Cajita in páramo de Chisaca, 3600 m, 04 Sep 1983, *Sarmiento 1998* (COL). **Risaralda:** Santa Rosa, Cordillera Central, hacienda La Sierra, valley of Quebrada Betania, 3700 m, 25 Jan 1980, *Jaramillo Mejía et al. 5898* (COL). **Santander:** Coromoro, Laguna La Fiquera, in páramo de Carnicera, origin of the Quebrada de Coromoro, 3850 m, 29

Nov 1967, *Jaramillo Mejia & van der Hammen 4360* (COL); Pamplona (Norte de Santander), SW of the city, towards Pinhuelal, 30 Jun 1945, *de Garganta Fábrega 1026* (COL).

This species and its closer allies have been much confused. Morphologically, the *Melpomene pilosissima* group can be characterized by short rhizomes which are usually erect to decumbent, rarely horizontally creeping, with the fronds caespitose (less than 5 mm apart), by lanceolate to very narrowly lanceolate scales with thick dark brown cell walls, and long to very long, usually dark brown to atropurpureous hairs. All species of *Melpomene* with eglandular hairs regularly present on margins and adaxial laminar surfaces and/or having only few or none hydathodes belong to this group. It includes two main lineages, one consisting of *M. xiphopteroides* (vars. *xiphopteroides* and *acrodontium*) and *M. vernicosa*, the other of *M. pilosissima* (vars. *pilosissima* and *tsatchelae*), *M. huancabambensis*, *M. michaelis*, and *M. jimenezii*. Within its range, *Melpomene pilosissima* is most similar to epiphytic *M. xiphopteroides*: scale width, gland number of the scales, and hairiness are the same in both species. *Melpomene xiphopteroides* differs mainly in patent to weakly ascending pinnae, laminae that are broadest at or above their center with the bases long-decurrent or truncate proximally, and petioles that are usually marginate (wings sometimes thin and ephemeral) to alate from the proximal pinnae. In contrast, *M. pilosissima* var. *pilosissima* always has ascending pinnae, laminae that are broadest at or below their center with the bases rounded or cuneate; the petioles are terete to weakly marginate in the distal half. The laminar hairs of *M. pilosissima* are generally longer than those of *M. xiphopteroides* (mean length 1.5-2.2 mm vs. 0.8-1.5 mm), but may be between 1.2-2.0 mm in both species. Plants with fewer hairs than usual occur in both species; these differ in the sori, which have usually more hairs in *M. xiphopteroides* (3-5) than in *M. pilosissima* (1-3); the latter species generally has more hairs on the laminae than within the sori.

While *Melpomene xiphopteroides* and *M. vernicosa* represent a species pair with different elevational preferences, *M. pilosissima* s.l. is divided into a grade of populations with comparable elevation patterns but clearcut distributions. In Mexico and Guatemala, we find mainly *M. pilosissima* var. *pilosissima*. From Costa Rica south through the northern Andes to the Tumbesian region in northern Peru, var. *pilosissima* is largely replaced by the var. *tsatchelae*, which differs in weakly visible costae and marginate to weakly alate petioles. In northern Peru, we find *M. huancabambensis*, which has no hydathodes and patent pinnae (vs. hydathodes well developed and ascending pinnae in *M. pilosissima* and its var. *tsatchelae*), and also terete petioles (vs. marginate to weakly alate in var. *tsatchelae*). In the

central Andes, *M. pilosissima* is replaced by *M. michaelis* and *M. jimenezii*. Contrary to the northern species (*M. pilosissima* and *M. huanacabambensis*), *M. michaelis* and *M. jimenezii* have the hairs clustered in the sori, but like *M. huanacabambensis* they lack hydathodes or have them sporadically developed.

*Melpomene pilosissima* var. *pilosissima* is often confused with *M. personata*, which see for distinguishing characters.

**19b. *Melpomene pilosissima* var. *tsatchelae*** (P. Labiak) Lehnert, comb. et stat. nov.  
*Melpomene tsatchelae* P. Labiak, Brittonia 52: 251. 2000. Type. Ecuador. Pichincha, carretera Quito-Santo Domingo, 2500 m, 24 May 1987, *van der Werff & Palacios 9598* (holotype, NY; isotypes, AAU, MO n.v., US). Figs. 18A, 28A.

Etymology: The name refers to the Tsatchela Indians, who live near the type locality.

*Plants* predominately saxicolous, sometimes epiphytic. *Rhizomes* short to very short-creeping, ascending to erect, 0.8-1.2 mm diam. *Fronde*s to 18-25 cm long, patent to stiffly pendent, inserted onto the rhizomes at acute angles, caespitose, closely placed (1-3 mm) (Fig. 28A). *Scales* to 4.0-4.2 x 0.6 mm, (9-)12-14(-16) cells wide at base, clathrate, dark brown to brown, strongly iridescent, lanceolate, narrowly cordate proximally, acute to attenuate at tips; apical glands 3-8 cells, linearly or palmately arranged. *Petioles* 50-80(-100) mm long, 0.5-0.8 mm diam., marginate to weakly alate from the laminar bases, with many dark brown to castaneous hairs 0.8-3.0 mm long; simple and branched glandular hairs of crossiers and young fronds sometimes persistent in older fronds. *Laminae* to 100-125 x 10-22 mm (2/3 of frond length), narrowly elliptic to lanceolate (broadest at and/or below the middle), rounded to cuneate at bases, short acute at tips (Fig. 28A); 1-3 proximal pinna pairs markedly smaller than the subsequent pinnae, sometimes remote, but not alariform. *Rhachises* dark brown to black, planar and slightly sunken adaxially (Fig. 28D), hemispherically protruding abaxially (Fig. 28E), scattered to densely hairy (as on petioles) abaxially and in the proximal half adaxially. *Pinnae* 5.0-9.0 x 1.0-2.0 mm (ca. 4-5 times as long as wide), weakly ascending (80-60°), inequilateral at base, fully adnate, oblong to linear deltate, the tips obtuse to acute; costae usually partially visible abaxially; margins sometimes undulate; hairs few to many, evenly distributed on the abaxial laminae, always some to many hairs along the margins, at least one at the tips, sometimes few on adaxial laminae; hairs not clustered in sori; hydathodes well

developed. *Sori* 1-6 pairs per segment, with hairs 1.5-2.0 mm long scattered in and around them (Fig. 28E).

**Distribution and habitat.** Elfin forests, moist montane forests at 2300-2950 m in Mexico, Costa Rica, Venezuela, Colombia, Ecuador, N Peru (Fig. 18A).

**Selected specimens examined. MEXICO. Chiapas:** San Cristobal Las Casas, W side of Zontehuiz near summit, 2743 m, 17 Oct 1981, *Breedlove 53604* (NY). **Guerrero:** Galeana, Piedra Ancha, 3050 m, 29 May 1939, *Hinton 14326* (NY).

**COSTA RICA. Alajuela:** above Lecheria on Volcán Poas, 2200 m, 30 Jul 1932, *Stork 3368* (UC).

**COLOMBIA. Cauca:** Canaan, Mount Purace, 3100-3300 m, 11-13 Jun 1922, *Pennell & Killip 6638* (NY). **Cundinamarca:** Guasca, Vereda Potreritos, secondary forest along the road Guasca-Cacheta, 2700 m, 03 Aug 1989, *Linares et al. 2871, 2879* (AAU). **Cesár:** Manaure, Serranía de Perija, 32 km SE of Manaure, above the laguna, 10°25'N, 72°53'W, 2950 m, 05 Nov 1993, *Rangel et al. 11091* (AAU). **Boyacá:** Villa de Leyva, Santuario de Flora y Fauna Iguaque, quebrada carrizal, 2700 m, *Murillo M. T. et al. 2932* (AAU).

**VENEZUELA. Lara:** Parque Nacional Dinira, Páramo de Jabón, NE slopes, 09°34'N, 70°06'W, 3000 m, 28 Dec 1999, *Riina et al. 883* (UC). **Mérida:** Valle de San Javier, at level with La Caña, NW facing slope (Serranía El Escorial), 08°43'N, 71°05'W, 3050-3080 m, 01 Apr 1999, *Schneider 2283* (UC); Dtto. Rangel, along road Santo Domingo-Apartaderos, 08°51'N, 70°44'W, 2400 m, 06 Aug 1983, *van der Werff & Ortíz 5946* (UC); road Santo Domingo-Apartaderos, 08°50'N, 70°46'W, 2700 m, 06 Aug 1983, *van der Werff & Ortíz 5981* (UC); Valle de San Javier, slope of ridge La Caña (Serranía Escorial), 08°43'N, 71°05'W, 2700-2750 m, 09-10 Mar 1999, *Schneider & Zipp 2153* (UC).

**ECUADOR. Bolivar:** forests between Guaranda and Bodegas, [ca. 01°36'S, ca. 79°00'W,] Nov 1836, *Rémy 1897* (P). **El Oro:** Chilla, track to the antennas, Km 7, 03°27'964"S, 79°36'243"W, 2975 m, 07 Nov 1997, *Lewis G. P. et al. 3689* (NY). **Imbabura:** Road Otavalo-selva Alegre, Km 57, 00°15'N, 78°30'W, 2800 m, 28 May 1980, *Balslev & Quintana F. 24052* (AAU). **Loja:** trails ca. 5 km ENE of San Pedro de Vilcabamba, Loma Solamaco to upper Quebrada Romerillos, 04°14'S, 79°10'W, 2300-2400 m, 01 Dec 1994, *Øllgaard et al. 105997* (AAU). **Morona-Santiago:** road Sigsig-Gualaquiza, app. 20 km from Sigsig, 03°12'S, 78°45'W, 2800 m, 31 Mar 1985, *Eriksen 59122* (AAU).

**PERU. Piura:** Prov. Ayabaca, ruins of Aypate, Tacalpo community, anexo Yanchalá, 04°42.094'S, 79°34.252'W, 2700-2800 m, 22 May 1996, *Quipuscoa-S. et al.* 575 (UC); surroundings of Ayabaca, 2650 m, 09 Sep 1976, *Sagástegui & Cabanillas* 8701 (UC). **Cajamarca:** Prov. Contumazá, Bosque de Cachiö, 2650 m, 14 May 1994, *Sagástegui et al.* 15269 (UC).

This variety replaces *Melpomene pilosissima* var. *pilosissima* in most areas of the northern Andes. The var. *pilosissima* differs in the pinna tips (obtuse to acute in var. *tsatchelae* vs. obtuse var. *pilosissima*) and the costae (partially visible vs. not visible). The var. *tsatchelae* also tends to have longer petioles (50-100 mm vs. 26-55 mm in var. *pilosissima*) and more apical glands on the scales (3-8 vs. 1-3). The partially visible costae and the acute pinna tips resemble those of *M. personata*, but that species has shorter hairs (to 2.0 mm vs. 2.5-3.0 mm in var. *tsatchelae*) that are clustered in the sori (vs. evenly distributed on the abaxial laminae) and usually has longer horizontally creeping rhizomes (vs. short and ascending to erect). Both taxa have different habitat preferences, *M. pilosissima* var. *tsatchelae* growing mainly saxicolously and *M. personata* epiphytically. Other similar species are *M. huancabambensis*, *M. michaelis*, and *M. xiphopteroides*, which see for discussion.

**20. *Melpomene pseudonutans*** (H. Christ & Rosenst.) A. R. Sm. & R. C. Moran, Novon 2: 431. 1992. *Polypodium pseudonutans* H. Christ & Rosenst., Repert. Spec. Nov. Regni Veg. 5: 15. 1908. *Ctenopteris pseudonutans* (H. Christ & Rosenst.) Copel., Phillip. J. Sci. 84: 389. 1955 (1956). *Grammitis pseudonutans* (H. Christ & Rosenst.) C. V. Morton, Contr. U.S. Natl. Herb. 38: 114. Type. Ecuador. Tungurahua, slopes of Mt. Tungurahua, *Rimbach s.n.* (holotype, S; isotypes, UC, US).

*Melpomene brevipes* (C. V. Morton) A. R. Sm. & R. C. Moran, Novon 2: 429. 1992. *Polypodium sodiroi* var. *brevipes* C. V. Morton, Phytologia 22: 79. 1971. Type. Ecuador. Tunguarhua, Mt. Tungurahua, *Spruce* 5279 (holotype, K)

*Melpomene rosarum* (Copel.) A. R. Sm. & R. C. Moran, Novon 2: 431. 1992. *Polypodium rosarum* Copel., Phillip. J. Sci. 84: 389. 1955 (1956). *Grammitis rosarum* (Copel.) C. V. Morton, Contr. U.S. Natl. Herb. 38: 116. 1967. Type. Ecuador. Chimborazo, vicinity of Huigra, *Rose* 22232 (holotype, US). Figs. 10B, 29.

**Etymology:** The species was compared with *Polypodium nutans* Blume from Malesia by Christ and Rosenstock, who saw a strong similarity between both species.

*Plants* predominately epiphytic or epilithic, sometimes growing in moss layers on the ground. *Rhizomes* horizontally creeping to weakly ascending, 1.8-2.5(-2.8) mm diam., posterior parts long-persisting (Fig. 29A). *Fronde*s 130-390(-520) mm long, erect, inserted onto the rhizomes at right angles, moderately to widely spaced ((2-)4-14 mm), often crowded towards the rhizome tips (Fig. 29A). *Scales* 6.0-8.0 x (0.8-)1.4-1.6 mm, (18-)24-40(-46) cells wide, clathrate (Fig. 29B), brown, strongly iridescent, broadly cordate to pseudopeltate, acute to attenuate at tips; tips usually undulate; apical glands 3-8 cells, in nodding clusters or palmately arranged (Fig. 29C). *Petioles* (5-)12-60 mm long, (0.8-)1.0-1.2(-1.8) mm diam., marginate to weakly alate throughout, glabrous to glabrescent, with few short dark brown hairs 0.75-1.2 mm long (Fig. 29D); simple and branched glandular hairs of crozier and young fronds sometimes persistent on older fronds; petiolar bases with several scales. *Laminae* to (120-)130-350(-470) mm long, (20-)32-45(-52) mm wide, obovate to lanceolate-elliptic (broadest at or above the middle), cuneate to decurrent at bases, acute at tips (Fig. 29A); firm chartaceous to subcoriaceous. *Rhachises* dark brown to black, planar to weakly protruding adaxially, hemispherically protruding abaxially; glabrous adaxially except for some scattered ephemeral brown hairs, sparsely hairy abaxially in sterile parts, moderately to densely hairy in fertile parts, hairs 0.8-1.5 mm. *Pinnae* (6.0-)12.0-26.0(-35.0) x 2.2-3.8 mm (2.5-6.0 times as long as broad), weakly ascending (80-60°), long deltate, broadly adnate, inequilateral, decurrent towards the bases, the tips obtuse to acute (Fig. 29E, F); costae straight to curved, weakly to clearly visible abaxially (Fig. 29E), not visible or obscurely so adaxially (Fig. 29F), with some hairs abaxially in fertile parts, margins entire or broadly dentate in large pinnae, without hairs (Fig. 29E); proximal pinna pairs markedly smaller than the central ones, but not alariform; hydathodes present, only weakly immersed in laminar tissue (Fig. 29F). *Sori* 2-11 pairs per segment, with some setae around them, but not directly within them, sometimes glabrous (Fig. 29E).

**Distribution and habitat.** Páramos, punas (jalca), and elfin forests at 2700-4100 m in Colombia, Ecuador, and Peru (Fig. 10B).

**Selected specimens examined. COLOMBIA. Bolivar:** below Páramo de Chaquiro, Cordillera Occidental, 2800-3100 m, 24 Feb 1918, *Pennell 4330* (NY). **Caldas:** Cerro



Tatama, Cordillera Occidental, 3400-3700 m, 08-10 Sep 1922, *Pennell 10548* (NY). **Cundinamarca:** Cordillera oriental, Cerro Negro, Hato Grande, ridge east of Río Muchindote, 1 km E of Gachetá, 2870 m, 13 Jun 1944, *Grant 9411* (COL). **Meta:** Macizo de Sumapaz, heading down to San Carlos, 3300 m, 08 Jul 1981, *Díaz-P. 2648-A* (COL); Macizo de Sumapaz, E slope of the cordillera, Quebrada El Buque, 3100 m, 09 Jul 1981, *Díaz-P. 2697* (COL). **Nariño:** Cordillera Oriental, on Cinchona Mission of FEA, W side of Volcan Doña Juana, 3200-3700 m, 16 Dec 1944, *Ewan 16616* (P, UC). **Norte de Santander:** páramo El Hatigo, en route from Toledo to Pamplona, 2900 m, 10-12 Mar 1927, *Killip & A. C. Smith 20645* (NY). **Tolima:** Murillo, 2200-2800 m 18 Dec 1917, *Pennell 3172* (NY). **Valle del Cauca:** Riófrio, Darién, páramo El Duende, 3300-3850 m, 23-28 Jul 1998, *Vargas W.G. 4766* (COL).

**ECUADOR. Carchi:** Montufar, within 3 km of pueblo of Colonia Huaqueña, 00°35.5'N, 77°42'W, 3500 m, 30 Jun 1994, *Fay & Fay 4338, 4340* (AAU); Valle de Maldonado, Km 53 on the road Tulcán-Maldonado, 00°50'N, 78°03'W, 3150-3250 m, 17-18 May 1973, *Holm-Nielsen et al. 5650* (AAU, UC); along road Tulcan-El Carmelo, 3300 m, 08 Aug 1989, *van der Werff & Gudiño 11002* (UC); about 1/2 h E of Huaca, past Colonia Huaceña, 3200-3400 m, 18 Feb 1989, *van der Werff & Palacios 10627* (UC); Canton Montufar, Guandera Reserve, ca. 6 km E of Fernández Salvador, 00°36'N, 77°42'W, 3315 m, 02 Jul 1996, *Wilson 2794* (UC); Canton Montufar, Guandera Reserve, ca. 6 km E of Fernández Salvador, 00°36'N, 77°42'W, 3270 m, 02 Jul 1996, *Wilson 2806A, 2807* (UC); Canton Montufar, Guandera Reserve, ca. 6 km E of Fernández Salvador, 00°36'S, 77°42'W, 3500 m, 02 Jul 1996, *Wilson 2814A* (UC). **Chimborazo:** road ca. 10 km NE of Alao, at Cuspipaccha, 01°48'S, 78°26'W, 3500 m, 06 May 1982, *Øllgaard et al. 38140* (AAU). **Cotopaxi:** the upper slopes of Río Langoa Valley, 00°55'S, 78°25'W, 3700 m, 17 Nov 1984, *Brandbyge & Møller Jørgensen 42879* (AAU); road Angamarca-El Corazón, just below Pinllopata, 01°09'S, 79°05'W, 1250 m, 07 Jul 1979, *Holm-Nielsen & Andrade 18542* (AAU); Quevedo-Latacunga road, above Pilaló, at the timberline, 00°58'S, 78°56'W, 3450-3500 m, 08 Apr 1973, *Holm-Nielsen et al. 3345* (AAU, UC). **Imbabura:** road Ibarra-Mariano Acosta, E of the pass (on Hda. Yura Cruz), 00°20'N, 78°00'W, 3500-3600 m, 09-10 Aug 1976, *Øllgaard & Balslev 8632* (AAU); small wooded quebrada 5 km N of Hacienda Pinnán, 10850 ft, 25 Jun 1944, *Wiggins 10359* (UC). **Loja:** Loma de Oro at Panamerican highway, 10 km S of Saraguro along turn-off 2 km to the E from the pass, 3300 m, 02 Jan 1981, *Balslev 1386* (AAU); road Pichig-Fierro Urco, ca. 11 km (app. 15 km SW of Saraguro), 03°41'S, 79°20'W, 3400 m, 30 Dec 1988, *Madsen 85443* (AAU); muletrack Amaluza-Palanda, western slope,

near the pass (W of Laguna Chuquiragua), 04°35'S, 79°20'W, 3100-3400 m, 22 Sep 1976, *Øllgaard & Balslev 9643* (AAU); road to páramo 4.2 km from Bellavista on Manu-Saraguro road km 4 from Manu, 03°32'S, 79°25'W, 3000 m, 21 Nov 1996, *Øllgaard et al. 2113* (AAU); road Loma del Oro (S of Saraguro) toward Fierro Urcu, ca. km 9, 03°42'S, 79°19'W, 3400 m, 12 Mar 1989, *Øllgaard et al. 91040* (AAU); along small road leading to the antennas from Loma del Oro, between San Lucas and Saraguro, 03°40'S, 79°13'W, 3200 m, 27 Jun 1995, *Pedersen & Lozano 104360* (AAU); Cordillera del Loro, 50 km N of Loja, just before descending towards Saraguro, along road to radar station, 3000-3200 m, 08 May 1987, *van der Werff & Palacios 9407* (UC). **Loja/Zamora-Chinchipe:** limit of Parque Nacional Podocarpus, new road Loja-Zamora, E of the pass, 03°58'S, 79°07'W, 2900 m, 17 Jan 1989, *Madsen 85540* (AAU). **Morona-Santiago:** 0-4 km E of (below) the pass on the Alao-Huamboya trail, 01°47'S, 78°22'W, 3650-3950 m, 05 Jan 1988, *Molau et al. 2373* (AAU); road Gualaceo-Limón, Km 33.3, E of the pass, 03°02'S, 78°38'W, 3010 m, 27 Dec 1990, *Øllgaard et al. 98543* (AAU); vía Plan de Milagro-Gualaceo, 03°02'S, 78°35'W, 3000-3200 m, 06 Feb 1989, *Palacios & van der Werff 3760* (UC). **Napo:** 10 km above Laguna de Papallacta on road Quito-Papallacta, 00°20'S, 78°07'W, 3800 m, 05 Jun 1973, *Holm-Nielsen et al. 6766* (AAU); Cordillera de los Llanganatis, NE side of Laguna Encantada, 01°11'S, 78°12'W, 3430 m, 16 Mar 1983, *Holm-Nielsen et al. 41839* (AAU); Cerro Sumaco, loma 315 deg. of summit, 00°34'S, 77°43'W, 3200 m, 03 May 1979, *Holm-Nielsen et al. 17668* (AAU); páramo, ca. 6 km NE of Km 45 on road Salcedo-Napo, 00°56'S, 78°23'W, 3600 m, 16-18 Nov 1984, *Laegaard 53349* (AAU); N side of Cerro Sumaco, at the timber-line, 00°35'S, 77°39'W, 3300 m, 25 Apr 1979, *Løjtnant & Molau 12776* (AAU); Oyacachi, Yarupaccha, 00°12'S, 78°07'W, 3620-3680 m, 28 Dec 1996, *Navarrete 1365*,(AAU); road San Miguel (Salcedo)-Puerto Nuevo (Napo) (under construction), 54 km from San Miguel, 00°59'S, 78°16'W, 3200-3300 m, 29 Sep 1976, *Øllgaard & Balslev 9821* (AAU); Llanganati, steep slope along Río Topo, immediately SE of Aucacochoa, 01°09'S, 78°18'W, 3370-3420 m, 18 May 1982, *Øllgaard & Holm-Nielsen 38764, 38788* (AAU); Oyacachi, ca. 1.5 km SE of the village, 00°13'S, 78°03'W, 3200 m, 27 Oct 1995, *Øllgaard & Navarrete 1247* (AAU). **Pichincha:** Nevado Cayambe, ladera N, cerca Olmedo, 00° 06.08'N, 77° 58.82'W, 3800 m, 30 Jun 2002, *Lehnert 119, 120* (GOET, QCA, UC); Nevado Cayambe, ladera N, cerca Olmedo, [ca. 00° 06.07'N, ca. 77° 58.80'W,] 4100 m, 30 Jun 2002, *Lehnert 123* (GOET, QCA, UC); road and trail from Chaupi, W of pass between Iliniza and Corazón, 00°33'S, 78°42'W, 3780-3930 m, 15 Mar 1995, *Øllgaard et al. 1188* (AAU). **Zamora-Chinchipe:** Pass *El Tiro* between Loja

and Zamora, 03°59'46"S, 79°08'49"W, 2860 m, 23 Aug 2003, *Lehnert 812, 813, 820* (GOET, QCA, UC).

**PERU. Cajamarca:** Prov. Jaén, Sallique, localidad El Páramo, 05°40'50"S, 79°16'20"W, 3200 m, 23 Jun 1998, *Campos et al. 5087*(UC). **San Martín:** Prov. Mariscal Caceres, Near Mirador. Río Abiseo National Park, 3000-3100 m, 13 Jul 1988, *León 2132* (UC); P.N. Río Abiseo, 3400 m, 13 Mar 1988, *León & Young 1516* (USM); forest patch (C6) at timberline, Chochos, 07°XX'S [sic], 77°XX'W [sic], 3425 m, 25 Nov 1985, *Young 2154* (USM); forest patch (C11) at timberline, Chochos, 07°XX'S [sic], 77°XX'W [sic], 3400 m, 24 Nov 1985, *Young 2509* (USM).

The elevation of 1250 m for the collection *Holm-Nielsen & Andrade 18542* (AAU) from Prov. Cotopaxi, Ecuador, appears to be much too low and is probably an error.

*Løjtnant & Molau 12776* (AAU) from Ecuador nicely shows the transition from narrow, glabrous subcoriaceous laminae to wide, hairy chartaceous laminae.

This species is extremely variable in pubescence. In Ecuador, it shows these general tendencies: forms in the south are glabrous or with few hairs around the sori, those from the eastern and western cordillera always have some hairs around the sori, and often also on the rhachises; plants from the Cordillera de Llanganatis and the Prov. Carchi are very densely hairy. Glabrous specimens have been described as *Polypodium sodiroi* var. *brevipes* C. V. Morton; depauperate plants from the western escarpment of the Cordillera Occidental were described as *Ctenopteris rosarum* Copel. The latter has rather narrow scales and resembles large specimens of *M. wolfii*, but the truncate segment tips typical of that species are missing. The laminar characters of *M. rosarum* with the acute pinnae (vs. obtuse to truncate in *M. wolfii*) fit better into the concept of *M. pseudonutans*. The differences between *M. pseudonutans* and *M. wolfii* are the maximum size (larger in *M. pseudonutans*), the segment form (rounded to long-deltate in *M. pseudonutans* vs. trapezoid to obtusely oblong in *M. wolfii*) and the scale size (more than 1 mm wide in *M. pseudonutans* vs. less than 1 mm wide in *M. wolfii*). Both species exhibit similar variation in pubescence from glabrous to densely hairy and are apparently closely related as shown by molecular data (Lehnert et al., in prep. a).

Constant features of *Melpomene pseudonutans* are the broad scales, which have characteristically undulate tips and persist on the petiolar bases. The rhizomes are among the thickest of the genus (to 2.8 mm diam.) and small plants that may be mistaken for other

species, i.e., *M. vulcanica*, *M. sklenarii*, and *M. flabelliformis*, have thicker rhizomes than these.

*Luteyn et al. 5970* (AAU) from Venezuela resembles *M. flabelliformis* in laminar shape and scale size, but is unusually densely hairy between the sori, which fits neither species. It is placed in *M. pseudonutans* because it agrees better in size and having glabrous sori. Specimens of *M. flabelliformis* with similarly glabrous sori and many hairs around them of are known from Costa Rica, Prov. San José (*Hennipman et al. 6992*, UC; *Smith A. R. & Béliz 1994*, UC; *Stolze 1507*, AAU, UC).

**21. *Melpomene sklenarii*** Lehnert, sp. nov. Type. Ecuador. Azuay: Cajas National Park, E flanks of Cerro Amarillo (4451 m), 02°45'S, 79°15'W, 13 Jul 1997, 4300-4400 m, *Sklenar & Sklenarova 2592* (holotype, UC, isotype, PRC). Figs. 30, 31.

A *Melpomene peruviana* in squamis ovato-lanceolatis (vs. angusto-lanceolatis), segmentis fere rotundis obtusis (vs. deltatis obtusis vel acutis), frondibusque erectis (vs. frondibus pendentibus), a *M. moniliforme* pilis aequaliter distributis in lamina abaxiale (vs. pilis in sori restrictis), pinnis basalibus interdum remotis (vs. pinnis semper concinnis) differt.

Etymology: The name honours Petr Sklenar from Charles University, Prague, who collected most of the known specimens during his studies of Ecuadorian páramos.

*Plants* terrestrial or epilithic, growing in moss layers, rock crevices or open soil. *Rhizomes* moderately to long-creeping, 0.6-1.0 mm diam. (Figs. 30A, B), regularly branching in a wide to right angle (Fig. 30B). *Fronde*s erect, inserted onto the rhizomes at right angles, distantly placed ((5-)11-14 mm) (Fig. 30A, B). *Scales* 2.8-4.0 x 0.6 mm, (10-)14-18(-26) cells wide across their bases, clathrate (Fig. 30 C), dark brown to brown, weakly to rarely strongly iridescent, broadly cordate to pseudopeltate, acute to attenuate at tips; apical glands 3-8 cells palmately arranged; scales soon shed from rhizomes, especially between the fronds. *Petioles* (6-)12-55 mm long, 0.4-0.8(-1.0) mm diam., alate from the laminar bases, marginate to the rhizomes, glabrescent or hairy, with dark brown hairs 0.75-1.5(-2.0) mm long (Fig. 30D); simple and branched glandular hairs rarely present; petiolar bases with persistent scales. *Laminae* 40-80(-90) mm long, to 7-12 mm wide, linear to narrow-lanceolate (widest from below the middle), rounded to cuneate at bases, acute at tips (Fig. 30A, B). *Rhachises* dark

brown to black, planar and slightly sunken adaxially (Fig. 30E), weakly protruding to planar abaxially, with scattered brown acicular hairs (to 1.2 mm) abaxially (Fig. 30F). *Pinnae* to 4.2 x (2.0-)2.4-3.0 mm (ca. 1.5-2.5 times as long as broad), patent, inequilateral and decurrent towards the bases, fully adnate, deltate to oblong, the tips rounded to obtuse (Fig. 30E, F), slightly gibbose, pale green to whitish from below; costae not visible, or obscurely so; basal pairs not notably smaller than the following segments, or only one pair weakly so, often remote (Fig. 30B); glabrous to densely hairy with evenly distributed brown hairs 0.8-1.5 mm long (Fig. 30F); hyaline margins one cell wide (2 cells wide in sinuses and in junction with petioles), without glandular hairs (Fig. 30E, F); hydathodes present. *Sori* 1-3(-4) pairs per segment, surrounded by 5-8 dark brown acicular hairs to 1.0 mm long.

**Distribution and habitat.** Páramos, punas (jalca), and elfin forests at 2900-4600 m in Colombia and Ecuador (Fig. 31).

**Selected specimens examined. COLOMBIA. Nariño:** Prov. Pasto, Volcán Galeras, ca. 01° 12'N, ca. 77° 28'W, 3950 m, 06 Aug 1977, *Pinto et al. 1828* (COL). **Boyacá:** Cordillera Oriental, Sierra Nevada del Cocuy, surroundings of Salto de Correlitos. Sta. 13 above and E of Salto, E of Laguna San Paulito, ca. 05° 34'N, ca. 72° 37'W, 4200 m, 14 Apr 1959, *Barclay & Juajibioy 7370* (COL); Sierra Nevada del Cocuy, páramo Cocavo, Cuchilla Puente Piedra ca. 2 km to the NE of Laguna Pintada, 4510 m, 30 Sep 1972, *Cleef 5668* (COL). **Caldas:** Cordillera Central, surroundings of the refuge of Ruiz, road to El Silencio, ca. 05° 28'N, ca. 75° 39'W, 4310 m, 07 Oct 1978, *Rangel et al. 1735-A* (COL); Páramo del Ruiz, [ca. 05° 28'N, ca. 75° 39'W,] 4200-4630 m, 29 Aug 1957, *Barclay 5240* (COL); Nevado del Ruiz, sandy area 2 km SW of the refuge with many outcrops of volcanic rock, [ca. 05° 28'N, ca. 75° 39'W,] 4520 m, 18 Mar 1972, *Cleef & van't Hart 2446* (COL); Nevado del Ruiz, [ca. 05° 28'N, ca. 75° 39'W,] 4700 m, 06 Aug 1958, *Bishler 1482* (COL); road from Manizales to Nevado, above the “termales,” 3500 m, 07 Jun 1966, *Murillo M. T. et al. 874* (COL); road from Manizales to Nevado, above the “termales,” 3500 m, 07 Jun 1966, *Murillo M. T. et al. 861* (COL); road from Manizales to Nevado, 4230 m, 05 Jul 1959, *Pinto 437* (COL).

**ECUADOR. Carchi:** road Tulcán-Maldonado, Km 34 from Tulcán, 06 Jul 2002, *Lehnert 156* (GOET, QCA, UC); carretera Tulcán-Maldonado, Km 32 from Tulcán, base of Volcan Chiles, 06 Jul 2002, *Lehnert 155a* (GOET, QCA, UC); S slopes of volcán Chiles, 02°49'N, 77°57'W, 4100 m, 21 Oct 1987, *Ramsay & Merrow-Smith 872* (AAU). **Chimborazo:** El Altar, N side of the volcano, on the ridge below the Canonigo peak,

01°41'S, 78°24'W, 4200-4400 m, 19 Aug 1995, *Sklenar & Kosteckovar 967* (UC); El Altar, N side of the volcano, on the ridge below the Canonigo peak, 01°41'S, 78°24'W, 4500 m, 19 Aug 1995, *Sklenar & Kosteckovar 88\_7* (UC); Chimborazo volcano, base of the terminal moraine on the E side of the mountain, 01°28'S, 78°46'W, 4500 m, 03 Jul 1997, *Sklenar & Sklenarova 2198* (UC); Chimborazo volcano, on the E slope of the mountain, 01°28'S, 78°46'W, 4200-4250 m, 02 Jul 1997, *Sklenar & Sklenarova 2308* (UC). **Chimborazo/Morona-Santiago:** Cerro Yanaurcu, N ridge of the mountain, 02°14'S, 78°30'W, 4200-4300 m, 29 Oct 1995, *Sklenar & Kosteckovar 1499* (AAU); Cerros Yuibug-Pailacajas (4730 m), E side of the mountain ridge, 01°45'S, 78°27'W, 4300-4350 m, 31 Jul 1997, *Sklenar & Sklenarova 3025* (UC). **Imbabura:** SW slopes of the volcano Cotacachi, 00°22'N, 78°21'W, 4100-4320 m, 09 Nov 1983, *Boysen Larsen et al.* (AAU); slopes of Volcán Cotacachi, 00°35'N, 78°20'W, 4150 m, 11 Oct 1987, *Ramsay & Merrow-Smith 796* (AAU); Cerro Imbabura, in a gully on the S side of the volcano, 00°15'N, 78°10'W, 4400 m, 05 Jun 1995, *Sklenar & Kostekova 520* (AAU); Nevado Cotacachi, SE ridge of the volcano, 00°21'N, 78°21'W, 4200-4400 m, 09 Sep 1995, *Sklenar & Kosteckovar 1237* (UC); Cerro Imbabura, 00°15'S, 78°10'W, 4300 m, 05 Jun 1995, *Sklenar & Kosteckovar 31-16* (QCA), *31-17* (AAU). **Loja:** Cerro Toledo, E of Yangana, between Loja and Valladolid, 04°23'S, 79°07'W, 3000-3100 m, 26 Oct 2004, *Lehnert 1465* (GOET, QCA, UC). **Napo:** Laguna Yuragcocha, 3 km E of Cerro Quilindaña, 00°47'S, 78°21'W, 4050 m, 31 Mar 1979, *Holm-Nielsen 16375* (AAU); the SW slope 1.5 km from Cerro Quilindaña, 00°47'S, 78°21'W, 4100 m, 01 Apr 1979, *Holm-Nielsen 16416* (AAU); Cordillera de los Llanganatis, NE side of Laguna Encantada, 01°11'S, 78°12'W, 3430 m, 16 Mar 1983, *Holm-Nielsen et al. 41858* (AAU); around Laguna Yuragcocha, 3 km E of the peak of Cerro Quilindaña, Cordillera Oriental, 00°47'S, 78°21'W, 4100 m, 31 Mar 1979, *Løjtnant & Molau 11567* (AAU); Volcán Antisana, rocky slopes on the W side of the mountain, 00°30'S, 78°10'W, 4500-4550 m, 21 Jul 1997, *Sklenar & Sklenarova 2803* (UC); Volcán Antisana, rocky slopes on the W side of the mountain, 00°30'S, 78°10'W, 4500-4550 m, 21 Jul 1997, *Sklenar & Sklenarova 2806* (UC). **Pichincha:** heading down W-SW from the highest point of Sincholagua, 00°35'S, 78°21'W, 4600 m, 02 Jun 1985, *Bosco Nowak 171* (QCA); NE side of Cayambe mountain, 14500 ft, 10 Dec 1961, *Cazalet & Pennington 5750* (B, UC); Volcán Atacazo, SW slope, Km 19 from San Juan, 00°21'S, 78°39'W, 2900 m, 25 Aug 1980, *Holm-Nielsen & Azanza 25180* (AAU); Nevado Cayambe, ladera S, 00°00.5'N, 78°00.95'W, 3700-3800 m, 29 Jun 2002, *Lehnert 108* (GOET, QCA, UC); “*In Monte Pichincha,*” 3500 m, 1921, *Mille s.n.* (P). **Pichincha/Cotopaxi:** NE slope of Illiniza Sur, 00°40'S, 78°42'W, 4400 m, 28 May 1995,

*Sklenar & Sklenarova 19\_2* (UC). **Pichincha/Napo:** W side of a mountain ridge, ca. 2 km to the W from cerro Sara Urcu, 00°06'S, 77°57'W, 4400 m, 29 Aug 1995, *Sklenar & Kosteckovar 100-9* (AAU). **Tungurahua:** Volcán Tungurahua, N side of the mountain, steep slope to the right of the summit, 01°27'S, 78°27'W, 4100 m, 08 Aug 1997, *Sklenar & Sklenarova 3207* (UC).

This species is easily confused with *M. peruviana* but can be distinguished by the evenly distributed hairs on the abaxial laminae (vs. clustered in sori in *M. peruviana*), more widely spaced fronds, and paler, more broadly lanceolate rhizome scales (vs. dark brown to blackish and narrowly lanceolate) which are often shed between the fronds (vs. usually persistent). *Melpomene sklenarii* grows in loose formations with the distant fronds held erect whereas *M. peruviana* tends to form dense mats and holds the fronds stiffly tip-downwards.

The rather small range of *M. sklenarii* matches that of *M. vulcanica*. Even though large specimens of the latter are easily separated from *M. sklenarii* (segments long-deltate with acute tips, costae visible on both sides vs. segments oblong to round with obtuse tips, costae not visible adaxially), small plants may be confused with *M. sklenarii*. Even if equal in size, *Melpomene vulcanica* still has larger scales than *M. sklenarii* (6.2 x 1.0 mm, 20-30 cells wide across bases vs. to 3.5 x 0.6 mm, 14-18(-26) cells wide across bases); both species have hyaline pinna margins, but those of *M. vulcanica* are two cell rows wide and beset with glandular cells or hairs whereas those of *M. sklenarii* are just one cell row wide in most parts and lack glands.

Small plants of *M. flabelliformis* can be distinguished from *M. sklenarii* by their hairs clustered in the sori and the only weakly marginate petioles (vs. hairs not clustered in sori and petioles marginate to alate throughout in *M. sklenarii*); the laminae are proximally more strongly cuneate in *M. flabelliformis*, too. The two species have not been found growing together so far, and especially the small forms of *M. flabelliformis* occur mainly outside the range of *M. sklenarii* (i.e., Mexico and Africa).

- 22. *Melpomene sodiroi*** (H. Christ & Rosenst.) A. R. Sm. & R. C. Moran. Novon 2: 431. 1992. *Polypodium sodiroi* H. Christ & Rosenst., Repert. Spec. Nov. Regni Veg. 5: 14. 1908. *Grammitis sodiroi* (H. Christ & Rosenst.) C. V. Morton, Contr. U.S. Natl. Herb. 114. 1967. *Xiphopteris sodiroi* (H. Christ & Rosenst.) Crabbe, Brit. Fern Gaz. 9: 319.

1967. Type. Ecuador. Tungurahua, base of Mt. Tungurahua, *Rimbach 24* (holotype, P; isotypes, UC, US). Figs. 26D, 32.

*Plants* predominately epiphytic or epilithic, growing in moss layers. *Rhizomes* moderately to long horizontally creeping, 0.8-1.6 mm diam. (Fig. 32A). *Fronde*s 100-320 mm, pendent, inserted onto the rhizomes at right angles, remotely placed (5-15 mm). *Scales* to 6.0-9.0(-10.0) x 1.0-1.2 mm, (20-)24-30(-34) cells wide (some scales of the inner layers much smaller), clathrate (Fig. 32B), dark brown to brown, iridescent, broadly cordate to pseudopeltate, attenuate to long attenuate at tips; apical glands 1-5 cells linearly arranged (Fig. 32C). *Petioles* 45-90(-110) mm long, 0.5-0.8(-1.0) mm diam., terete, glabrous to glabrescent with few dark brown hairs 0.75-1.2 mm long (Fig. 32 D); simple and branched glandular hairs of crosiers and young fronds may persist in older fronds. *Laminae* to (70-)170-230 mm long, 12-40 mm wide, lanceolate to elliptic (widest around the middle), rounded to truncate at bases, short acute to attenuate at tips (Fig. 32A). *Rhachises* dark brown to black, planar and slightly sunken adaxially (Fig. 32E), hemispherically protruding abaxially, glabrous (Fig. 32F). *Pinnae* (7.0-)8.0-17.0(-22.0) x (2.2-)2.6-3.2(-3.5) mm (3-7 times as long as wide, rarely less), gibbose, patent to ascending (85-60°), inequilateral and decurrent towards their base, fully adnate, deltate to linear-oblong, the tips obtuse (Fig. 32E, F); costae not visible (Fig. 32F), but sometimes protruding abaxially in dried specimens; 1-3 proximal pinna pairs markedly smaller than subsequent segments, rounded but not alariform; hydathodes present (Fig. 32E). *Sori* 2-12 pairs per segment, without or with 1-12 short hairs (less than 1 mm) (Fig. 32F).

**Distribution and habitat.** Elfin forests and wet montane forests at 2800-4000 m in Colombia and Ecuador (Fig. 26D).

**Additional specimens examined. COLOMBIA. Nariño:** “in monte ignivomis Azufral, Cord. merid. n. gr.”, 3800 m, 18 May 1876, *André 3286* (NY).

**ECUADOR. Azuay:** Las Cajas; near laguna Toreadora, 02°43'S, 79°12'W, 3900 m, 13 Sep 1983, *Boysen Larsen & Eriksen 45127* (AAU); Cajas, Laguna Dos Chorreras, ca. 02°50'S, ca. 79°10'W, 3600-3650 m, 16 Nov 2003, *Lehnert 1106* (GOET, QCA, UC), surroundings of Laguna Toreadora, 02°47.17'S, 79°13.10'W, 3700-3800 m, 14 Nov 2004, *Lehnert 1555* (GOET, QCA, UC). **Chimborazo:** El Altar, N side of the volcano, on the ridge below the Canonigo peak, 01°41'S, 78°24'W, 4200 m, 20 Aug 1995, *Sklenar & Sklenarova*



94-1 (AAU). **Chimborazo/Morona Santiago**, Cerro Yuibug-Pailacaja (4730 m a.s.l.), E side of the mountain ridge, 01°45'S, 78°27'W, 4100-4200 m, 30 Jul 1997, *Sklenar & Sklenarova 3070* (AAU). **Loja**: PN Podocarpus, Cajanuma, trail to "Lagunas del Compadre," 2975 m, 08 Aug 2003, *Lehnert 791* (GOET, QCA, UC); road Pichig-Fierro Urco, ca. 10 km, 03°41'S, 79°20'W, 3000-3500 m, 20 Jan 1990, *Madsen 86752* (AAU); road Pichig-Fierro Urco, ca. 10 km, 03°41'S, 79°20'W, 3000-3500 m, 20 Jan 1990, *Madsen 86753* (AAU). **Loja/Zamora-Chinchipe**: road Amaluza-Zumba (in construction), Km 37, 04°44'36"S, 79°25'28"W, 3500 m, 12 Aug 2001, *Madsen et al. 8257* (AAU). **Morona-Santiago**: Parque Nacional Sangay, Peace Corps Sangay Mountaineering Expedition, between Plazapamba and Yanayacu, 02°02'S, 78°25'W, 3200-3600 m, 23-31 Dec 1995, *Clark et al. 1825* (UC). **Napo**: NE slope of Volcán Cayambe, 00°05'N, 77°59'W, 3900-4000 m, 21 May 1980, *Holm-Nielsen & Jaramillo 23676* (AAU); Páramo de Soguillas, near las Torres de Llanganatis, 01°08-09'S, 78°15-16'W, 3850-4000 m, 16-17 May 1982, *Øllgaard & Holm-Nielsen 38758* (AAU); Llanganati, N facing slope towards the Río Golpe, just N of Chosa Aucacocha, 01°08'S, 78°18'W, 3500-3600 m, 15-16 May 1982, *Øllgaard et al. 38629, 38702* (AAU); Páramo de Guamaní, 14000 ft, 16 Jan 1981, *Proctor 38737* (QCA). **Pichincha**: Páramo de La Virgen, 4050 m, 16 Mar 1994, *Cornejo & Laegaard 2087, 2091* (AAU); Cayambe, northern slope, 00°05'N, 78°00'W, 3800-3900 m, 03 Jul 1980, *Holm-Nielsen & Øllgaard 24328* (AAU), Cayambe-Olmedo-Laguna San Marcos, turnoff towards Cerro Mirador, 00°05'N, 78°01'W, 3880 m, 01 Jan 1988, *Jørgensen 61967* (AAU); 2 km S of Paso de la Virgen on road Quito-Baeza, 00°20'S, 78°13'W, 4000-4200 m, 19-20 May 1984, *Laegaard 52141* (AAU); carretera Quito-Baeza, Km 256, 4300 m, 08 Jul 2002, *Lehnert 171, 173* (GOET, QCA, UC); road Olmedo-Laguna San Marcos, W of the pass, 00°05'N, 78°01-02'W, 3600 m, 10 Jul 1980, *Øllgaard et al. 34342* (AAU); Volcán Cayambe, N slopes, 00°03-05'N, 77°59'W, 3750-3850 m, 09 Jul 1980, *Øllgaard et al. 34235* (AAU); along road Quito-Papallacta, 2800-3900 m, 23 Feb 1994, *van der Werff & Gray 13355* (UC). **Tungurahua**: Cordillera de los Llanganates NW of saddle between Río Topo and Río Verde Grande on W slopes of Cerro Hermoso, 2.4 km from the summit, 01°13'S, 78°18'W, 3850-3950 m, 10 Nov 1980, *Holm-Nielsen & Jaramillo J. 28350, 28367* (AAU), Volcán Tungurahua, trail from Baños to refugio of Tungurahua, 01°27'S, 78°27'W, 2000-3800 m, 31 May-01 Jun 1983, *Lawesson et al. 44137* (AAU).

*Melpomene sodiroi* is one of the most distinct species of the genus. Surprisingly, it has often been confused with *M. pseudonutans*. Both species often grow side-by-side and are among the larger *Melpomene* species, but there the similarities end. *Melpomene sodiroi* is

characterized by gibbose pinnae with immersed sori and often whitish abaxial laminae, dark reddish brown rhizome scales with long-attenuate, straight tips and long terete petioles; *Melpomene pseudonutans* has flat pinnae with green surfaces and superficial sori, the tips of the brown to auburn scales usually undulate, and at least marginate petioles. Furthermore the costae are usually visible in *M. pseudonutans* and not so in *M. sodiroi*. Other similar species are *M. occidentalis*, which can also be distinguished by the visible costae, and *M. personata*, with which a real relationship apparently exists (Lehnert et al., in prep. a). The latter species sometimes has obscure costae and generally has the hairs clustered in the sori, but differs in smaller rhizomes scales (to 4.5 mm long, 10-14 cells wide vs. 6.0-9.0 mm long, 24-30 cells wide in *M. sodiroi*) and flat pinnae with green abaxial surfaces (vs. usually gibbose and whitish). *Melpomene youngii*, from northern Peru, is another species with whitish abaxial laminae and gibbose pinnae, although to lesser extent than in *M. sodiroi*. It also lacks brown acicular hairs (vs. some hairs present in sori and scattered on petioles in *M. sodiroi*) and has stronger ascending pinnae by (60-30° vs. 85-60° in *M. sodiroi*).

- 23. *Melpomene vernicosa*** (Copel.) A. R. Sm. & R. C. Moran, Novon 2: 431. 1992. *Ctenopteris vernicosa* Copel., Philipp. J. Sci. 84: 452, t. 9. 1955 (1956). *Grammitis vernicosa* (Copel.) C. V. Morton, Contr. U.S. Natl. Herb. 38. 110. 1967. Type. Costa Rica. Cartago, Alto de Estrella, *Standley 39140* (lectotype, US, designated by Morton, U.S. Natl. Herb. 38. 110. 1967).
- Melpomene pennellii* (Copel.) A. R. Sm. & R. C. Moran, Novon 2: 430. 1992. *Grammitis pennellii* (Copel.) C. V. Morton, Phytologia 22: 82. 1971. *Ctenopteris pennellii* Copel., Philipp. J. Sci. 84: 397. 1955 (1956). Type. Colombia. Cauca: "San José," San Antonio, *Pennell & Killip 7379* (holotype, US). Figs. 33, 34A.

Etymology: Named for the shiny adaxial surfaces of the laminae (Latin *vernix* = laquer).

*Plants* epiphytic in moss layers, sometimes terrestrial. *Rhizomes* stout, very short-creeping to erect, (1.5-)1.8-2.2 mm diam. (Fig. 33A). *Fronde*s erect to patent, inserted onto the rhizome in a narrow angle, fasciculate (0.5-2.0 mm apart) (Fig. 33A). *Scales* 4.0-6.2 x 0.4-0.5 mm, 10-18(-20) cells wide across their bases, the cells prosenchymatic, clathrate (Fig. 33B), dark brown to blackish, strongly iridescent, narrowly cordate at bases, long acute to attenuate at tips; apical glands 3-8 cells in nodding clusters or palmately arranged. *Petioles* (20-)45-66

mm long, (0.8-)1.0-1.2 mm thick, terete or rarely very narrowly marginate, densely hairy, with stiff, dark brown hairs (0.6-)1.0- 2.0 mm long (Fig. 33C); simple and branched glandular hairs very sparse or absent. *Laminae* to 150-210 x 36 mm, broadly elliptic (broadest in the middle), decurrent in proximal half, truncate at bases, acute at tips (Fig. 33A). *Rhachises* very dark brown to black, planar adaxially (Fig. 33D), strongly hemispherically protruding abaxially (Fig. 33E), strongly hairy abaxially, glabrous adaxially or only weakly hairy proximally; hairs castaneous to black, 0.8-1.2 mm long, some basally with 2-3 vesiculose hyaline cells, with branches identical to glandular hairs. *Pinnae* 16.0-20.0 x 3.0-3.5 mm (7-9 times as long as wide), patent or nearly so (90-80°), equilateral at bases, fully adnate, linear-oblong, the tips obtuse, somewhat gibbose; costae obscurely visible in dried specimens (Fig. 33E); proximal pinna pairs sometimes markedly smaller than subsequent segments (one half to one third of longest pinnae), but not alariform; hairs like those on rhachises clustered in sori (Fig. 33D), scattered along the costae, but also evenly distributed on laminae abaxially, absent adaxially and on the margins (Fig. 33D); hydathodes present, weakly immersed in tissue (Fig. 33E). *Sori* 3-14 pairs per segment, 3-8 hairs to 1.5 mm long within each sorus (Fig. 33E).

**Distribution and habitat.** Wet montane forests at 1200-2650 m in Mexico, Honduras, Costa Rica, Colombia, Ecuador, and northern Peru (Fig. 34A).

**Specimens examined. MEXICO. Chiapas:** 1902, *Münch 101* (P). **Oaxaca:** Sierra de Juárez, Km 85 ruta 175 Tuxtepec-Oaxaca, 1800 m, 20 Nov 2005, *Kessler 13502* (GOET).

**HONDURAS. Lempira:** Celaque National Park; between Camp 1 and first summit, ca. 8 km WSW of the town of Gracias, 14°33'N, 88°41'W, 2400 m, 18 Nov 1991, *Moran & Rohrbach 5634* (UC).

**COSTA RICA. San José:** Massif of Cerro de La Muerte, 2900 m, 23 Jul 2003, *Kluge 7018* (GOET). **Puntarenas:** Canton de Coto Brus. Z.P. Las Tablas, Cuenca Térraba-Sierpe, Cerro Chai, Las Alturas de Coton, Coto Brus, 08°57'50"N, 82°49'44"W, 1900-2100 m, 23 Jun 1997, *Coto 35* (UC).

**COLOMBIA. Antioquia:** Belmira, vereda La Salazar (lower part), quebrada El Diablo, 2625 m, 06°35'57.3"N, 75°39'15.6"W, 20 Jun 2002, *Rodriguez W. D. & Arboleda 3448* (NY). **Cundinamarca:** Soacha, Sabaneta, 2850 m, 19 Oct 1961, *Murillo M. T. 447* (NY). **Huila:** Cordillera Central, Cordillera del Buey, hike from Finca Loyola over the páramo down to San Antonio, 2100 m, 14 Dec 1975, *Bishop 1992* (UC). **Nariño:** Quebrada de Imbé at Rio Coaiquer, W slopes of the cordillera of Pasto, 1200 m, 27 Jul 1880, *Lehmann 76* (B).

**Santander del Norte:** Herrán, Parque Nacional Natural Tama, sector Orocué, towards Alto del Pesebre, 2650-3020 m, 02 Apr 1987, *Lozano et al. 5484, 5500* (COL).

**VENEZUELA. Merida:** “Merida,” 1856, *Moritz 216* (B, P); Dtto. Andres Bello, La Carbonera, ca. 13 mi NNW of Jají along Highway 4, property of the Universidad de los Andes, 08°40'N, 71°26'W, 2000 m, 20 Nov 1982, *Smith A. R. et al. 1471* (UC). **Trujillo:** Dtto. Boconó, 22 km SE of Boconó, road to Guaramacál, 09°12'N, 70°10'W, 2300 m, 25-26 Nov 1982, *Smith A. R. et al. 1570* (UC); 24-28 km SE of Boconó, road to Guaramacál, 09°12'N, 70°10'W, 1700-2000 m, 25-26 Nov 1982, *Smith A. R. et al. 1593* (UC).

**ECUADOR. Azuay:** 9.9 km N of Sevilla de Oro, 2250-2300 m, 14 Aug 1982, *Clemants 2332* (NY). **Loja:** road Loja-Zamora, app. Km 10, 03°59'S, 79°10'W, 2400-2600 m, 17 Sep 1988, *Madsen 75342* (AAU); trails ca. 5 km ENE of San Pedro de Vilcabamba, Loma Solamaco to upper Quebrada Romerillos, 04°14'S, 79°10'W, 2300-2400 m, 01 Dec 1994, *Øllgaard et al. 105984* (AAU). **Pastaza:** Carretera Mera-Baños, ca. 2 km después Mera, 01°27.3'S, 78°09.7'W, 1000 m, 09 Jul 2002, *Lehnert 186* (GOET, QCA, UC). **Zamora-Chinchipe:** area of ECSF Research Station, around km 30 on road Loja-Zamora, E of Ceja Andina., 03°58'18"S, 79°04'44"W, 2200 m, 28 Apr 1999, *Bussmann et al. 12728* (UC); road Loja-Zamora, km 24-25, 03°59'S, 79°05'W, 1950-2100 m, 15 Apr 1973, *Holm-Nielsen et al. 3515* (AAU), new road Loja-Zamora, ca. 4 km E of pass "El Tiro," 03°59'S, 79°08'W, 2650 m, 23 Sep 2004, *Lehnert 1331, 1333, 1334* (GOET, QCA, UC).

**PERU. Amazonas:** Chachapoyas, Carretera Chachapoyas–Mendoza, Km 52 from Chachapoyas, 10 km behind Molinopampa, 06° 14.26'S, 77° 35.96'W, 2700 m, 04 Aug 2002, *Lehnert 237* (GOET, UC, USM); a few km from Molinopampa, 14 Mar 1998, *van der Werff et al. 14898* (UC); road Chachapoyas-Mendoza, a little past Molinopampa, 06°14'11"S, 77°35'49"W, 2400 m, 15 Mar 1998, *van der Werff et al. 15068* (UC).

*Melpomene vernicosa* is a large representative of the genus. It differs mainly the size of all parts from *M. xiphopteroides*: rhizome diam. 1.8-2.2 mm vs. 0.6-0.8 mm, and petiolar diam. 1.0-1.2 mm vs. 0.6-0.8 mm. *Melpomene vernicosa* is found mainly at the upper limit of its elevational range, i.e., above 1800 m, whereas *M. xiphopteroides* occurs mainly below 2000 m. However, their elevational ranges overlap completely. Geographically, the overlap is also considerable: Both occur from Mexico to Colombia and south to northern Peru, but whereas *M. vernicosa* is restricted to the continent north of the Amotape-Huancabamba region, *M. xiphopteroides* extends to the Greater Antilles and south to Bolivia and SE Brazil (in latter region as var. *acrodontium*).

The Venezuelan collections *Smith et al. 1570* and *1593* (UC) have petioles weakly marginate but clearly belong otherwise to *M. vernicosa*; this is a good example of the ambiguity of this character.

Within the genus, the hairs of *Melpomene vernicosa* with branched glandular bases and dark acicular tips (Fig. 1G), which are borne on the rhachises abaxially, are unique. Unfortunately, they are not present in all specimens and are thus not a reliable distinguishing character. Similar hairs occur in other grammitid genera, e.g., *Lellingeria tungurahuae* (Rosenst.) A. R. Sm. & R. C. Moran (de la Sota et al., 2000).

**24. *Melpomene vulcanica*** Lehnert, sp. nov. Type. Ecuador. Napo: road Olmedo-Laguna San Marcos, E of the pass, 00°07'N, 77°59'W, 3640 m, 08-09 Jul 1980, *Øllgaard et al. 34159* (holotype, AAU, isotype, QCA). Figs. 34B, 35.

A *Melpomene pseudonutante* frondibus lanceolatis basin versus truncatis vel breve cuneatis (vs. frondibus longe obovatis basin versus decurrentibus) rhizomatibusque tenuioribus (0.8-1.5 mm vs. 1.8-2.5 mm), a *M. personata* pilis laminarum abaxialium aequaliter dispersis (vs. pilis in soribus confertis) frondibusque erectis (vs. pendentibus) differt.

Etymology: This species has been found mainly on the slopes of volcanoes in Ecuador and Colombia.

*Plants* epiphytic or terrestrial; in mosslayers on trunks of trees or the caudices of *Blechnum*, in ditches; sometimes directly in soil. *Rhizomes* horizontal, moderately to long-creeping, regularly branching in wide to right angles, (0.8-)1.2-1.5 mm diam. (Fig. 35A, B). *Fronde* 100-250 mm, erect, inserted onto the rhizomes in a right angle, or in narrow angles and strongly ascending; widely placed ((2-)10-20 mm) (Fig. 35A). *Scales* 3.5-6.2 x 0.6-1.0 mm, (18-)20-30(-46) cells wide, clathrate, cell walls thick and dark brown to thin and brown, weakly iridescent, broadly cordate to pseudopeltate, acute to attenuate at the flat to flaring tips (Fig. 35C); apical glands 3-8 cells (rarely more), palmately or linearly arranged, rather small and fugacious. *Petioles* (20-)35-65(-80) mm long, 0.6-1.0 mm diam., marginate from the laminae bases to semiterete, glabrescent to hairy, with brown acicular or catenate, flaccid hairs 1.0-1.5 mm long (Fig. 35D); simple and branched glandular hairs to 0.2 mm long rarely

present; petiolar bases with scales. *Laminae* (10-)16-30(-34) x (45-)90-220 mm, lanceolate (broadest below the middle, normally after the second pinna pair), rather abruptly ending at base, i.e., truncate or widely cuneate, acute to attenuate at tips (Fig. 35A). *Rhachises* dark brown to black, planar and slightly sunken adaxially (Fig. 35E), hemispherically protruding abaxially (Fig. 35F), with scattered brown, acicular hairs, 1.0-1.2 mm long. *Pinnae* (9.0-)10.0-14.5(-17.0) x (2.8-)3.2-3.8 mm (3-4 times as long as broad), patent or weakly ascending (80-60°), inequilateral, decurrent towards the bases, fully adnate, linear-oblong, the tips acute to obtuse (Fig. 35E, F); green from below, with scattered hairs like those on the rhachises; costae visible at least abaxially, black, with some scattered hairs like those on the rhachis (Fig. 35F); pinna margins hyaline, 1-2 cells wide, with few glandular hairs; proximal 1-3 pairs markedly smaller than the subsequent segments, but not alariform. *Sori* 2-4 pairs per segment, surrounded by (0-)2-8 brown hairs to 1.2 mm long (Fig. 35F).

**Distribution and habitat.** Páramos, elfin forest; most frequent on the northern and eastern volcanoes. (2600-)3200-4500 m in Colombia and Ecuador (Fig. 34B).

**Specimens examined. COLOMBIA.Cauca:** Cordillera Central, Parque Nacional del Puracé, camino de Pimabalá al volcán del Puracé, 3700 m, 19 Jul 1976, *Jaramillo Mejia & van der Hammen 5218* (COL); left side of road Tóez-Tacueyo, 3640 m, Sep 1980, *Rangel 2396* (COL). **Huila:** Cordillera Central, Cordillera del Buey, hike from Finca Loyola over the páramo down to San Antonio (2100 m according to residents), 2600 m, 14 Dec 1975, *Bishop 1986* (UC). **Huila-Cauca:** Macizo Colombiano, páramo Las Papas, cerros y alrededores de la laguna La Magdalena, 3530 m, 16 Oct 1958, *Idrobo et al. 2954* (AAU). **Nariño:** Páramo El Tabano, Alto de la Cordillera, entre Pasto y El Encano, vertiente occidental, 3200 m, 11 Jan 1941, *Cuatrecasas 11920* (COL); Pasto, Volcán Galeras, páramo al S de la cima, 3700 m, 24 Dec 1972, *Hagemann & Leist 1783* (COL); vertientes de Cumbal, 3400-4300 m, 22 Jan 1973, *Hagemann & Leist 1974* (COL). **Risaralda:** Santa Rosa, Cordillera Central, entre la hacienda La Sierra y Termales de Santa Rosa, Quebrada La Sierra, 3525 m, 26 Jan 1980, *Jaramillo Mejia et al. 5931* (COL).

**ECUADOR. Carchi:** Páramo El Angel, in the pass on road El Angel-Tulcán, 00°41'N, 77°54'W, 3750-3850 m, 15 May 1973, *Holm-Nielsen et al. 5476* (AAU); carretera Tufiño-Maldonado- Lagunas Verde, 01°28'S, 79°13'W, 3900-4000 m, 01 Oct 1994, *Navarrete 756* (AAU); Volcán Chiles, along gully on the SW side of the volcano, 00°48'N, 77°57'W, 4150-4200 m, 23 Jun 1995, *Sklenar & Sklenarova 637* (UC). **Chimborazo:** El Altar, N side of the

volcano, on the ridge below the Canoningo peak, 01°41'S, 78°24'W, 4200-4400 m, 19 Aug 1995, *Sklenar & Kosteckovar 950, 93-15* (UC). **Imbabura:** E slopes of Cayambe peak, 3200 m, 16 Jul 1944, *Wiggins 10407* (NY). **Morona Santiago:** trail Alao-Huamboya, around the pass, between Cuspipaccha and alt. 3700 m on E slope, 01°47'S, 78°25'W, 3550-3950 m, 07 May 1982, *Øllgaard et al. 38233* (AAU); trail Alao-Huamboya, around the pass, 01°47'S, 78°25'W, 3550-3950 m, 07 May 1982, *Øllgaard et al. 38290* (AAU); Cerros Yuibug-Pailacajas, E side of the mountain ridge, 01°45'S, 78°27'W, 4300 m, 31 Jul 1997, *Sklenar & Sklenarova 2968* (UC). **Napo:** Cordillera de los Llanganates, loma between Río Topo and Río Verde Grande, 3 km WNW of Cerro Hermoso, 01°13'S, 78°18'W, 4000 m, 10 Nov 1980, *Holm-Nielsen & Jaramillo J. 28329* (AAU); Cordillera de los Llanganatis, NE side of Laguna Encantada, 01°11'S, 78°12'W, 3430 m, 16 Mar 1983, *Holm-Nielsen et al. 41769, 41802, 41811, 41842* (AAU); S side of the crater of Cerro Sumaco, 00°34'S, 77°43'W, 3780-3820 m, 26 Apr 1979, *Holm-Nielsen et al. 17334* (AAU); E side of Cerro Sumaco, 00°34'S, 77°43'W, 3750 m, 30 Apr 1979, *Holm-Nielsen et al. 17469* (AAU); SE side of Cerro Sumaco, 00°34'S, 77°43'W, 3750 m, 30 Apr 1979, *Holm-Nielsen et al. 17489* (AAU); *ibid.*, 3750-3800 m, 01 May 1979, *Holm-Nielsen et al. 17550, 17577, 17590* (AAU); *ibid.*, 3200 m, 02 May 1979, *Holm-Nielsen et al. 17699* (AAU); *ibid.*, 3350 m, 05 May 1979, *Holm-Nielsen et al. 17969* (AAU); carretera Quito-Baeza, Quijos, 4300 m, 08 Jul 2002, *Lehnert 176* (GOET, QCA, UC); N-facing slopes at the W side of Laguna Parcacocha, 00°16'S, 78°09'W, 4100 m, 18 Mar 1979, *Løjtnant & Molau 11164* (AAU); NE-facing ridge on the N side of Cerro Sumaco, 00°35'S, 77°39'W, 3600-3700 m, 24 Apr 1979, *Løjtnant & Molau 12664* (AAU); S side of Cerro Sumaco, 100-200 m S of the main crater, 00°35'S, 77°39'W, 3700-3800 m, 29 Apr 1979, *Løjtnant & Molau 12954B, 12954C* (AAU); Oyacachi, 5 km después del paso, bosques en los márgenes del carretero, 00°12'S, 78°06'W, 3500 m, 28 Dec 1996, *Navarrete 1367* (AAU, QCA) Oyacachi, Yarupaccha, 00°12'S, 78°07'W, 3620-3680 m, 16 Jan 1996, *Navarrete 1416* (AAU), road Quito-Baeza, 7-8 km NW of the Laguna Papallacta (Páramo de Guamani), 00°19'S, 78°08'W, 3800 m, 20 Jul 1976, *Øllgaard & Balslev 8162* (AAU); Páramo de Soguillas, near Las Torres de Llanganati, 01°08-09'S, 78°15-16'W, 3850-4000 m, 16-17 May 1982, *Øllgaard & Holm-Nielsen 38752* (AAU); Llanganati, páramo SE of Chosa Aucacocha, between Aucacocha and Pan de Azucar, 01°09'S, 78°18'W, 3800-3900 m, 15 May 1982, *Øllgaard et al. 38496* (AAU); Volcán Antisana, rocky gully on the W side of the mountain, 00°30'S, 78°10'W, 4400-4500 m, 22 Jul 1997, *Sklenar & Sklenarova 2784* (AAU, UC); NE side of Volcán Antisana, 00°27'S, 78°08'W, 4300 m, 17 Aug 1997, *Sklenar & Sklenarova 3402* (AAU, UC); *ibid.*, 00°27'S, 78°08'W, 4200 m, 18 Aug 1997, *Sklenar &*

*Sklenarova 3438* (AAU, UC); Hacienda Yanahurco, 3800 m, 28 Aug 2001, *Smith A. R. et al. 2875* (UC). **Pichincha:** Guamani pass, E of Pifo, Cordillera Oriental, 4000 m, 10 Nov 1944, *Ewan 16447* (UC); 2 km S of Paso de la Virgen on road Quito-Baeza, 00°20'S, 78°13'W, 4000-4200 m, 19-20 May 1984, *Laegaard 52148* (AAU); Carretera Quito-Baeza, 00°20.2'S, 78°13.2'W, 4200 m, 08 Jul 2002, *Lehnert 168* (GOET, QCA, UC); *ibid.*, Km 256, 4300 m, 08 Jul 2002, *Lehnert 174* (GOET, QCA, UC); Páramo de Guamaní, Carretera Pifo-Papallacta, 00°19'S, 78°12'W, 3960 m, 13 Jan 1990-26 May 1991, *León S. 1164* (AAU); Volcán Cayambe, N slopes, 00°03-05'N, 77°59'W, 3750-3850 m, 09 Jul 1980, *Øllgaard et al. 34235A* (AAU); road and trail from Chaupi-páramo of Volcán Corazón, 00°34'S, 78°41'W, 4140 m, 15 Mar 1995, *Øllgaard et al. 1194* (AAU); W side of a mountain ridge ca. 2 km to the west from cerro Sara Urcu, 00°06'S, 77°57'W, 4100 m, 30 Aug 1995, *Sklenar & Sklenarova 108-2* (AAU); Pichincha/Napo border, edge of Antisana reserve, 3800 m, 28 Aug 2001, *Smith A. R. et al. 2871* (UC); along road Quito-Pallapacta, 2800-3900 m, 27 Feb 1994, *van der Werff & Gray 13356* (UC); at pass of road Quito-Pallapacta, 4000 m, 14 Jul 1991, *van der Werff & Palacios 12357* (AAU). **Pichincha/Napo:** Volcán Cayambe, N slopes, 00°03-05'N, 77°59'W, 3750-3850 m, 09 Jul 1980, *Øllgaard et al. 34290* (AAU); road Olmedo-Laguna San Marcos, E of the pass, 00°07'N, 77°59'W, 3620-3800 m, 10-11 Jul 1980, *Øllgaard et al. 34462* (AAU); W side of a mountain ridge, ca. 2 km to the west from cerro Sara Urcu, 00°06'S, 77°57'W, 4400 m, 29 Aug 1995, *Sklenar & Kosteczkovar 1118* (AAU). **Tungurahua:** Santiago de Pillaro Cantón, páramos de Pisayambo, surroundings of laguna de Pisayambo, 01°05'S, 78°23'W, 3600-3900 m, 11 Oct 1998, *Cueva 249* (UC); Santiago de Pillaro, Parque Nacional Llanganates, W of Cerro Hermoso, near saddle between headwaters of Río Verde and Río Topo, 01°11'40"S, 78°19'34"W, 3950 m, 12 Nov 1999, *Neill et al. 12005* (UC); Cerro Hermoso, SW ridge of the mountain, 01°14'S, 78°18'W, 4100 m, 06 Sep 1997, *Sklenar & Sklenarova 3625* (AAU); Patate Cantón, Parque Nacional Llanganates, slopes of Cerro Pan de Azúcar, on transect Páramo de Soguillas-Cerro Pan de Azúcar, 01°09'S, 78°17'W, 3800 m, 13 Oct 1998, *Vargas H. et al. 2820* (UC).

The size of the laminae and the thickness of the cell walls in the scales vary considerably in this species, and every extreme of one character can be found within the whole range of the other without apparent correlation to the life form. However, plants with large fronds seem to grow in sheltered spots, i.e., they are present in nearly all epiphytes, but also in terrestrial plants from sheltered spots, e.g., rock gullies. Smaller scales with thick cell walls are found in terrestrial plants growing directly on soil; large scales with wide, iridescent



lumina are produced if the rhizomes grow in thick moss layers, i.e., in all epiphytes and some terrestrial plants from páramos. However, the scales are always larger than in *M. sklenarii*, which is similar to the small forms of *M. vulcanica*.

Rhizomes of *M. vulcanica* are usually long creeping and do not bear any developed fronds over a length of the apices. This clearly separates this species from *M. pseudonutans*, which has a rather compact growth (although the posterior parts of the rhizome persist and contribute greatly to the total length). The rhizomes of *Melpomene pseudonutans* are thicker (usually more than 2.0 mm diam. vs. usually less than 1.5 mm in *M. vulcanica*), its petioles are less hairy and thicker (1.0-1.2(-1.8) mm vs. 0.6-1.0 mm), and its blades are long-obovate (vs. lanceolate).

Other species with long-creeping rhizomes have hairs clustered in the sori, like *M. moniliformis* and *M. personata*, and/or the costae not or only partially visible on the abaxial laminae, like *M. flabelliformis*.

*Ollgaard et al. 1194* (AAU) and *Sklenar & Sklenarova 3019* (UC), both from Ecuador, are good examples of plants with strongly branching the rhizomes. *Bishop 1986* (UC), from Colombia, has extraordinarily thick but nevertheless long-creeping rhizomes.

**25. *Melpomene wolfii*** (Hieron.) A. R. Sm. & R. C. Moran, *Novon* 2: 431. 1992. *Polypodium wolfii* Hieron., *Hedwigia* 48: 249. 1909. *Ctenopteris wolfii* (Hieron.) C. V. Morton, *Contr. U.S. Natl. Herb.* 38: 115. 1967. Type. Ecuador. Pichincha: near Mindo, at base of Mount Pichincha, *Stübel 745* (holotype, B).

*Melpomene assurgens* (Maxon) A. R. Sm. & R. C. Moran, *Novon* 2: 429. 1992. *Polypodium assurgens* Maxon, *Contr. Gray Herb.* 165: 73. 1947. *Ctenopteris assurgens* (Maxon) Copel., *Philip. J. Sci.* 84: 386. 1955. *Grammitis assurgens* (Maxon) C. V. Morton, *Contr. U.S. Natl. Herb.* 38: 116. 1967. Type. Ecuador. Pichincha: Quito-Santo Domingo road, *Haught 3226* (holotype, US). Figs. 5D, 36.

*Plants* predominantly epiphytic, also in moss layers on rocks, rarely directly on soil. *Rhizomes* erect to ascending, posterior parts long-persisting, 1.5-2.0 mm diam. (Fig. 36A). *Fronds* erect, fasciculate, inserted onto the rhizome at acute angles, closely placed (1-2(-4) mm) (Fig. 36A). *Scales* 3.0-5.0(-6.0) x 0.5-0.8(-1.0) mm, (12-)16-26(-32) cells wide across the bases, clathrate (Fig. 36B), reddish brown to brown, strongly iridescent, broadly cordate to pseudopeltate, acute to attenuate at tip; apical glands 1-5 cells linearly to palmately arranged (Fig. 36C).

*Petioles* 9-35(-50) mm long, 0.8-1.0(-1.2) mm diam., marginate to alate from the lamina base, glabrous to glabrescent (Fig. 36D); simple and branched glandular hairs of crozier and young fronds may persist partially in older fronds. *Laminae* 130-410 x 3.5-15.0 mm, narrowly elliptic (broadest in the middle), strongly decurrent towards the bases, acute to attenuate at tips (Fig. 36A). *Rhachises* dark brown to black, planar or slightly protruding adaxially, hemispherically protruding abaxially; glabrous or with scattered branched glandular hairs on both sides, rarely sparsely short hairy abaxially in fertile portions (Fig. 36F). *Pinnae* 3.2-5.6(-6.0) x 3.5-4.5(-7.0) mm (0.75-2.0 times as long as wide), planar to weakly concave adaxially, often reflexed, weakly to strongly ascending (80-55°), equilateral at base or weakly decurrent towards the bases, fully adnate, usually truncate (Fig. 36E, F) to erose at tips (Fig. 36G), fertile segments often rounded, in large plants also oblong, with obtuse tips; costae not visible or obscurely so abaxially, costae and veins obscurely visible on both sides in most dried specimens; glabrous, rarely with some hairs (<1 mm) abaxially if sori hairy (Fig. 36F); proximal pinna pairs markedly smaller than the central segments, the lowermost pinnae always alariform; stomata sometimes visible as small red dots in dried specimens; hydathodes yellowish white, narrow elliptic, flat or weakly protruding (Fig. 36G). *Sori* 2-5 pairs per segment, without or with 1-5 short brown hairs less than 1.0 mm long (Fig. 36E, F).

**Distribution and habitat.** Moist montane forests at 1000-3400 m in Venezuela, Colombia, Ecuador, and Peru (Fig. 5D).

**Selected specimens examined.**

**COLOMBIA. Antioquia:** Sonsón, páramo of Las Palomas, 2720 m, 19 Aug 1974, *Acosta Arteaga 753* (COL); Mun. de Urrao, 2350 m, *Atehortúa & Hoyos* (QCA); Medellín, corregimiento Santa Elena, vereda Mazo, camino que conduce hacia la Bocatoma (Patos), 06°15'51.5"N, 75°30'47.4"W, 2400 m, 10 Jan 2001, *Rodríguez W. et al. 3186* (COL); Belmira, camino hacia la cabaña El Refugio, 06°38'46"N, 75°40'27"W, 3210 m, 30 May 2002, *Rodríguez W. et al. 3352* (COL); vereda la Amoladora, sector Montefrío, border between municipios San Pedro de los Milagros and San Jerónimo, 06°30'16.8"N, 75°39'16.3"W, 2920 m, 10 Oct 2002, *Rodríguez W. et al. 3706* (COL). **Caldas:** Río San Rafael, below Cerro tatama, Cordillera Occidental, 2600-2800 m, 07-11 Sep 1922, *Pennell 10353* (NY). **Chocó:** Mun. San José del Palmar, Cerro del Torrá, filo de cumbre, 2700-2800 m, 21 Aug 1988, *Silverstone-Sopkin et al. 4628* (UC). **Cundinamarca:** San Bernardo, Cordillera Oriental, Cuchilla de Paquilo, hacienda La Soledad, 2900 m, 22 Jul 1981,

*Jaramillo Mejía et al. 6914* (COL). **Huila:** Cordillera Central, Cordillera del Buey, hike from Finca Loyola over páramo down to San Antonio (2100 m according to resident), 2500 m, 14 Dec 1975, *Bishop 1988* (UC). **Nariño:** carretera La Victoria-Monopamba, Km 32, Motilón, 2500 m, 10 Jan 1973, *Hagemann & Leist 1837* (COL); San Francisco, carretera San Francisco-Mocoa, 2700-2800 m, 26 Nov 1967, *Mora 4368* (COL). **Putumayo:** Cordillera Portachuelo, campamento Los Obreros, vertiente W, 75 km al W de El Peino, 2460 m, 22 Nov 1972, *Hagemann & Leist 1592* (COL); Mpio. Colón, Reserva Natural La Rejoja, 01°18'N, 76°52'W, 2750 m, 10 Nov 1996, *Ramírez B. R. 10188* (UC). **Risaralda:** Mistrato, corregimiento de Jeguadas, cordillera occidental, vertiente occidental, 1500 m, 28 Mar-02 Apr 1992, *Betancur et al. 3187* (COL); Santuario, vereda La Colonias, 400 m arriba del campamento, 2910 m, 02 Feb 1983, *Torres J. H. et al. 1467* (COL). **Santander:** limite entre los departamentos Santander y Boyacá, corregimiento Virolín, finca La Sierra., 2500-2600 m, 14 May 1976, *Lozano et al. 2495* (COL); Charalá, corregimiento Virolin, camino El Reloj, en vallecito y alrededores de la quebrada La Lanosa, 1900 m, 20 Oct 1983, *Torres J.H. et al. 2675* (COL).

**VENZUELA (?). Prov. Unknown:** “Caracas,” 17 Sep 1854, *Gollmer s. n.* (B).

**ECUADOR. Carchi:** Valle de Maldonado, Km 67 on the road Tulcán-Maldonado, 00°53'S, 78°04'W, 2400 m, 20 Apr 1973, *Holm-Nielsen et al. 6165* (AAU); road Tulcán-Maldonado, 53-54 km from Tulcán, 00°50'N, 78°03'W, 3100-3200 m, 31 Jul 1976, *Øllgaard & Balslev 8310* (AAU); above Maldonado, 2400 m, 31 Jul 1989, *van der Werff & Gudiño 10805* (UC); Maldonado-Tulcán road ca. Km 20, 2400-2600 m, 07 Oct 1981, *Werling & Leth-Nissen 340* (QCA). **Cotopaxi:** Cantón Pilalo, along shore of Río Pilaló, 00°05'S, 79°09'W, 1800-2000 m, 04 Dec 1987, *Cerón & Villavicencio 2774* (QCA, UC); Cantón Pujili, along road between El Corozon and Angamarca, along side road to Yasaicho, 0.3-0.4 km off main road, 3.1 km above main square in El Corozon, 01°08'S, 79°03'W, 1780 m, 07 Apr 1992, *Croat 73673* (UC). **Imbabura:** road to Intag valley above Apuela, 00°23'N, 78°28'W, 2500 m, 07 May 1980, *Holm-Nielsen 23341* (AAU). **Loja:** Nudo de Sabanilla, W slope on road to Yangana, 2600 m, 06 Feb 1985, *Harling & Anderson 21725* (QCA); road Loja-Zamora, ca. Km 10, 03°59'S, 79°10'W, 2400-2600 m, 17 Sep 1988, *Madsen 75354* (AAU). **Morona-Santiago:** road Gualaceo-Limón, Km 33.3, E of the pass, 03°02'S, 78°38'W, 3010 m, 27 Dec 1990, *Øllgaard et al. 98542* (AAU); road Plan de Milagro-Gualaceo, Km 10.8, 03°00'S, 78°32'W, 2200-2250 m, 24-25 Nov 1997, *Øllgaard & Navarrete 2754* (AAU); *ibid.*, Km 8.9 to antennas, 03°00'S, 78°31'W, 2300-2350 m, 20 Mar 1997, *Øllgaard & Navarrete 2539* (AAU). **Napo:** Cantón Archidona, Sumaco-Napo-Galeras National Park, Sumaco

Mountain, between summit crater and high camp, 00°36'S, 77°38'W, 2600 m, 17 Mar 1996, *Clark J. L. 2238* (UC); cantón Tena, Cordillera de Huacamayos, entre Carachupa-Chacana, 00°48'S, 78°07'W, 1940-2200 m, 07 Aug 1995, *Jaramillo & Tapia 18447* (QCA); Cerro Huacamayos, on road Baeza-Tena, ca. 34 km from Baeza, 00°41'S, 77°50'W, 2000 m, 9-10 Aug 1980, *Øllgaard et al. 35887* (AAU); Quijos, Reserva Ecológica Antisana, Cordillera de los Guacamayos, sector oriental, crossing of ARCO pipeline, between El Mirador and La Virgen, 00°38'S, 77°51'W, 2300 m, 12-14 Jan 1999, *Vargas H. & Narvaéz 3522* (UC).

**Pichincha:** Estación Biológica Río Guajalito in Quebrada Las Palmeras, Km 59 along road Chilligallo-Alluriquin, 00°14'S, 78°49'W, 1860 m, 01-05 Apr 1995, *Ankersen & Kragelund 112* (AAU); road Aloág-Tandapi, W of the pass, 00°27'S, 78°43'W, 2600 m, 04 Jul 1979, *Holm-Nielsen 18400* (AAU); Bellavista; entre Tandayapa y Mindo (vieja carretera Quito-Puerto Quito), 2300 m, 10 Sep 2004, *Lehnert 1163* (GOET, QCA, UC); Santa Rosa, 18 km al S de Nanegalito, 00°00'50"S, 78°39'10"W, 1900-2000 m, 01 Jan 1995, *Navarrete 776* (AAU); Canton Quito, Reserva Forestal Maquipucuna, on ridge N of Cerro de Sosa, ca. 6 km airline SE of Nanegal, 00°07'N, 78°38'W, 1750 m, 28 Aug 1989, *Webster & Urtecho 27106* (UC, US).

**Sucumbios:** Reserva Ecológica Cayambe Coca, Volcán Reventador, collections from crater rim and slopes, 00°04'S, 77°37'W, 3400 m, 22 Nov 1997, *Clark J. L. 4415* (UC).

**Zamora-Chinchipe:** Parque Nacional Podocarpus, road Yangana-Valladolid, Km 21, 04°28'S, 79°09'W, 2700 m, 28 Oct 1989, *Bøgh 86596* (AAU); road Loja-Zamora, Km 24-25, 03°59'W, 79°05'W, 1950-2100 m, 15 Apr 1973, *Holm-Nielsen et al. 3510* (AAU); Estación Científica San Francisco, channel trail between Q1 and Q2, 03°58'S, 79°04'W, 1900 m, 05 Oct 2003, *Lehnert 958* (GOET, QCA, UC); Reserva Tapichalaca, study plot B1, nearby Ventanillas, 04°29'S, 79°07'W, 2600 m, 26 Oct 2003, *Lehnert 985* (GOET, QCA, UC); Reserva Tapichalaca, sector Ventanillas., 04°29'S, 79°07'W, 2520-2600 m, 17 Sep 2004, *Lehnert 1279* (GOET, QCA, UC); Loja-Zamora, Km 13.5, old road to Zamora, 03°58'S, 79°08'W, 2750 m, 06 May 1997, *Lewis G. P. et al. 3244* (AAU); limit of Parque Nacional Podocarpus, new road Loja-Zamora, E of the pass, 03°58'S, 79°07'W, 2500-3000 m, 25 Mar 1990, *Madsen 87093* (AAU); Parque Nacional Podocarpus, quebrada Río San Francisco, at new road Loja-Zamora (in construction), 03°58'S, 79°05'W, 2040-2250 m, 23 Jun 1988, *Øllgaard 74970* (AAU); along new road Loja-Zamora, 2500 m, 25 Apr 1987, *van der Werff & Palacios 8960* (AAU); area of ECSF Research Station, around km 30 on road Loja-Zamora, E of ceja andina, 03°58'18"S, 79°04'44"W, 2400 m, 11 Jun 2000, *Werner 436* (UC).

**PERU. Amazonas:** Condorcanqui, Cordillera del Condor, top of tepui Cerro Machinaza, 03°52.7'S, 78°25.8'W, 2160 m, 30 Jul 1994, *Beltran & Foster 1468* (USM).

**Cajamarca:** Prov. Jaén, San Ignacio, San José de Lourdes, Picorana, 04°58'S, 78°53'W, 2470-2560 m, 18 Aug 1998, *Campos J. et al. 5592* (UC); San Ignacio, Santuario Nacional Tabacondas-Namballe, Tabacondas, 05°15'S, 79°19'W, 2300-2400 m, 14 Nov 1998, *Campos J. et al. 5691* (UC). **Cuzco:** Prov. La Convención, Los Palmitos, cabeceras del Koribeni, 9000 ft, Sep 1932, *Bües 1964* (CUZ); Distrito Echarati, E Río Apurimac, NE Pueblo Libre, up mountain of Anchiuay and Bellavista, S Cordillera Vilcabamba, 12°51'S, 73°30'W, 2445 m, 03 Aug 1998, *Nuñez et al. 23296, 23343* (USM). **Huanuco:** Prov. Huanuco, Carpish, 2700-2750 m, 1964, *Ferreyra R. 16154* (USM); road from Huanuco to Tingo Maria, N of Carpish pass, 48.6 km NE of Huanuco, 2490 m, 06 Dec 1981, *Plowman & Rury 11125* (USM); Carpish, 2800 m, 12 Dec 1953, *Coronado 63* (UC). **Junin:** Prov. Satipo, N Cordillera Vilcabamba, E slope, upper Río Puyeni watershed, 11°33'35"S, 73°38'28"W, 2050 m, 01 Jul 1997, *Boyle et al. 4937* (USM). **Pasco:** Prov. Oxapampa, camino a la cumbre del San Gutardo, distrito Chontabamba, 2700-2800 m, 03 Feb 1982, *León B. 525* (USM). **San Martín:** Prov. Riojas, Buenos Aires, along road Pedro Ruiz-Rioja, 05°42'09"S, 77°53'06"W, 2000 m, 21 Mar 1998, *van der Werff et al. 15372* (UC).

The stiffly erect, fasciculate fronds with their very short segments characterize this species. It is one of only three *Melpomene* species in which truncate to emarginate segments occur. A geographical correlation can be observed in this character: whereas most plants from the southern range have most of their segments with blunt tips, the plants from the north have this segment type only in the base of the blades. With most of their segments rounded or even oblong, they resemble small and juvenile plants of *M. pseudonutans*, another species with thick, short-creeping rhizomes. However, that species usually has visible costae, predominantly deltate segments with acute tips, and thicker rhizomes. *Fay & Fay 3035* (AAU) shows both extremes of segment shape in one plant of *M. wolfii*. Plants from the northwestern Andean slopes tend to be more densely hairy in fertile segments than plants from the south or from the eastern slopes. The type of *M. wolfii* is a small, glabrous plant from a shady forest whereas the type of the synonymous *M. assurgens* (*Haught 3226*, US) is a large plant from an open spot along a road. There are many collections that display the morphological transition between these two extremes.

Other relatives with truncate to emarginate segment tips are *M. flagellata* from Bolivia and *M. moniliformis* var. *tepuiensis* from Venezuela. These species are readily distinguished by the long-hairy petioles and long hairs clustered in the sori (vs. glabrous petioles and evenly distributed, short hairs on the laminae of *M. wolfii*).

Plants of *M. wolfii* from southern Peru differ from the northern Andean populations by longer petioli (to 70 mm), more arching fronds, and longer, narrower scales (to 7.0 x 0.5 mm). There are no records of *M. wolfii* from the southern Amotape-Huancabamba region, which is quite well investigated.

**26. *Melpomene xiphopteroides* (Liebm.) A. R. Sm. & R. C. Moran, Novon 2: 431. 1992.**  
Figs. 37, 38.

*Plants* epiphytic or saxicolous. *Rhizomes* short-erect to short-creeping, 0.6-0.8 mm diam. (Fig. 37A, B). *Fronds* patent, inserted onto the rhizomes at narrow angles, or appressed to them, fasciculate (0.5–1.0 mm apart). *Scales* 1.2-1.4(-4.5) x 0.3-0.8 mm, (8-)10-12(-14) cells wide across their bases, clathrate (Fig. 37C, F), dark brown to brown, weakly iridescent, lanceolate, cordate to pseudopeltate at bases, long acute at tips; apical glands 5-10 cells linearly to palmately arranged (Fig. 37G). *Petioles* 15-35 mm long, 0.6-0.8 mm thick, alate to marginate (Fig. 37D), with many dark brown hairs 1.2-2.0 mm long (Fig. 37H); simple and branched glandular hairs often absent even in crosiers and young fronds. *Laminae* to 140 mm long, 26-29 mm wide, linear to broadly elliptic (broadest in the middle), cuneate to truncate at bases, short acute at tips (Fig. 37B). *Rhachises* dark brown to black, planar and slightly sunken adaxially, hemispherically protruding abaxially, moderately to abundantly hairy abaxially, sparsely hairy to glabrous adaxially, the hairs to 1.5 mm abaxially, shorter adaxially. *Pinnae* 12.0-14.0 x 2.5-3.0 mm (4-5 times as long as wide), patent to weakly ascending (90-70°) (Fig. 37B), equilateral at base, fully adnate, linear-oblong, the tips obtuse; costae not visible, or obscurely so abaxially in dried specimens (Fig. 37E); basal pinna pairs notably smaller than subsequent segments; hairs 0.8-1.5 mm long, brown, with rather flaccid bases; clustered in sori, scattered along costae, also some on tips and margins of segments; stomata often dark; hydathodes present. *Sori* 2-8 pairs per segment, with several hairs to 1.5 mm long in and around them.

*Melpomene xiphopteroides* is defined here according to the concept of A. R. Smith (1981; Mickel & Smith, 2004) as having the hairs clustered in sori, which is the main difference to *M. pilosissima*; it is also characterized by having the petioles at least narrowly marginate, often distinctly alate (vs. terete in *M. pilosissima*). The type of synonymous

*Ctenopteris megaloura* has alate petioles, rather short hairs and is less hairy on the laminae; its larger pinnae tend to have auriculate bases, as is observed in large specimens of *M. firma*.

In addition to the hair distribution, *M. pilosissima* differs from *M. xiphopteroides* in having stiffer hairs and longer petioles; the laminar bases are cuneate to round. Specimens of *M. xiphopteroides* with short petioles have proximally decurrent laminae; plants with longer petioles have truncate bases laminae that look like proximally decurrent laminae with removed proximal segments. The often mentioned difference of the pinnae of *M. pilosissima* being more ascending than in *M. xiphopteroides* (Tryon & Stolze, 1993; Mickel & Smith, 2004) is ambiguous: the segments of *M. xiphopteroides* can be nearly patent to ascending to ca. 70° with respect to the rhachis, thus falling into the range of *M. pilosissima*. In fact, most plants of *M. xiphopteroides* from the central Andes have definitely ascending pinnae (if the margins are folded in dried specimens, the degree of ascent may appear even stronger) and may at first sight appear like Mexican plants of *M. pilosissima*. Comparison of the hair distribution (hairs clustered in sori) and the petioles (at least marginate, often alate) clearly align them with *M. xiphopteroides*. Based on this observation, nearly all Brazilian specimens of what has been previously determined as *M. pilosissima* can be transferred to the *M. xiphopteroides* group. This does include *Polypodium acrodontium* Fée, a former synonym of *M. pilosissima*. I place the Brazilian population here separately as a distinct variety, *M. xiphopteroides* var. *acrodontium* (Fée) Lehnert, which see for further discussion.

Compared to *Melpomene vernicosa*, both varieties of *M. xiphopteroides* are generally smaller with thinner petioles (0.6-0.8 mm vs. 1.0-1.2 mm), have more chartaceous laminar texture (vs. subcoriaceous in *M. vernicosa*), and differ in predominantly marginate-alate petioles (vs. usually terete in *M. vernicosa*).

Two varieties are recognized:

**26a. *Melpomene xiphopteroides* (Liebm.) A. R. Sm. & R. C. Moran var. *xiphopteroides*.**

*Polypodium xiphopteroides* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. 5, 1: 196. 1849. *Grammitis xiphopteroides* (Liebm.) A. R. Sm., Amer. Fern J. 70: 26. 1980. Type. Mexico. Veracruz, "Hac. de Mirador", *Liebmann* [Liebm. Pl. Mex. 2548, Fl. Mex. 189] (lectotype, C, designated by Smith, Amer. Fern J. 70: 26. 1980).

*Ctenopteris megaloura* Copel., Philipp. J. Sci. 84:391. 1955 (1956). Type. Guatemala. Alta Verapaz, Cobán, *von Türckheim II. 1855* (holotype, US).

*Polypodium rigens* Maxon, Proc. U.S. Natl. Herb. Mus. 27: 741. 1904. *Ctenopteris rigens* (Maxon) Copel., Philipp. J. Sci. 84: 422. 1955 (1956). *Grammitis rigens* (Maxon) Proctor,

Brit. Fern Gaz. 9: 219. 1965. Type. Jamaica. John Crow Peak, *Maxon 1346* (holotype, US). Fig. 37A-E, 38.

*Plants* predominantly epiphytic. *Rhizomes* short-erect to short-creeping, 0.6-0.8 mm diam. (Fig. 37A, B). *Fronde*s patent, inserting into the rhizome in a narrow angle, or appressed to it, fasciculate (0.5–1.0 mm apart). *Scales* 1.2-1.4(-4.5) x 0.3-0.8 mm, (8-)10-12(-14) cells wide, clathrate (Fig. 37C), dark brown to brown, weakly iridescent, lanceolate, cordate to pseudopeltate at bases, long acute at tips; apical glands 5-10, linearly to palmately arranged. *Petioles* 15-35 mm long, 0.6-0.8 mm thick, weakly marginate in large plants (Fig. 37D), usually alate or marginate in small plants, with many dark brown hairs 1.2-2.0 mm long; simple and branched glandular hairs often absent even in crosiers and young fronds. *Laminae* to 140 mm long, 26-29 mm wide, linear to broadly elliptic (broadest at or above the middle), decurrent or cuneate to truncate at bases, short-acute at tips; whitish abaxially; stomata sometimes dark. *Rhachises* dark brown to black, planar and slightly sunken adaxially, hemispherically protruding abaxially, moderately to abundantly hairy abaxially, sparsely hairy to glabrous adaxially (Fig. 37E), hairs to 1.5 mm long abaxially, shorter adaxially. *Pinnae* 12.0-14.0 x 2.5-3.0 mm (4-5 times as long as wide), patent to weakly ascending (90-70°), equilateral at base or weakly auriculate basiscopically, fully adnate, linear-oblong, the tips obtuse; costae not visible, or obscurely so abaxially in dried specimens (Fig. 37E); basal pinna pairs notably smaller than subsequent pinnae; if laminae broadest beyond the middle and strongly decurrent towards the base then lowermost pinnae alariform; hairs 0.8-1.5 mm long, brown, with rather flaccid bases; clustered in sori, scattered along costae, usually also some on the tips and the margins of some segments; hydathodes present. *Sori* 2-8 pairs per segment, with several hairs to 1.5 mm long (Fig. 37E).

**Distribution and habitat.** Wet montane forests at 900-2400(-2800) m in Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Cuba, Jamaica, Dominican Republic, Venezuela, Guayana, Colombia, Ecuador, Peru, Bolivia, and northern Brazil (Fig. 38).

**Selected specimens examined. MEXICO. Chiapas:** E of Comitán Domínguez, along dirt road 1.8 mi E of turnoff to Ejido Tzisco, 07 Jan 1984, *Hardison et al. 92B* (UC). **Oaxaca:** Sierra de Juárez, Km 77 route 175 Tuxtepec-Oaxaca, 1300 m, 19 Nov 2005, *Kessler 13479, 13484* (GOET); Ixtlán, trail from San Pedro Nolasco N to the Llano Verde, 6000-72000 ft, 05 Oct 1969, *Mickel & Hellwig 3776a* (UC); Dto. Mixes, N slope of Cerro



Zempoaltepetl, trail from Totontepec to La Candelaria, 2700-7200 ft, 20 Sep 1970, *Mickel & Leonard 4723* (UC); Ixtlán, 23 km S of Valle Nacional, 5 km N of Vista Hermos, 3800-4000 ft, 23 Sep 1972, *Mickel & Pardue 6704* (UC). **Veracruz:** surroundings of Jalapa, Maneru, 1410 m, 23 Feb 1997, *Endlich 1687* (B); 3000 m, Jun-Oct 1840, *Galeotti 6310* (P).

**GUATEMALA. Alta Verapaz:** Cobán, 1350 m, Jul 1906, *von Türckheim III347* (NY). **Chiquimula:** Cerro Tixixi (Tishishi), 3-5 miles N of Jocotán, 500-1500 m, 10 Nov 1939, *Steyermark 31655* (NY).

**HONDURAS. Prov. unknown:** near El Achote, hills above the plains of Siguatepeque, 1350 m, 13 Jul 1938, *Yuncker et al. 5850* (NY).

**NICARAGUA. Jinotega:** Macizo de Peñas Blancas, top and N slope of steep ridge SW of finca of Manuel Estrada (El Cielo), S of Río Gusaneras, 13°15'N, 85°42'W, 1200-1330 m, 16 Jan 1979, *Stevens & Krukoff 11521* (NY, UC).

**COSTA RICA. Cartago:** hills near Navarro Valley, 6-8 mi SW of Cartago, 6000 ft, 01 May 1928, *Stork 1710* (UC). **Heredia:** Vera Blanca, 2000 m, 17 Aug 1967, *Bishop 883, 884* (UC). **Poas:** forests of Achioté, 2200 m, Nov 1896, *Tonduz 10734* (P). **Puntarenas:** Monte Verde, Walter James' driveway, 1500 m, 18 Jul 1979, *Koptur SK-158* (UC). **San José:** near summit between Aserri and Tarbaca 1-2 km N of Tarbaca, 1750 m, 05 Jul 1967, *Bishop 801* (UC); Naranjo, S of Cartago, 5500 ft, 04 May 1928, *Stork 1817* (UC).

**PANAMA. Chiriquí:** along trail between N fork of Río Palo Alto and Cerro Pate Macho, ca. 6 km NE of Boquete, 08°48'N, 82°23.5'W, 1600-2000 m, 06 Feb 1986, *Smith A. R. et al. 2383* (UC); along Río Caldera (Boquete region) and on slope to the E, ca. 3, 5 km NW of Bajo Mono, 08°50'N, 82°28'W, 1600 m, 08 Feb 1986, *Smith A. R. et al. 2457* (UC); 3.7 km along road through Bajo Grande from bridge NE of Cerro Punta., 08°50'N, 82°32'W, 2250-2400 m, 09 Nov 1980, *Sytsma & Stevens 2084* (UC).

**CUBA. Oriente:** "In Cuba Orientali," Sep 1859-Jan 1860, *Wright 1050* (B, UC); crest of Sierra Maestra between Pico Turquino and La Bayamesa, 27-28 Oct 1941, *Morton & Acuña 3545* (UC).

**JAMAICA.** Blue mountains, 01 Jun 1926, *Johnson s.n.* (UC); near Cinchona, 4907 ft, 19 Mar 1909, *Watt 187* (P).

**DOMINICAN REPUBLIC. La Vega:** Cordillera Central, 5.4 km S of Constanza (via road to Pueblo Río Grande) and 6-8 km on the road to Pinar Parejo, 2000-2100 m, 24 Feb 1982, *Mickel et al. 8440* (UC). **Monte Cristi:** Cordillera Central, Monción, high ridge between Río Cenobi and Río San Juan, 02 Jun 1929, *Ekman 12823* (NY).

**COLOMBIA. Antioquia:** La Unión, road from La Unión to San Miguel, 2340-2430 m, 05°56'N, 75°15'W, 05 Jul 1987, *Arbeláez A. L. et al. 56* (NY); Belmira, Vereda Yermalito, 2825 m, 06°36'27.8"N, 75°39'29.7"W, 02 Jul 2002, *Rodriguez W. et al. 3467* (NY). **Boyacá:** Cordillera Oriental, E slope, road Sogamoso to Pajarito, Río Cusiana valley, 1500 m, *Jaramillo Mejia et al. 3868* (COL); Río Cusiana valley, between Sogamoso and Corinto, 2200-2300 m, *Murillo M. T. 1408* (COL). **Cauca:** Santa Rosa, Serranía de los Churumbelos, Bota caucana, 1400 m, *Gonzales C. 761* (COL); El Tambo, 2000 m, *von Sneidern 148* (B). **Cundinamarca:** Junin, Vereda La Aldea, 2300 m, *Murillo M. T. 955* (COL); Albán, Vereda La Maria Alta, cerro Pan de Azucar, W slope of Cordillera Oriental, 2100-2200 m, *Triana-M. et al. 94* (COL). **Huila:** La Plata, Vereda Agua Bonita, finca Merenberg, 1200-1300 m, *Diaz-P. et al. 570* (COL); La Argentina, above the finca Palmira, 2100 m, *Lozano et al. 4142* (COL). **Meta:** El Calvario, police station San Francisco, Vereda San Isidro, 2410 m, *Camargo-G. & Huertas-G. 7965* (COL). **Santander:** Charalá, Vereda El Taladro, Km 50-55, road Duitama-Virolin, 2250-2300 m, *Diaz-P. et al. 1644* (COL).

**VENEZUELA. Amazonas:** Dtto. Atabapo, headwaters of Río Yudi, opposite to Trabajo No. 17, 1600 m, 05°29'N, 65°18'W, Mar 1992, *Delgado 1765A* (NY); Dtto. Atures, 115 km SE of Puerto Ayacucho, 1500 m, 04°54'N, 66°54'W, Sep 1989, *Fernandez A. et al. 5948* (NY); valley of Río Coro-Coro, W of Serranía de Yutaje, E base of forested mountain 5 km W of river, 1100 m, 05°41'00"N, 66°09'30"W, 13 Mar 1987, *Holst & Liesner 3449A* (NY). **Anzoátegui:** Dtto. Freites, Cerro Peonía, above Los Pajaritos, 31 airline km NE of Bergatín and N of Mundo Nuevo, Serranía de Turimiquire, 10°06'N, 64°06'W, 2300 m, 02-03 Dec 1981, *Davidse & Gonzáles A. C. 19883* (UC). **Aragua:** Dtto. Ricaurte, ridge El Socorro-Topo El Paují; SE of La Victoria, 10°11'N, 67°15'W, 1400-1600 m, 09 Jan 1999, *Meier W. & Speckmaier 4416* (UC). **Bolívar:** Dtto. Piar, Macizo del Chinantá, Amurí-tepui, 05°10'N, 62°07'W, 1850 m, 02-05 Feb 1983, *Steyermark et al. 128572* (UC). **Carabobo:** Dtto. Valencia, old hacienda Aguacatal, property of "Electricidad de Valencia," W of Valencia, headwaters of Río Tocuyito, Cerro El Amparo and NW ridge, 10°15'N, 68°07'30"W, 1350 m, 23 May 2000, *Meier W. & Borjas 7229* (UC). **Dtto. Federal:** Cordillera de la Costa, Cerro El Avila, S slope, near point "Los Pinabetes," 10°32.6'N, 66°53.2'W, 1880 m, 09 Nov 1991, *Meier W. 726* (UC). **Falcon:** Sierra de San Luis, arriba de Santa Maria, 1000 m, 02 Mar 1979, *van der Werff 3391* (UC). **Lara:** Dtto. Morán, through Páramo "Las Rosas," 4 km from Caserío "Buenos Aires," 09°37'N, 70°05'W, 2450 m, 23 Dec 1984, *Rivero & Escalona 803* (UC); Dtto. Palavecino, road to Parque Nacional Terepaima, ca. 10-11 km SE of town of Río Claro, beyond summit, 09°53'N, 69°19'W, 1500 m, 14 Nov 1982, *Smith A. R. & Burandt 1309*

(UC). **Mérida:** Valle San Javier, slope exposed to NW, at level with La Caña, 08°43'N, 71°05'W, 2750-2800 m, 04-06 Nov 1997, *Schneider J. 1595* (UC); Dtto. Andres Bello, La Carbonera, ca. 13 min NNW of Jají along Highway 4, property of the Universidad de los Andes, 08°40'N, 71°26'W, 2000 m, 20 Nov 1982, *Smith A. R. et al. 1435, 1474* (UC); Dtto. Rangel, along road Santo Domingo-Apartaderos, 08°51'N, 70°44'W, 2400 m, 06 Aug 1983, *van der Werff & Ortíz 5952* (UC). **Monagas:** Dtto. Acosta, serranía del Turumiquire; high plateau on mountain ridge, headwaters of Río Negro (tributary of Río Colorado), on S edge of the meseta, 10°02'N, 63°52'W, 1600 m, 12 May 1982, *Huber et al. 6312* (UC). **Portuguesa:** Dtto. Unda, A 20 km NE de Chabasquen, ridge El Helechal, 09°03'N, 69°59'W, 1600-2000 m, 07 Sep 1983, *Ortega F. et al. 1778, 1780, 1781, 1782* (UC); Dtto. Guanare, ESE of Paraíso de Chabasquén, along road to Cordoba, ca. 27 min. from Chabasquén, just below summit and below road, 09°23'N, 69°54'W, 1500 m, 07 Nov 1982, *Smith A. R. 1119* (UC); ESE of Paraíso de Chabasquén, along road to Cordoba, ca. 20-25 min. from Chabasquén, 09°23'N, 69°59'W, 1300-1500 m, 05 Nov 1982, *Smith A. R. et al. 1019* (UC). **Sucre:** climb to Cerro Turimiquire via Las Piedras over the mountain ridge, 10°07'N, 63°53'W, 1950-2000 m, 14-16 Mar 1993, *Meier W. & Bronner 3561* (UC). **Táchira:** Dtto. Uribante, surroundings of camp Siberia (CADAPE), 08°01'N, 71°43'W, 1200 m, 21 Nov 1985, *Ortega & van der Werff 2848* (UC); ca. 3 km outside Siberia on road to Pegonero, 08°55'N, 71°40'W, 1300 m, 11 Jul 1983, *van der Werff & Gonzáles A. 5337* (UC). **Trujillo:** Dtto. Boconó, 33.5 km SE of Boconó, road to Guaramacál, 09°12'N, 70°06'W, 1300 m, 25-26 Nov 1982, *Smith A. R. et al. 1553* (UC). **Vargas:** Monumento Natural Pico Codazzi, road Arco de la Colonia Tovar-Pto Cruz, 2 km from Arco, on the trail that leads to Río Petaquire from the pasarela of Hotel Casa Campo Tovar, 10°26'N, 67°14'W, 1900-1950 m, 25 Sep 1999, *Mostacero et al. 338* (UC).

**GUAYANA. Roraima:** Mt. Roraima, on the "ledge" above Rondon Camp, 2800 m, Dec 1927, *Tate 463* (NY).

**ECUADOR. Pastaza:** road Mera -Baños, ca. 2 km behind Mera, 01° 27.3'S, 78° 09.7'W, 1000 m, 09 Jul 2002, *Lehnert 187, 190* (GOET, QCA, UC); road N of Mera, toward Río Anzu, Km 68.2, 01°27'S, 78°04'W, 1450 m, 11 Nov 1994, *Øllgaard et al. 105533* (AAU); toward Río Anzu, Km 6.7, 01°27'S, 78°04'W, 1480 m, 12 Nov 1994, *Øllgaard et al. 105576, 105634* (AAU). **Zamora-Chinchipec:** Campamento Shaime (Shaimi) along Río Nangaritzá, trail to the ridge N of the village, trail starting from behind the visitor cabañas, 04°19'S, 78°40'W, 930-1100 m, 08 Nov 2004, *Lehnert 1532* (GOET, QCA, UC); hills with pasture and disturbed forest immediately S and SE of Zamora, 04°04'S, 78°57'W, 1000-1250 m, 14 Jun 1988, *Øllgaard et al. 74862* (AAU); Parque Nacional Podocarpus, at Río Bombuscaro, 6

km SW of Zamora, 04°07'S, 78°58'W, 1140 m, 24 Nov 1994, *Øllgaard et al.* 105705, 105706 (AAU).

**PERU. Amazonas:** Prov. Chachapoyas, Cerros Calla Calla, E side, 15 km above Leimebamba on the road to Balsas, vicinity of Sisumachay, Km 419, 2950 m, 27-28 Mar 1964, *Hutchinson & Bennet* 4792 (UC); road Chachapoyas-Mendoza, Km 52 from Chachapoyas, 10 km behind Molinopampa, 06°14.26'S, 77°35.96'W, 2700 m, 04 Aug 2002, *Lehnert* 237, 238, (GOET, UC, USM); road Leymebamba-Balsas, Km 25, 06° 43, 35'S, 77° 52, 60'W, 07 Aug 2002, *Lehnert* 260 (GOET, UC, USM); road Chachapoyas-Mendoza, a little past Molinopampa, 06°14'11"S, 77°35'49"W, 2400 m, 15 Mar 1998, *van der Werff et al.* 15068 (UC); remnants of forest around Laguna Pomacochas, 05°50'11"S, 77°57'47"W, 2250 m, 20 Mar 1998, *van der Werff et al.* 15251 (UC). **Junin:** Prov. Tarma, Schunke Hacienda, above San Ramón, 1400-1700 m, 08-12 Jun 1929, *Killip & A. C. Smith* 24847, 24848 (NY). **Loreto:** Sierra del Pongo, crest of mountain, 800 m, 15 Dec 1931, *Mexia* 6292a (UC). **Ucayali:** Prov. Coronel Portillo, Divisoria, between Tingo María and Pucallpa, 1500-1600 m, 18 Feb 1947, *Ferreyra* 1689 (USM).

**BOLIVIA. Beni:** Ballivian, 25 km on Yucumo-Quiquibey road, in the Pilon Lajas, 15°17'S, 67°04'W, 950 m, 18 Jul 1990, *Fay & Fay* 2760 (LPB, MO). **Cochabamba:** Prov. Chapare, Territorio Indígena Parque Nacional Isiboro-Secure, Cordillera de Mosestenez, crest above laguna Carachupa, 16°14'S, 66°25'W, 1550 m, 02 Sep 2003, *Kessler et al.* 13149, 13150, 13386, 13436, 13438 (GOET, LPB, UC). **La Paz:** Prov. Bautista Saavedra, Cerro Asunta Pata, entre Apolo y Charazani., 15°03'S, 68°29'W, 1500 m, 21 Jun 1997, *Kessler et al.* 10230, 10232 (LPB, UC); Prov. Caranavi, Serrania Bellavista, between Carrasco and Km 52, 15°40.48'S, 67°28.10'W, 1350 m, 12 Apr 2003, *Lehnert* 767 (GOET, LPB, UC); Prov. Franz Tamayo, headwaters of Yana Mayu, E of Virgen del Rosario, 14°36'06"S, 68°42'47"W, 1750 m, 08 Nov 2003, *Fuentes et al.* 5760 (LPB, MO); Prov. Larecaja, ca. 7 km from Consata along trail (soon to be the road) towards Mapiri, 1400 m, 16 Dec 1981, *Sperling & King* 5493 (GH, LPB); Prov. Murillo, Valle del Zongo, 44 km behind Abra de Zongo, 1650-1750 m, 19 Nov 1981, *Beck* 7237 (LPB); Prov. Nor Yungas, Coroico, Cerro Uchumachi, 16° 12'S, 67° 50'W, 2300 m, 24 Sep 2002, *Lehnert* 365 (GOET, LPB, UC); Estación Biológica Tunquini, 16°17'S, 67°50'W, 1600-2000 m, 02 Nov 2002, *Lehnert* 462, 464, 471, 472, 475, 477, 478, 479, 481 (GOET, LPB, UC); Cantón Pacollo, Cerro Omuni, 16°11'S, 67°52'W, 1870 m, 27 Nov 1998, *Portugal et al.* 506 (LPB, UC).

**26b. *Melpomene xiphopteroides*** (Liebm.) A. R. Sm. & R. C. Moran var. ***acrodontium*** (Fée)

Lehnert, comb. et stat. nov. *Polypodium acrodontium* Fée, Crypt. Vasc. Brésil 2: 58, t. 99. 1872. Type. Brazil. *Glaziou 4409* (holotype, P; isotype, B). Fig. 37B, F-H, 38.

Etymology: from Greek “akros-” = top, upper part of something, and “dons” = tooth. Probably referring to pinnatifid frond tips; Fée (1872) does not give an explanation for the name, but describes the frond tips as dentate.

*Plants* predominately epiphytic, sometimes saxicolous. *Rhizomes* short-erect to short-creeping, 0.6-0.8 mm diam. (Fig. 36B). *Fronde*s patent, inserted onto the rhizomes at narrow angles, or appressed to them, fasciculate (0.5–1.0 mm apart). *Scales* 1.2-1.4(-4.5) x 0.3-0.8 mm, (8-)10-12(-14) cells wide across their bases, clathrate (Fig. 37F), dark brown to brown, weakly iridescent, lanceolate, cordate to pseudopeltate at bases, long acute at tips; apical glands 5-10 cells linearly to palmately arranged (Fig. 37G). *Petioles* 15-35 mm long, 0.8 mm thick, usually alate or marginate, with many dark brown hairs 1.2-2.0 mm long (Fig. 37H); simple and branched glandular hairs often absent even in crosiers and young fronds. *Laminae* to 140 x 26-29 mm, linear to broadly elliptic (broadest in the middle), cuneate to truncate at bases, short acute at tips (Fig. 37B). *Rhachises* dark brown to black, planar and slightly sunken adaxially, hemispherically protruding abaxially, moderately to abundantly hairy abaxially, sparsely hairy to glabrous adaxially, the hairs to 1.5 mm abaxially, shorter adaxially. *Pinnae* 12.0-14.0 x 2.5-3.0 mm (4-5 times as long as wide), weakly ascending (80-70°) (Fig. 37B), equilateral at bases, fully adnate, linear-oblong, the tips obtuse; costae not visible; proximal pinna pairs notably smaller than the subsequent segments; hairs 0.8-1.5 mm long, brown, with rather flaccid bases; hairs clustered in sori, scattered along costae, usually also some on the tips and along margins of some segments; stomata often dark; hydathodes present. *Sori* 2-8 pairs per segment, with several hairs to 1.5 mm long in and around them.

*Melpomene xiphopteroides* var. *acrodontium* includes all Brazilian specimens previously determined as *M. pilosissima*. Both taxa are habitally identical, and there are almost no differences between *M. pilosissima* var. *tsatchelae* and *M. xiphopteroides* var. *acrodontium* except for the sori, which have hairs clustered in them in the latter species and hairs scattered around them in *M. pilosissima* var. *tsatchelae*. However, there is a large geographical gap between them, which makes intergradation between these two forms unlikely. *Melpomene pilosissima* is substituted in the central Andes by the related species

*M. jimenezii* and *M. michaelis*, which differ from *M. xiphopteroides* var. *acrodontium* in terete petioles and the partial or entire lack of hydathodes (vs. marginate to alate petioles and well developed hydathodes in var. *acrodontium*). A morphological grade between the *M. pilosissima* group in the Andes and the Brazilian population that has been formerly considered to be that species cannot be documented. Better fitting is *M. xiphopteroides* var. *xiphopteroides*, which has marginate to alate petioles like *M. pilosissima* var. *tsatchelae* and the Brazilian population, and is even morphologically closer to the latter by having hairs clustered in the sori and having hidden costae (vs. hairs not clustered in sori and costae visible in *M. pilosissima* var. *tsatchelae*). Furthermore, *M. xiphopteroides* forms a continuous population along the eastern Andean slope, reaching the Andean deflection in central Bolivia, and grows at an elevation (900-2400 m) similar to the Brazilian var. *acrodontium* (800-2500 m), thus coming closer also spatially than does *M. pilosissima* (2300-3500 m; southern limit in northern Peru).

Plants of *M. xiphopteroides* from the Amboró National Park in Bolivia, Dept, Santa Cruz, are indistinguishable from the Brazilian population and are thus assigned to the var. *acrodontium*.

**Distribution and habitat.** Montane Andean forest in central Bolivia and Mata Atlântica in Brazil, at 800-2500 m (Fig 38).

**Selected specimens examined. BRAZIL. Espírito Santo:** Município Castelo, Forno Grande, 1500 m, 18 May 1949, *Brade 19856* (RIO), Forno Grande, 1000 m, 18 May 1949, *Brade 19809* (RIO). **Minas Gerais:** Caraca, behind the grotto of Lourdes, 28 Feb 1976, *WelsWindisch & Ghillány 474* (RIO). **Paraná:** Serra do Monte Ypiranga, 29 Jan 1904, *Dusén 3338* (RIO). **Rio de Janeiro:** Parque Nacional de Itatiaia, trail to Prateleiras, 2400 m, 01 Aug 1973, *Barcia 650, 653* (RIO); Itatiaya, new street Km 1, 2500 m, 01 May 1950, *Brade 20305* (RIO); Morro Friburgo, Morro Possolé, sitio Dr. Dungs, 28 Jan 1968, *Pabst 9120* (BHCB, RIO); Petropolis, Rocio, 700 m, 16 Mar 1968, *Sucre & Braga 2454* (RIO). **Santa Catarina:** Estrada Dona Francisco, Joinville, 700 m 25 Jul 1957, *Reitz & Klein 4614* (US). **São Paulo:** Campos do Jordão, road to Pindamohangaba, 1900 m, 29 Jun 1998, *Labiak 654, 668* (SP); Serra da Bocaina, sertão da Bocaina, along rio Paca, near Casa do Peixe, 10 Feb 1959, *Pabst 4767* (RIO).

**BOLIVIA. Santa Cruz:** Prov. Ichilo, Cerro Amboro, 17°50'S, 63°48'W, 1150-1300 m, 23 Sep 1990, *Lewis M. & Clark 37743* (LPB, MO); P.N. Amboro, summit of Cerro Amboro, 1470 m, 17°45'30"S, 63°39'W, 09 Oct 1990, *Nee 9125* (NY, LPB).

**27. *Melpomene youngii*** (Stolze) B. León & A. R. Sm., *Amer. Fern J.* 93(2): 88. 2003. *Grammitis youngii* Stolze, *Fieldiana Bot.*, n.s. 32: 97. 1993. Type. Peru. San Martin, Prov. Mariscal Cáceres, Parque Nacional Río Abiseo, Puerta del Monte, 3600 m, 19 Nov 1985, *Young 1684* (holotype, USM; isotype, F n.v.). Figs. 34, 39.

Etymology: Named after Ken Young, who collected most of the known specimens in Río Abiseo National Park, Peru.

*Plants* predominantly epiphytic and pendent (Fig. 39A), growing in moss layers, rarely terrestrial, then fronds ascending. *Rhizomes* horizontal, moderately to short-creeping, 0.8-1.0 mm diam., rarely branched, branches short (<10 mm). *Fronde*s pendent, inserted onto the rhizomes at right angles, moderately spaced to closely placed (2-5 mm), not fasciculate (Fig. 39A). *Scales* 3.0 x 0.6 mm, (12-)14-16(-18) cells wide across bases, clathrate, dark brown to brown, strongly iridescent, broadly cordate to pseudopeltate, acute to attenuate at tip (Fig. 39B); apical glands 2-5 cells, V-shaped or palmately arranged (Fig. 39C). *Petioles* 25-50(-70) mm long, 0.6-0.8 mm diam., marginate near the laminar bases (Fig. 39D), terete for most of its length, glabrous to glabrescent, eglandular hairs absent but with few to many simple and branched glandular hairs 0.3 mm long on crosiers and young fronds (Fig. 39D), usually persisting on older fronds. *Laminae* 50-205 x 6-45 mm, linear to narrowly elliptic (broadest in the middle), cuneate to long decurrent at bases, long acute to attenuate at tips. *Rhachises* dark brown to black, planar and slightly sunken adaxially, hemispherically protruding abaxially; with many ephemeral branched glandular hairs abaxially. *Pinnae* 5.0-13.0(-20.0) x 1.2-1.5(-2.0) mm (ca. 4-7 times as long as broad) (Fig. 39E, F), weakly to rarely strongly ascending (60-30°), equilateral at bases or weakly decurrent towards the bases, fully adnate, linear-oblong to long-deltate, the tips obtuse; costae hidden, or obscurely visible abaxially in dried specimens (Fig. 39E); proximal 3-5 pinna pairs markedly smaller than the subsequent segments, lowermost pinnae usually alariform. *Sori* (2)3-10 pairs per segment, without hairs (Fig. 39 E).

**Distribution and habitat.** Endemic to elfin forests at 3300-3450 m in northern Peru.

**Additional specimens examined. PERU. San Martín:** Mariscal Caceres, P.N. Río Abiseo, Bosquecillo C18, 3450 m, 18 Jun 1988, *León 1945, 1957* (USM); Chochos, Río Abiseo Nat. Park, 3300 m, 23 Jun 1988, *León B. & Young 2052* (USM); in meadows of Pampa Hermosa, 3365-3390 m, 12 Aug 2000, *León B. & Young 4857* (LPB); Puerta del Monte, 3450 m, 19 Nov 1985, *Young 1620* (USM); Puerta del Monte, 3450 m, 20 Nov 1985, *Young 1763* (USM); first section of continuous forest on s side of river in Chochos valley, NW corner of Río Abiseo Nat. Park, 3450 m, 06 Jun 1986, *Young 3585* (USM); Chochos, Río Abiseo Nat. Park, 3400 m, 14 Jul 1987, *Young & León 4517, 4559, 4609a* (USM).

*Melpomene youngii* is distinguished from related species by the lack of hairs, especially in the sori. Species such as *M. sodiroi*, *M. personata* and *M. albicans* have at least some hairs in the sori, and *M. personata* and *M. albicans* also have hairs on the petioles.

#### DOUBTFUL NAMES AND EXCLUDED TAXA

***Melpomene alan-smithii*** A. Rojas, *Revista Biol. Trop.* 49: 444. 2001.

This species was described by a comparison with *M. anfractuosa* (Kunze ex Klotzsch) A. R. Sm. & R. C. Moran, which has been transferred to *Terpsichore* (León & Smith, 2004) in the meantime. The isotype at UC has calcareous deposits on the hydathodes, which are typical of certain groups of *Terpsichore*, but absent are in *Melpomene*. However, black fungi as are typical of *T. anfractuosa* have not been found in *M. alan-smithii*. The rhizome scales are very small and can not be assigned to either genus with certainty. Nevertheless, it is assumed here that this species belongs to the *Terpsichore taxifolia* group sensu Smith (1993).

***Melpomene anfractuosa*** (Desv.) A. R. Sm. & R. C. Moran, *Novon* 2: 429. 1992.

= *Terpsichore anfractuosa* (Desv.) B. León & A. R. Sm., *Amer. Fern J.* 93: 88. 2003.

***Melpomene dissimulans*** A. R. Sm. & R. C. Moran, *Novon* 2: 429. 1992.

= *Lellingeria dissimulans* A. R. Sm., *Novon* 5: 20. 1995.



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NUMERICAL LIST OF TAXA

1. *Melpomene albicans* Lehnert, sp. nov.
2. *Melpomene allosuroides* (Rosenst.) A. R. Sm. & R. C. Moran
3. *Melpomene caput-gorgonis* Lehnert, sp. nov.
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5. *Melpomene erecta* (C. V. Morton) A. R. Sm. & R. C. Moran
6. *Melpomene firma* (J. Sm.) A. R. Sm. & R. C. Moran
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12. *Melpomene leptostoma* (Fée) A. R. Sm. & R. C. Moran
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14. *Melpomene michaelis* Lehnert, sp. nov.
15. *Melpomene moniliformis* (Lagasca ex Sw.) A. R. Sm. & R. C. Moran
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## INDEX OF LOCAL NAMES

*Atarisi*: Tacana name for *Melpomene melanosticta* (Desv.) A. R. Sm. & R. C. Moran (Macia, 2004).

## INDEX OF SCIENTIFIC NAMES

New names and combinations in boldface, synonyms in italics.

*Ctenopteris aromatica*

*Ctenopteris assurgens*

*Ctenopteris calva*

*Ctenopteris firma*

*Ctenopteris leptostoma*

*Ctenopteris megaloura*

*Ctenopteris melanosticta*

*Ctenopteris moniliformis*

*Ctenopteris pennellii*

*Ctenopteris peruviana*

*Ctenopteris pilosissima*

*Ctenopteris pseudonutans*

*Ctenopteris rigens*

*Ctenopteris rigescens*

*Ctenopteris vernicosa*

*Ctenopteris wolfii*

*Grammitidaceae*

*Grammitis*

*Grammitis andicola*

*Grammitis aromatica*

*Grammitis assurgens*

*Grammitis deltata*

*Grammitis erecta*

*Grammitis firma*

*Grammitis flabelliforme*

*Grammitis katasophistes*

*Grammitis leptostoma*

*Grammitis melanosticta*

*Grammitis moniliformis*

*Grammitis pennellii*

*Grammitis peruviana*

*Grammitis pilosissima*

*Grammitis pseudonutans*

*Grammitis rigens*

*Grammitis rigescens*

*Grammitis rosarum*

*Grammitis sodiroi*

*Grammitis xiphopteroides*

*Grammitis vernicosa*

*Grammitis youngii*

*Grammitis zempoaltepetlensis*

*Jamesonia adnata*

*Lellingeria dissimulans*

*Lellingeria tungurahuae*

*Melpomene alan-smithii*

***Melpomene albicans***

*Melpomene allosuroides*

***Melpomene anfractuosa***

*Melpomene assurgens*

*Melpomene brevipes*

***Melpomene caput-gorgonis***

*Melpomene deltata*

*Melpomene dissimulans*

*Melpomene erecta*

*Melpomene firma*

*Melpomene flabelliformis*

***Melpomene flagellata***



Melpomene gracilis

**Melpomene huancabambensis**

**Melpomene jimenezii**

Melpomene leptostoma

Melpomene melanosticta

**Melpomene michaelis**

Melpomene moniliformis

var. **moniliformis**

var. minor

var. **adnata**

var. **tepuiensis**

var. **paradoxa**

var. **subdicarpon**

**Melpomene occidentalis**

*Melpomene pennellii*

**Melpomene personata**

Melpomene peruviana

Melpomene pilosissima

var. **pilosissima**

var. **tsatchelae**

Melpomene pseudonutans

*Melpomene rosarum*

**Melpomene sklenarii**

Melpomene sodiroi

*Melpomene tsatchelae*

Melpomene vernicosa

**Melpomene vulcanica**

Melpomene wolfii

Melpomene xiphopteroides

var. **xiphopteroides**

var. **acrodontium**

Melpomene youngii

*Melpomene zempoaltepetlensis*

Polypodiaceae

*Polypodium acrodontium*  
*Polypodium allosuroides*  
*Polypodium angustissimum*  
*Polypodium aromaticum*  
*Polypodium calvum*  
*Polypodium firmum*  
*Polypodium flabelliforme*  
*Polypodium gracile*  
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*Terspichore anfractuosa*  
*Xiphopteris flabelliforme*  
*Xiphopteris moniliformis*  
*Xiphopteris peruviana*

*Xiphopteris pilosissima*

*Xiphopteris rigescens*

*Xiphopteris sodiroi*

*Xiphopteris aromatica*

Figure captions

Fig. 1. Important characters of *Melpomene*. A-C. insertion of pinnae and segments into the rhachis: A. ascending (80-60°); B. patent (85-95°); C. deflexed (100-120°); D. measurement of a segment. E-G. hair types: E. pluricellular hair, *M. huancabambensis* (van der Werff & Ortega 13252, UC); F. glandular hairs, branched and simple, *M. moniliformis* var. *moniliformis* (Lehnert 262, GOET); G. hair with branched glandular base and unicellular acicular tip, *M. vernicosa* (Lehnert 868, GOET). H-J. sporangia from representative species of the genus: H. mature sporangium with trilete spores, opened partially during preparation, *M. gracilis* (Lehnert 1554, GOET); I. closed mature sporangia, spores not shown, *M. occidentalis* (Lehnert 1343, GOET); J. opened sporangium, *M. vulcanica* (Holm-Nielsen et al. 17235, AAU).

Fig. 2. Phylogenetic tree of *Melpomene* based on chloroplast genes (*rbcL*, *atpβ*) and morphology; numbers on branches are MP support/bootstrap values. (L. = *Lellingeria*; M. = *Melpomene*; Mi. = *Micropolypodium*; T. = *Terpsichore*).

Fig. 3. Worldwide distribution of *Melpomene*, arrows indicate noteworthy exclaves: A) southernmost occurrence in east Argentina (*Melpomene peruviana*), B) easternmost occurrence on the Mascarenes Islands (*M. flabelliformis*), and C) only Atlantic occurrence on Bioko (Fernando Póo) Island (*M. flabelliformis*).

Fig. 4. *Melpomene albicans*. A. habit; B. scales, different sizes; C. detail of scale apices; D. petiole, upper part; E. fertile segment abaxially; F. segment adaxially.

Fig. 5. Distribution maps. A. *Melpomene albicans*. B. *Melpomene caput-gorgonis*. C. *Melpomene erecta*. D. *Melpomene flagellata* (circles), *M. wolfii* (dots).

Fig. 6. *Melpomene allosuroides*. A. habit; B. scale; C. fertile segment abaxially; D. sterile segment abaxially (all from Solomon 12829, LPB).

Fig. 7. Distribution maps. A. *Melpomene allosuroides* (squares). *Melpomene gracilis* (dots). B. *Melpomene firma*. C. *Melpomene occidentalis*.

Fig. 8. *Melpomene caput-gorgonis*. A. habit (Kessler 1192, GOET); B. scale; C. detail of scale apices (Jiménez I. 534, LPB); D. petiole, upper part adaxially (Lehnert 868, GOET); E. segment adaxially (Lehnert 868, GOET); F. fertile segment abaxially, sporangia immature to primordial (Lehnert 367, GOET).

Fig. 9. *Melpomene deltata*. A. habit; B. segment abaxially, sporangia removed from most parts.

Fig. 10. Distribution maps. A. *Melpomene deltata*. B. *Melpomene flabelliformis*. C. *Melpomene leptostoma*.

Fig. 11. *Melpomene erecta*. A. habit; B. scale; detail shows cordate insertion and small marginal glands on short lobes; C. petiole, total length; D. fertile segment adaxially, sporangia mature and partially open; E. fertile segment abaxially, sporangia immature (all from *Lehnert 1570*, GOET).

Fig. 12. *Melpomene firma*. A. habit (*Lehnert 436*, GOET); B. scale (*Lehnert 1003*, GOET); C. detail of scale apex (*Lehnert 436*, GOET); D. petioles, left central part, right upper part (*Lehnert 417*, GOET); E. segment and rhachis adaxially (*Lehnert 196*, GOET); F. segment abaxially (*Lehnert 196*, GOET).

Fig. 13. *Melpomene flabelliformis*. A. habit, small African plant (*Hemp 494*, UBT); B. habit, medium sized Andean plant (*van der Werff 10497*, UC); C. habit, large Andean plant (*Young 4423*, USM); D. scale (*Lehnert 955*, GOET); E. detail of scale apex (*Lehnert 955*, GOET); F. petiole, central part (*Hemp 494*, UBT); G. segment and rhachis adaxially (*Hemp 494*, UBT); H. fertile segments abaxially, sporangia immature (*van der Werff 10497*, UC).

Fig. 14. *Melpomene flagellata*. A. habit (*Kessler & Kelschbach 107*, GOET); B. scale (*Kessler & Kelschbach 107*, GOET); C. petiole, left central part, right upper part (*Lehnert 517*, GOET); D. oblong segment abaxially, sporangia mature and open (*Kessler et al. 7138*, LPB); E. truncate segment abaxially, sporangia primordial (*Kessler & Kelschbach 107*, LPB).

Fig. 15. *Melpomene gracilis*. A. habit (*Lehnert 1554*, GOET); B. scale (*Lehnert 1554*, GOET); C. sterile segment abaxially, large and deeply crenate to pinnatisect (*Cruckshanks s.n.*, K); D. fertile segment abaxially, small and margins entire (*Lehnert 1596*, GOET).

Fig. 16. *Melpomene huancabambensis*. A. frond; B. scale; C. petiole, central part; D. segment adaxially; E. segment abaxially, sporangia immature (all from *van der Werff et al. 15353*, UC).

Fig. 17. Distribution maps. A. *Melpomene huancabambensis* (diamond); *M. jimenezii* (circles); *M. michaelis* (triangles); *M. pilosissima* var. *pilosissima* (dots), var. *tsatchelae* (squares); note the overlap of the varieties of *M. pilosissima*. B. *Melpomene melanosticta*.

Fig. 18. A-C. *Melpomene jimenezii*. A. habit; B. scale; C. segment abaxially, sporangia removed (all from *Jiménez I. 1859*, GOET). D-F. *Melpomene michaelis*. D. habit (*Lehnert 443*, GOET); E. scale, with unexpanded cells (*Lehnert 519*, GOET); F. scale, typical (*Lehnert 443*, GOET).

Fig. 19. *Melpomene leptostoma*. A. habit; B. scale; C. detail of scale apex; D. petiole, upper part; E. segment abaxially, sporangia immature; F segment adaxially (all from *Kessler 13500*, GOET).

Fig. 20. *Melpomene melanosticta*. A. habit (*Davidse & Huber 22756*, UC); B. scale with large marginal secondary apex (*Øllgaard et al. 979*, AAU); C. typical scale (*Fay & Fay 4180*, UC); D. detail of scale apex (*Fay & Fay 4180*, UC); E. petiole, upper part (frond apex points down) (*Øllgaard et al. 979*, AAU); F. segment abaxially, sporangia primordial (*Lehnert 1533*, GOET).

Fig. 21. *Melpomene moniliformis*. A-D. var. *moniliformis*. A. habit of plant growing in cushions (ca. 1/6 of original cushion); B. habit of shaded plant; C. petiole (*Lehnert 262*, GOET); D. segments abaxially, sori shown as outline (*Lehnert 262*, GOET). E-F. var. *minor*. E. habit (*Smith D. N. 7750*, USM); F. distal frond part with imbricately grown segments (*Lehnert 256*, GOET).

Fig. 22. *Melpomene moniliformis*, habit and characteristic features of the different varieties. A-D. var. *adnata*. A. habit (*Lehnert 1576*, GOET); B. fertile segment abaxially, present sporangia shown in outline (*Lehnert 1576*, GOET); C. scale (*Lehnert 118*, GOET); D. detail of scale apex (*Lehnert 118*, GOET). E-F. var. *paradoxa*. E. habit; F. fertile segments abaxially, sporangia primordial (all from *Kessler 6663*, UC). G. var. *tepuiensis*, habit (*Liesner 23170*, UC). H. var. *subdicarpon*, habit (*Labiak 659*, SP)

Fig. 23. Distribution maps. A. *Melpomene moniliformis* var. *moniliformis* (the var. *minor* has a nearly identical distribution and is not shown here separately). B. *Melpomene moniliformis* var. *adnata* (squares); var. *tepuiensis* (diamonds); var. *paradoxa* (circles); var. *subdicarpon* (dots).

Fig. 24. *Melpomene occidentalis*. A. habit of plant with patent linear pinnae (*Lehnert 1343*, GOET); B. habit of plant with weakly ascending long deltate pinnae (*Lehnert 1575*, GOET); C. petiole, upper part (*Lehnert 1343*, GOET); D. fertile segment abaxially (*Lehnert 1343*, GOET); E. rhachis adaxially (*Lehnert 1343*, GOET).

Fig. 25. *Melpomene personata*. A. habit (*Lehnert 405*, GOET); B. scale (*Lehnert 145*, GOET); C. petiole (*Bach et al. 1080*, GOET); D. rhachis and segments abaxially, costae clearly visible (*Jiménez I. 1773*, UC); E. segment adaxially, margins undulate (*Kessler et al 7234*, GOET); F. fertile segment abaxially, sporangia primordial, costae obscurely visible (*Bach et al. 1080*, UC).

Fig. 26. Distribution maps. A. *Melpomene personata*. B. *Melpomene peruviana*. C. *Melpomene pseudonutans*. D. *Melpomene sodiroi* (dots), *Melpomene youngii* (squares).

Fig. 27. *Melpomene peruviana*. A. habit (*Lehnert 779*, GOET); B. large scale (*Lehnert 278*, GOET); C. small scales (*Lehnert 571*, GOET); D. petiole (*Lehnert 779*, GOET); E. segment adaxially (*Krapovickas & Schinini 38663*, LPB); F. segments abaxially, sporangia immature (*Lehnert 779*, GOET).

Fig. 28. *Melpomene pilosissima*. A. habit representative of both varieties, var. *pilosissima* (*Kessler 13514*, GOET). B-C. var. *pilosissima*. B. scale (*Kessler 13514*, GOET); C. detail of scale apex (*Kessler 13514*, GOET). D-E. var. *tsatchelae*. D. segment adaxially (*van der Werff & Palacios 9698*, UC); E. segment abaxially, sporangia primordial (*Balslev & Quintana 24052*, AAU).

Fig. 29. *Melpomene pseudonutans*. A. habit; B. scale; C. detail of scale apex; D. petiole; E. segment abaxially, sporangia primordial; F. segment adaxially (all from *Laegaard et al. 53349*, AAU).

Fig. 30. *Melpomene sklenarii*. A. habit (*Lehnert 156*, GOET); B. habit (*Lehnert 108*, GOET); C. scale (*Mille s.n.*, P); D. petiole (*Lehnert 156*, GOET); E. segment adaxially (*Lehnert 156*, GOET); F. segment abaxially, sporangia primordial to immature, partly removed (*Lehnert 156*, GOET).

Fig. 31. Distribution of *Melpomene sklenarii*.

Fig. 32. *Melpomene sodiroi*. A. habit, left with wide pinnae and short frond apex (*Proctor 38737*, QCA), right with narrow pinnae and long tapering apex (*Lehnert 1106*, GOET); B. scales, small scale (*Lehnert 1106*, GOET) in detail, large scale shown as outline (*Laegaard 52141*, AAU); C. detail of scale apices (*Lehnert 1106*, GOET); D. petioles, hairy young one in the back, glabrous one in front (*Lehnert 1106*, GOET); E. segment adaxially (*Lehnert 1106*, GOET); F. segment abaxially, sporangia mature, partly removed (*Lehnert 1106*, GOET).

Fig. 33. *Melpomene vernicosa* A. habit (*Holm-Nielsen 3315*, AAU); B. scale (*Lehnert 803*, GOET); C. petiole (*Lehnert 803*, GOET); D. segment adaxially (*Lehnert 803*, GOET); E. segment abaxially, sporangia mature, closed (*Lehnert 803*, GOET).

Fig. 34. Distribution maps. A. *Melpomene vernicosa*. B. *Melpomene vulcanica*.

Fig. 35. *Melpomene vulcanica*. A. habit (*Øllgaard et al. 34159*, AAU); B. strongly branching rhizome, green fronds not shown; C. scale (*Holm-Nielsen et al. 17235*, AAU); D. petiole (*Holm-Nielsen et al. 17235*, AAU); E. segment adaxially (*Holm-Nielsen et al. 17235*, AAU); F. segment abaxially, sporangia immature (*Øllgaard et al. 34159*, AAU).

Fig. 36. *Melpomene wolfii*. A. habit (*Lehnert 1427*, GOET); B. scale (*Lehnert 869*, GOET); C. detail of scale apices (*Lehnert 869*, GOET); D. petiole (*Lehnert 1427*, GOET); E.

segment abaxially, glabrous, sporangia partially removed (*Lehnert 1427*, GOET); F. segment abaxially, hairy, sporangia removed (*Lehnert 1163*, GOET); G. truncate segment adaxially (*Lehnert 1427*, GOET).

Fig. 37. *Melpomene xiphopteroides*. A. habit of var. *xiphopteroides* (*Kessler 10232*, UC); B. habit representative of both varieties; from var. *xiphopteroides* (*Kessler 13484*, GOET). C-E. var. *xiphopteroides*. C. scale (*Mickel & Leonard 4723*, UC); D. petiole adaxially, narrowly marginate; E. segment abaxially, sporangia removed (*Kessler 10232*, UC). F-G. var. *acrodontium*. F. scale; G. detail of scale tip; H. petiole abaxially, alate. (F-H from *Schwacke 10695*, P)

Fig. 38. Distribution map. *Melpomene xiphopteroides*; var. *xiphopteroides* (dots), var. *acrodontium* (circles).

Fig. 39. *Melpomene youngii*. A. habit; B. scale; C. detail of scale tips (A-C. from *León & Young 2052*, USM); D. petiole (*León & Young 4857*, USM); E. segment adaxially, sporangia immature (*Young 1620a*, USM); F. segment adaxially (*León & Young 2052*, USM).



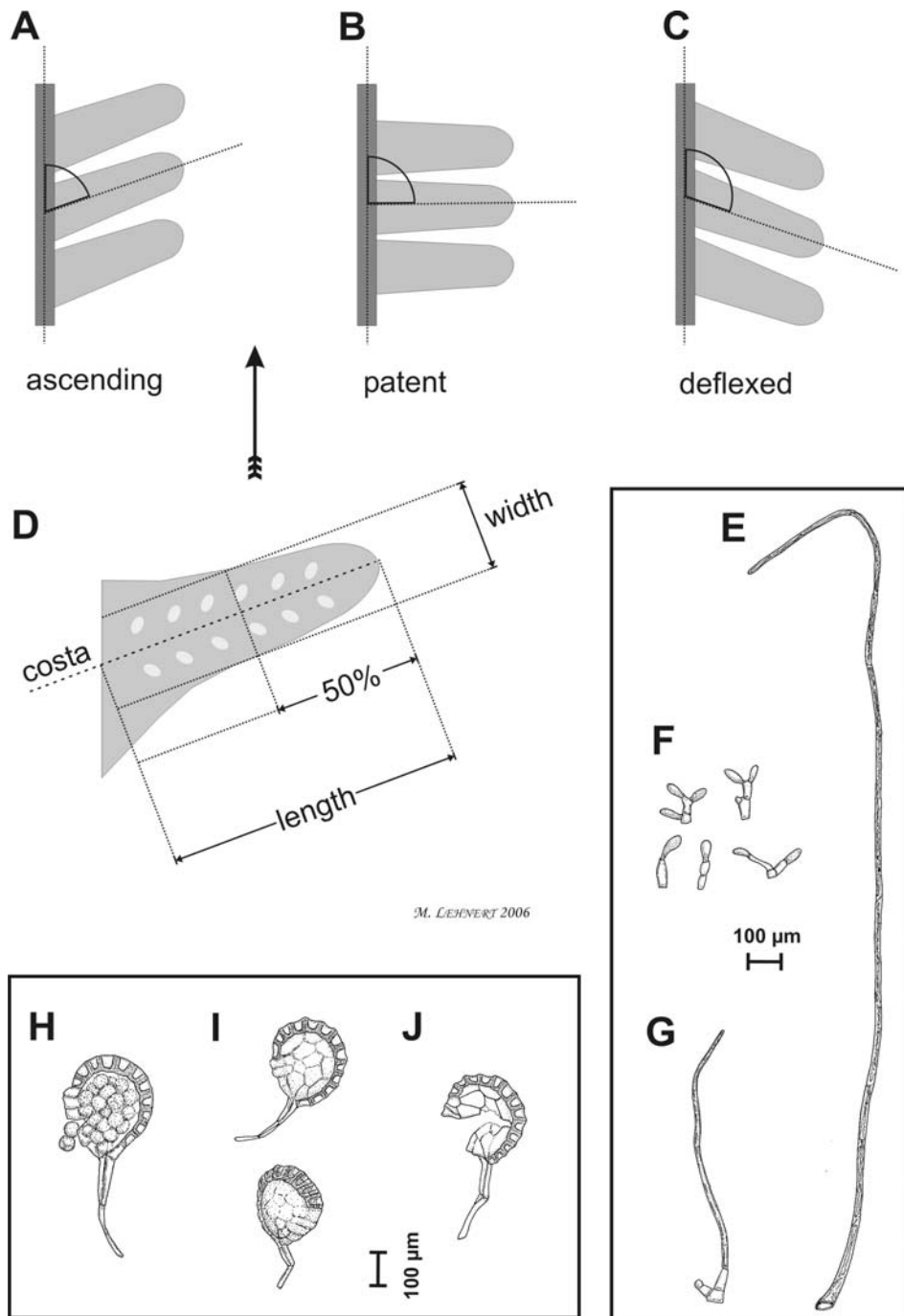


Fig. 1. Important characters of *Melpomene*. A-C. insertion of pinnae and segments into the rachis: A. ascending ( $80-60^\circ$ ); B. patent ( $85-95^\circ$ ); C. deflexed ( $100-120^\circ$ ). D. measurement of a segment. E-G. hair types: E. pluricellular uniseriate hair, *M. huancabambensis* (van der Werff & Ortega 13252, UC); F. glandular hairs, branched and simple, *M. moniliformis* var. *moniliformis* (Lehnert 262, GOET); G. hair with branched glandular base and unicellular acicular tip, *M. vernicosa* (Lehnert 868, GOET). H-J. sporangia from representative species of the genus: H. mature sporangium with trilete spores, opened partially during preparation, *M. gracilis* (Lehnert 1554, GOET); I. closed mature sporangia, spores not shown, *M. occidentalis* (Lehnert 1343, GOET); J. opened sporangium, *M. vulcanica* (Holm-Nielsen et al. 17235, AAU).

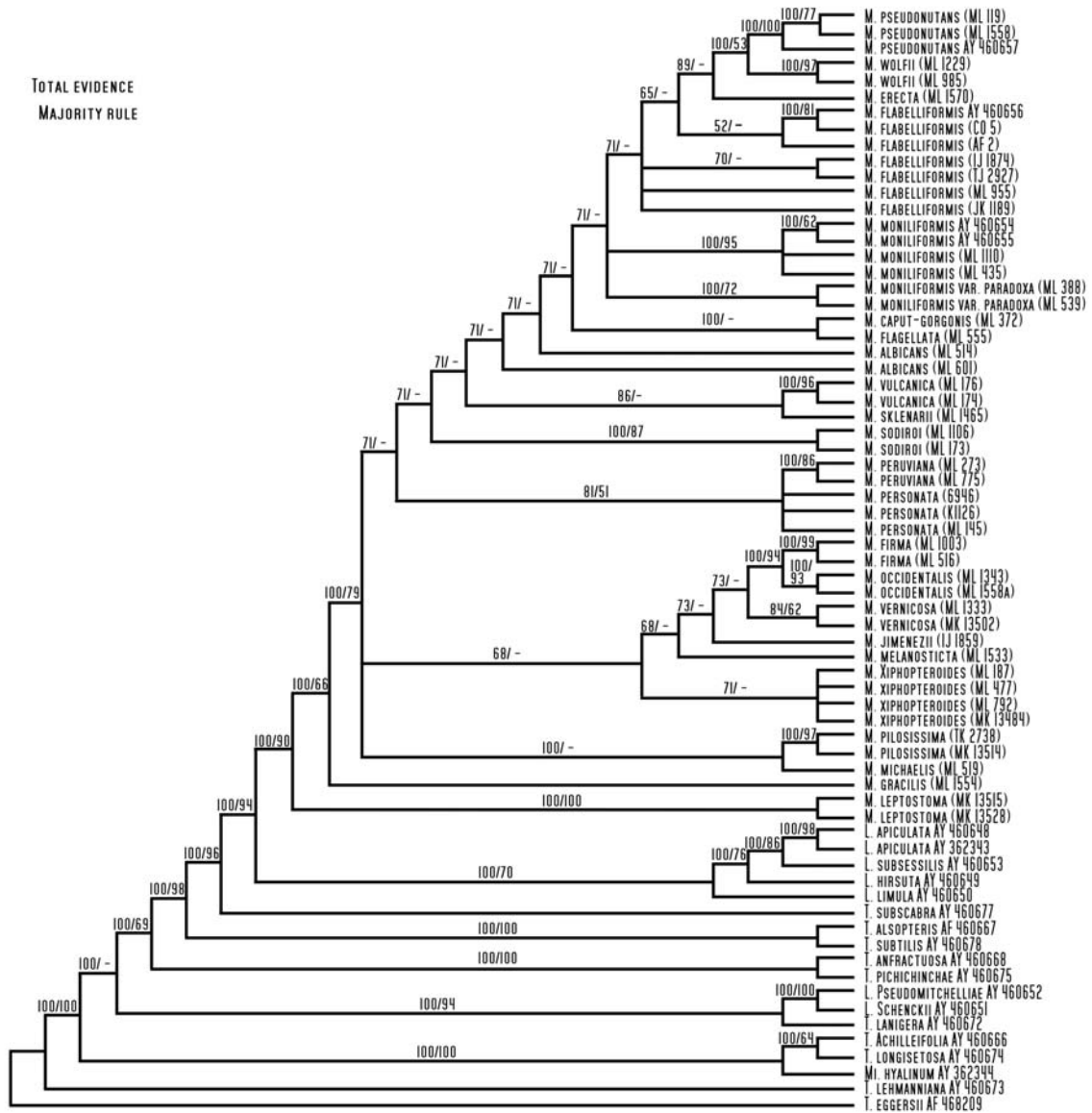


Fig. 2. Phylogenetic tree of *Melpomene* based on chloroplast genes (*rbcL*, *atpβ*) and morphology; numbers on branches are MP support/bootstraps values. (L. = *Lellingeria*; M. = *Melpomene*; Mi. = *Micropolypodium*; T. = *Terpsichore*).

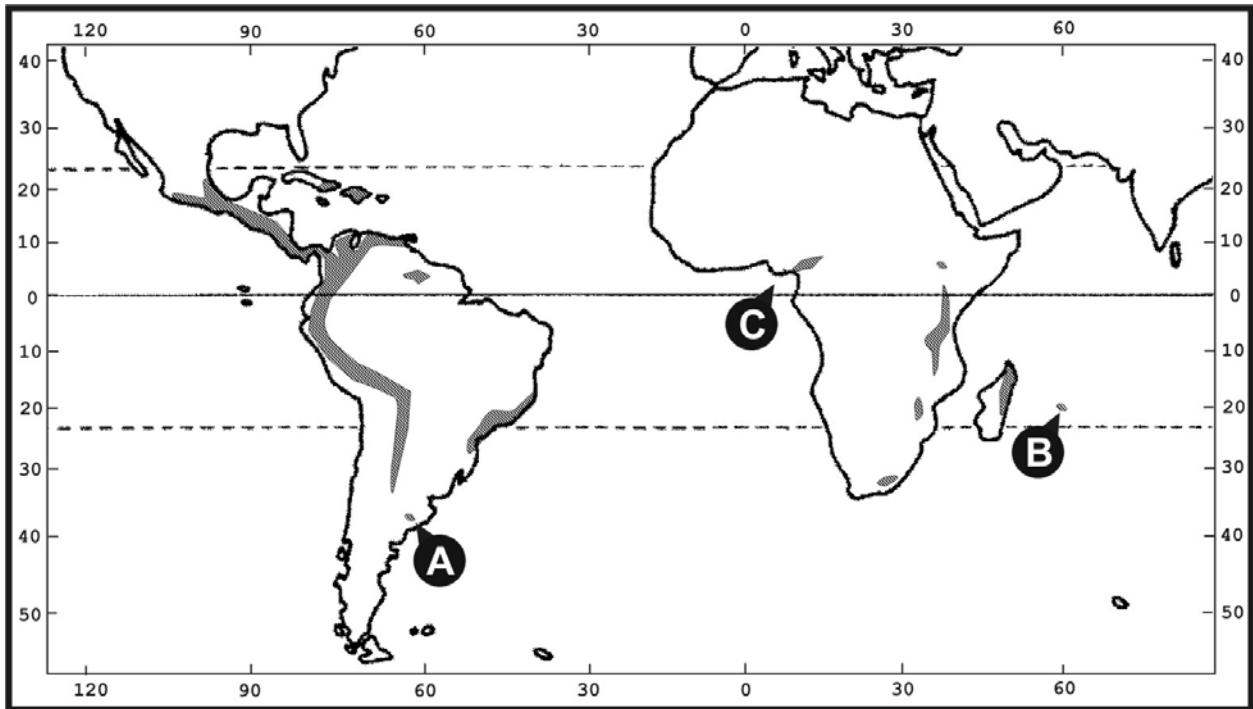


Fig. 3. Worldwide distribution of *Melpomene* (shaded area), arrows indicate noteworthy exclaves: A) southernmost occurrence in east Argentina (*Melpomene peruviana*), B) easternmost occurrence on the Mascarene Islands (*M. flabelliformis*, type locality), and C) only Atlantic occurrence on Bioko (Fernando Póo) Island (*M. flabelliformis*).

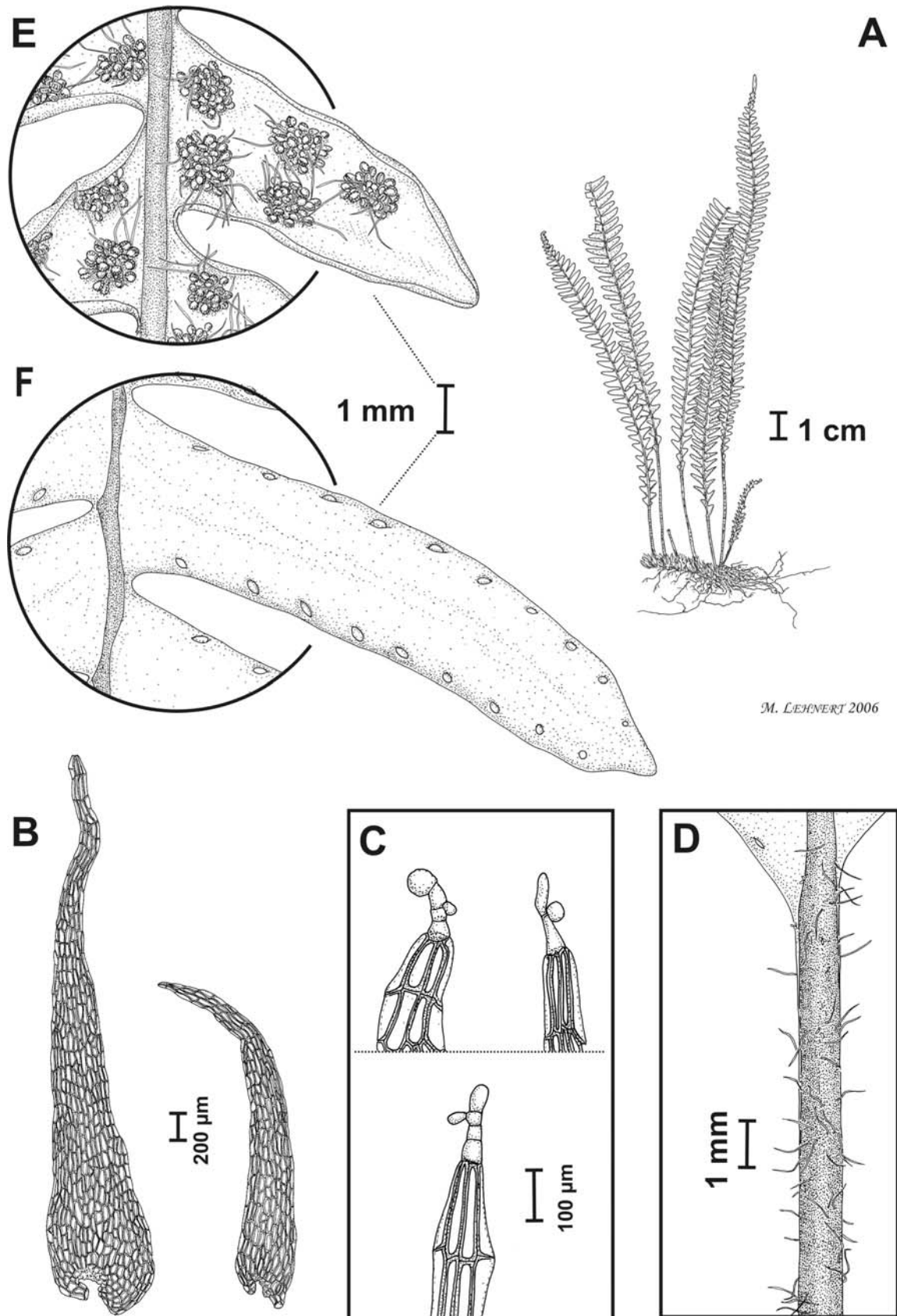


Fig. 4. *Melpomene albicans*. A. habit (*Lewis 39952*, LPB); B. scales, different sizes; C. detail of scale apices; D. petiole, upper part (*Lehnert 714*, GOET); E. fertile segment abaxially (*Lehnert 512*, LPB); F. segment adaxially (*Lehnert 714*, GOET).

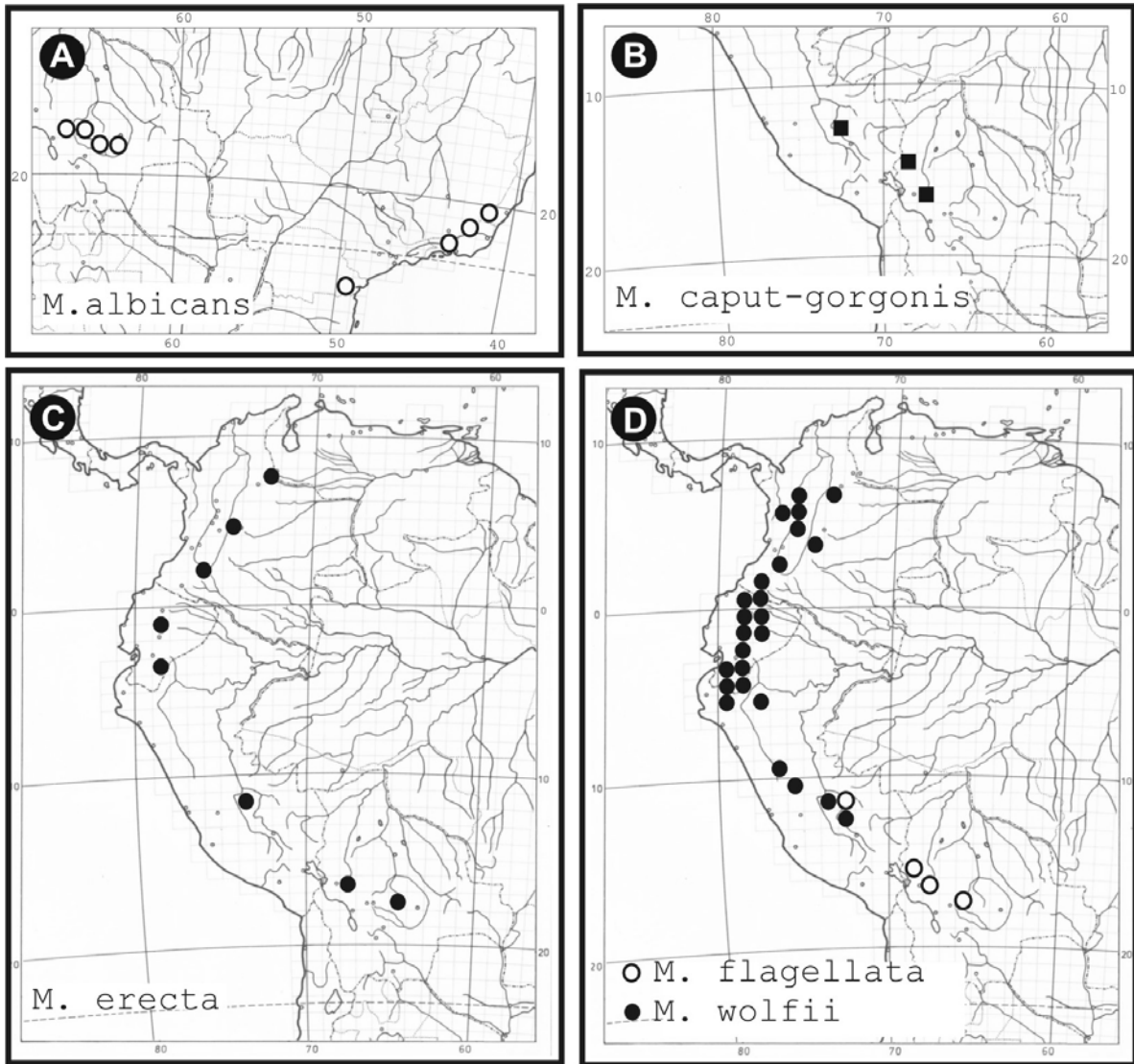


Fig. 5. Distribution maps. A. *Melpomene albicans*. B. *Melpomene caput-gorgonis*. C. *Melpomene erecta*. D. *Melpomene flagellata* (circles), *M. wolfii* (dots).

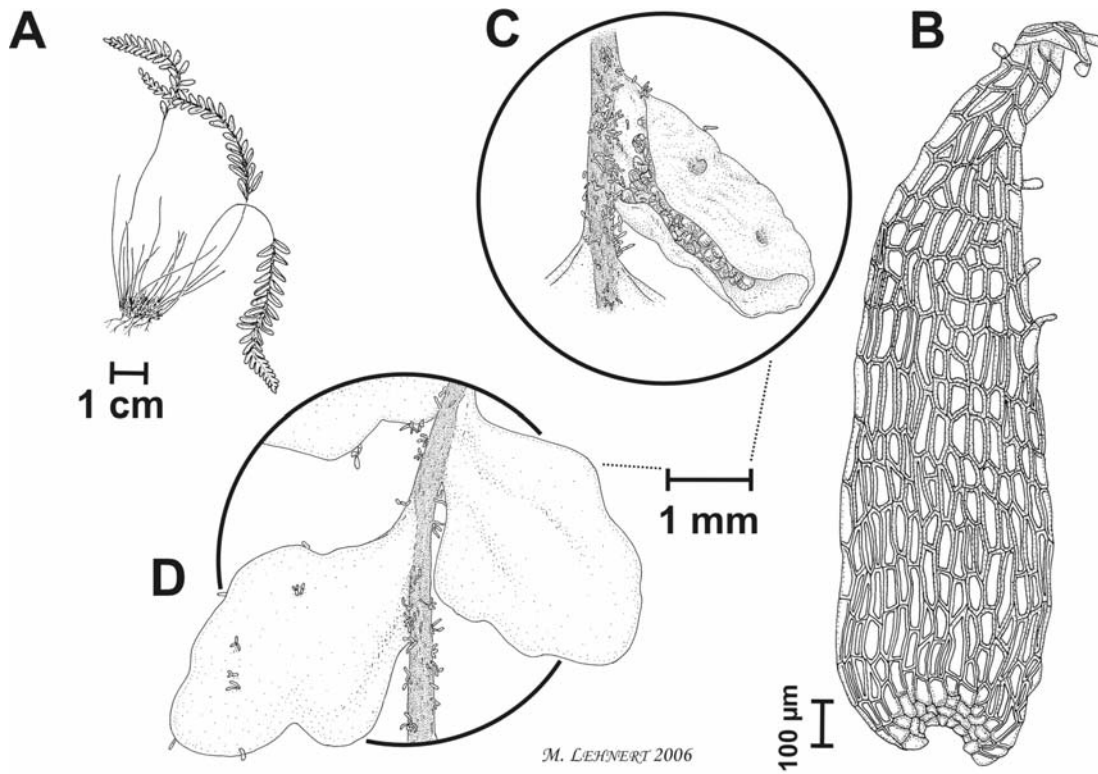


Fig. 6. *Melpomene allosuroides*. A. habit; B. scale; C. fertile segment abaxially. D. sterile segment abaxially.

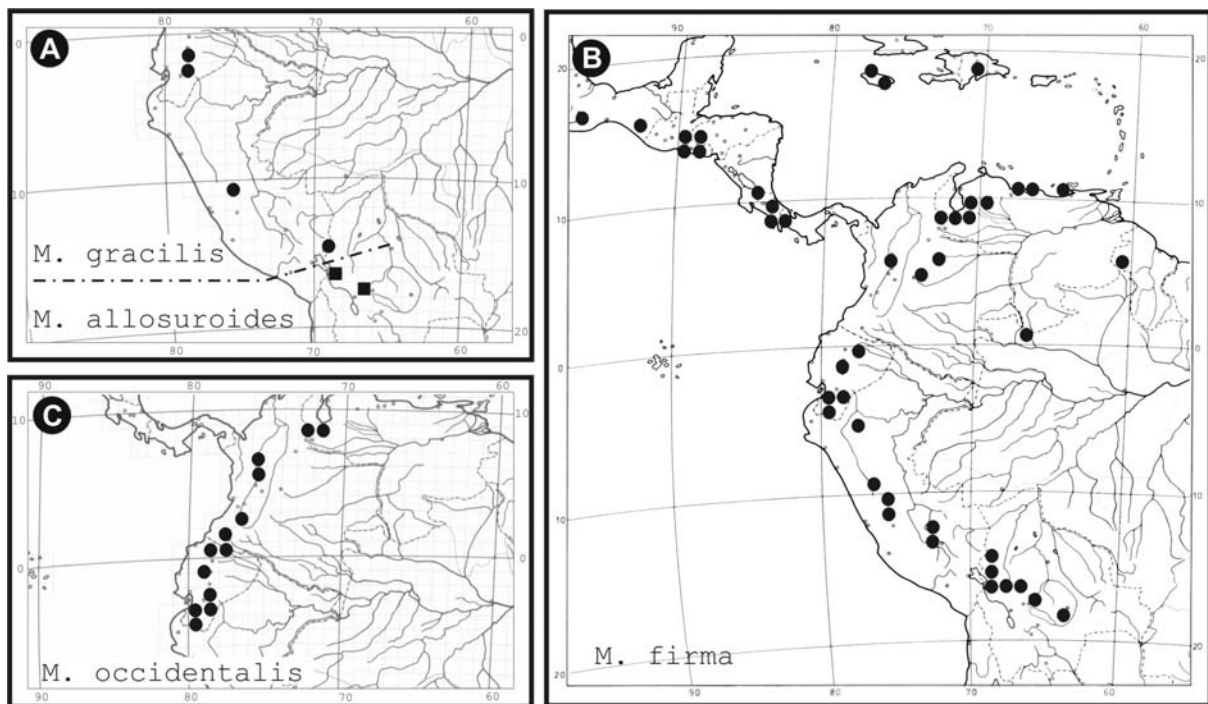


Fig. 7. Distribution maps. A. *Melpomene allosuroides* (squares). *Melpomene gracilis* (dots). B. *Melpomene firma*. C. *Melpomene occidentalis*.

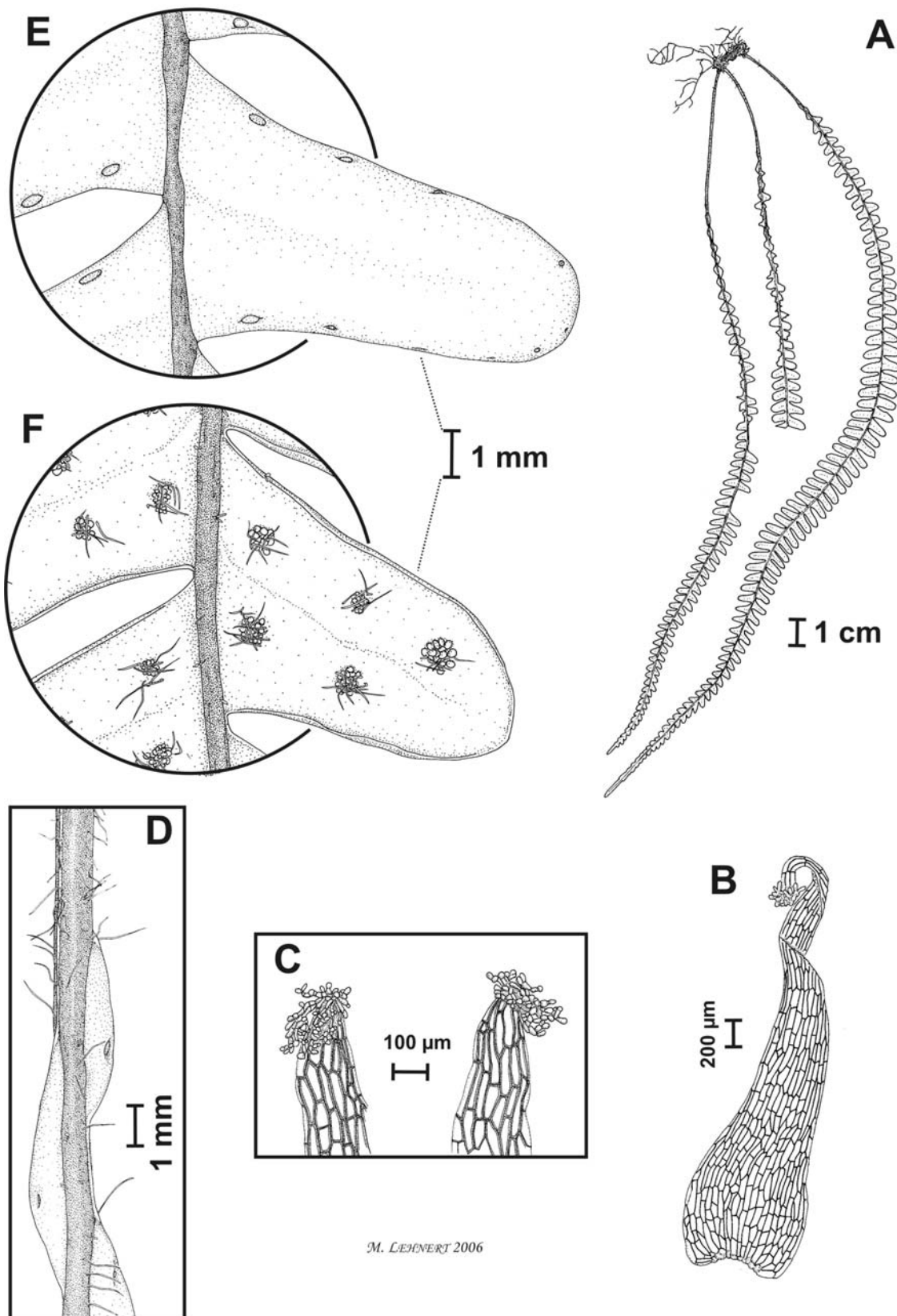
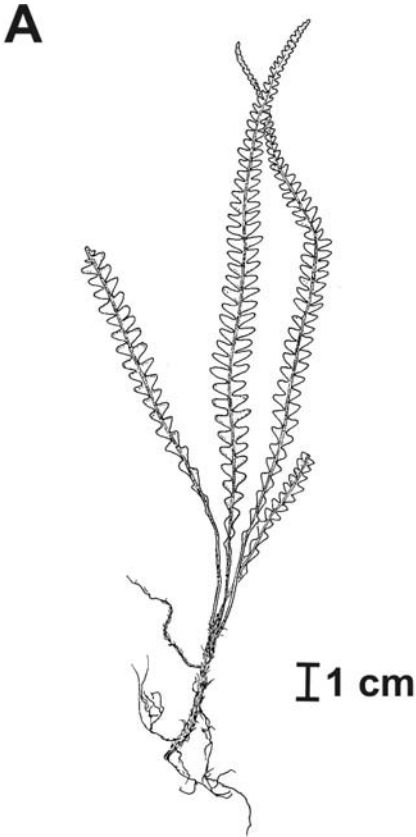


Fig. 8. *Melpomene caput-gorgonis*. A. habit (Kessler 1192, GOET); B. scale (Lehnert 368, GOET); C. detail of scale apices (Jiménez 534, LPB); D. petiole, upper part adaxially (Lehnert 368, GOET); E. segment adaxially (Lehnert 368, GOET); F. fertile segment abaxially, sporangia immature to primordial (Lehnert 367, GOET).



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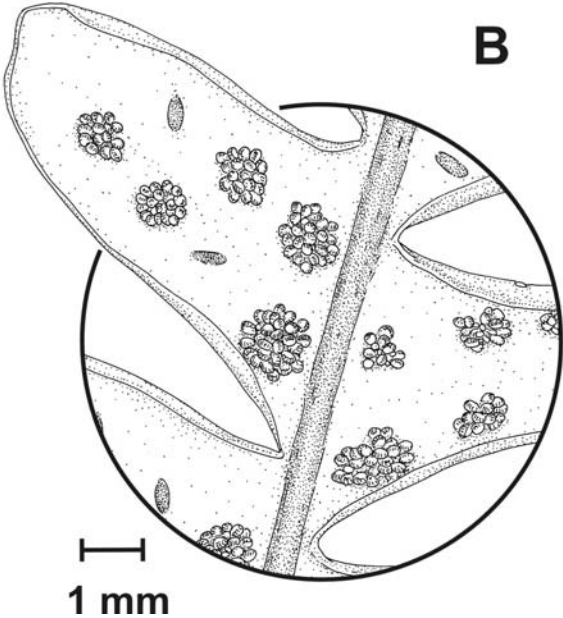


Fig. 9. *Melpomene deltata*. A. habit (Ortega & van der Werff 2246, UC); B. segment abaxially, sporangia removed from most parts (van der Werff et al. 8823, AAU).



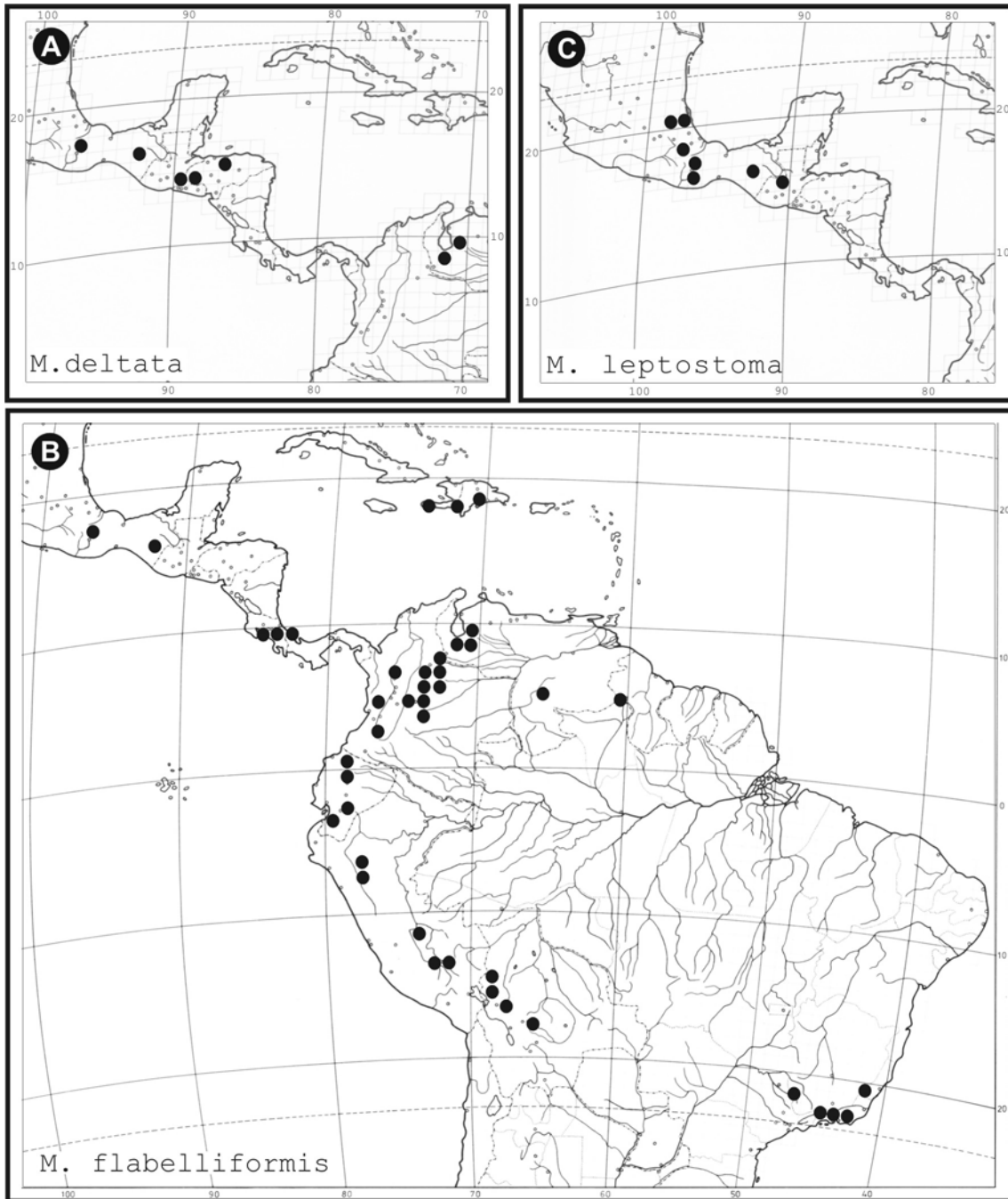


Fig. 10. Distribution maps. A. *Melpomene deltata*. B. *Melpomene flabelliformis*. C. *Melpomene leptostoma*.

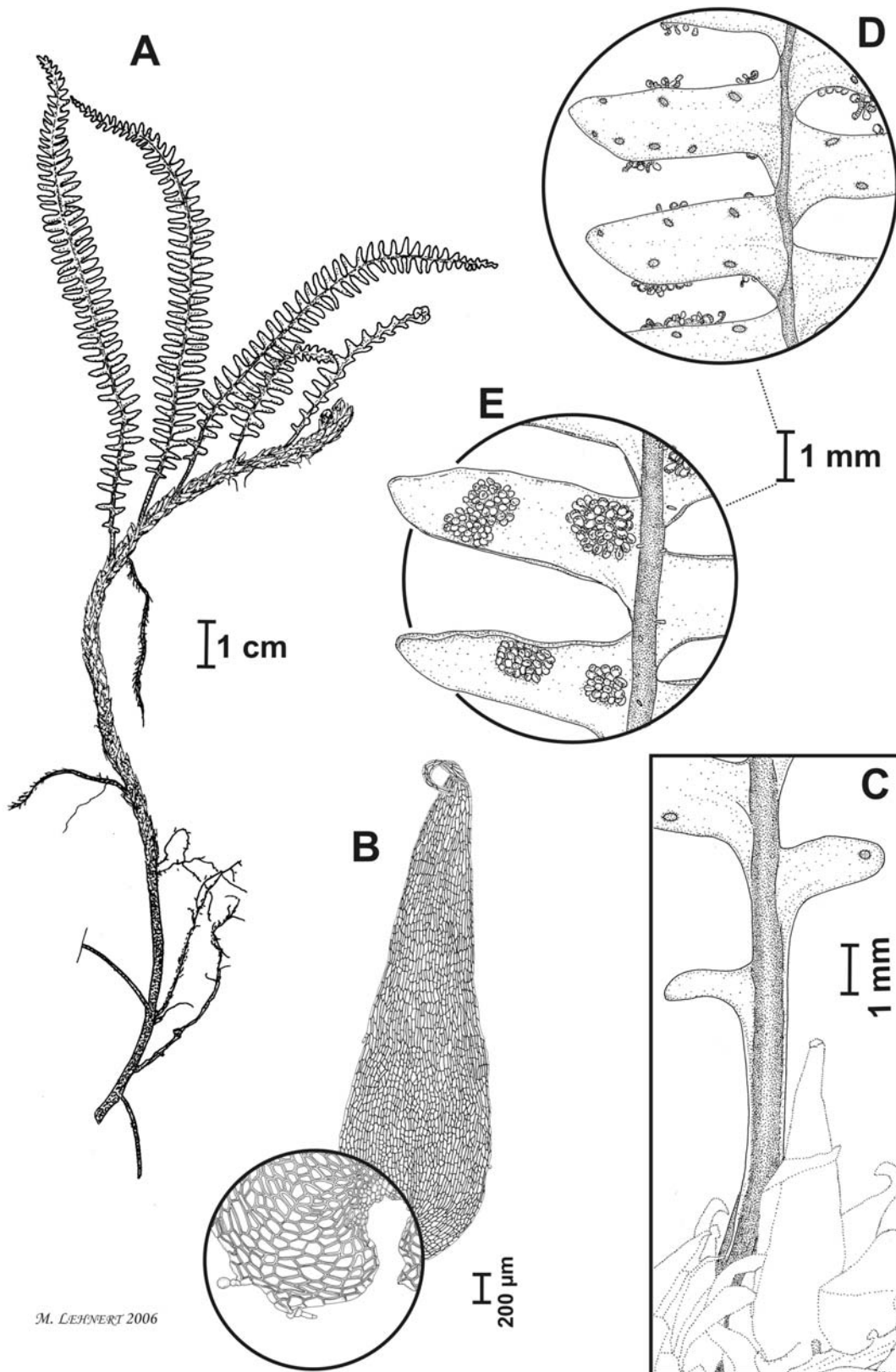


Fig. 11. *Melpomene erecta*. A. habit; B. scale; detail shows cordate insertion and small marginal glands on short lobes; C. petiole, total length; D. fertile segment adaxially, sporangia mature and partially open; E. fertile segment abaxially, sporangia immature (all from *Lehnert 1570*, GOET).

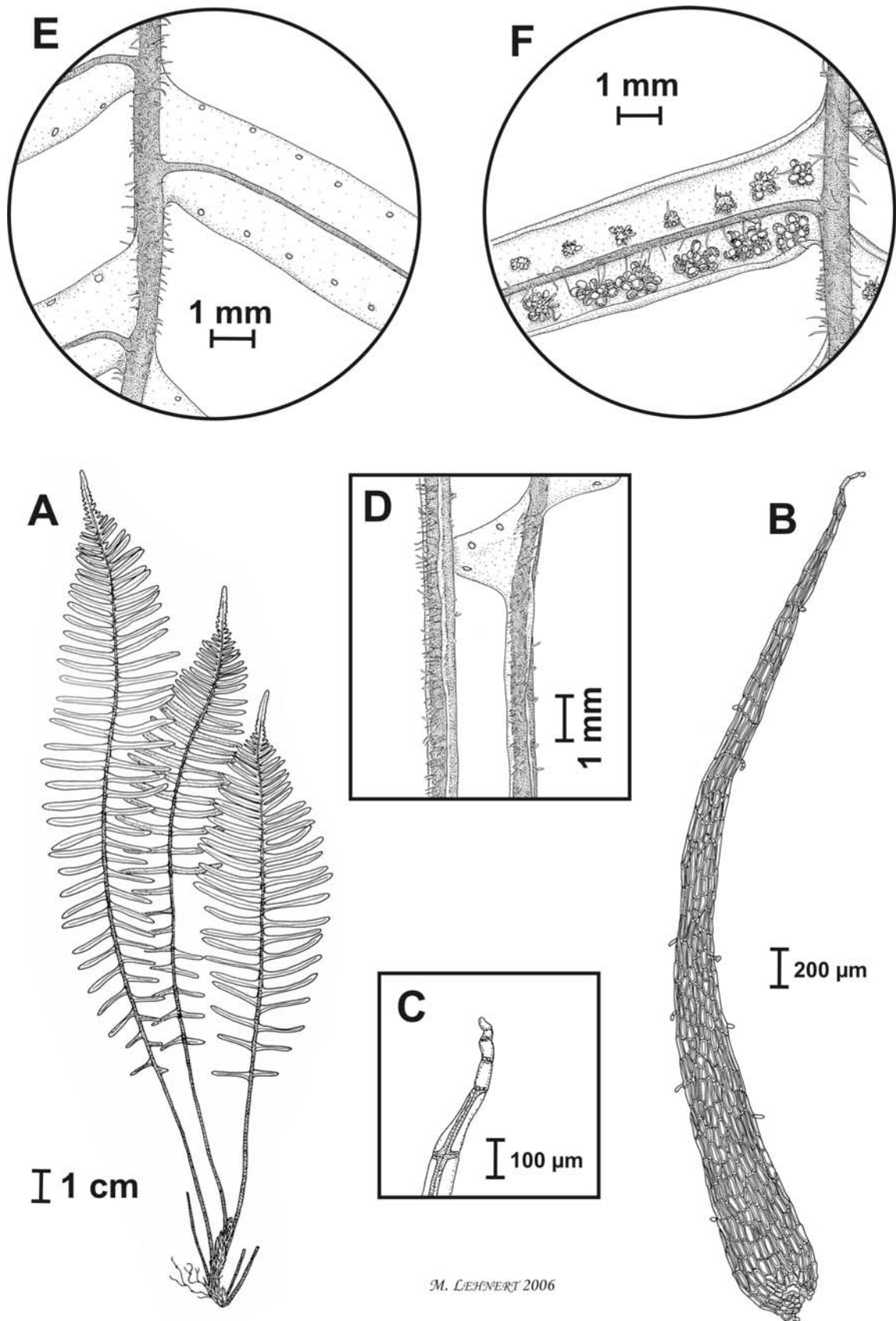


Fig. 12. *Melpomene firma*. A. habit (Lehnert 436, GOET); B. scale (Lehnert 436, GOET); C. detail of scale apex (Lehnert 436, GOET); D. petioles, left central part, right upper part (Lehnert 417, GOET); E. segment and rhachis adaxially (Lehnert 196, GOET); F. segment abaxially (Lehnert 196, GOET).

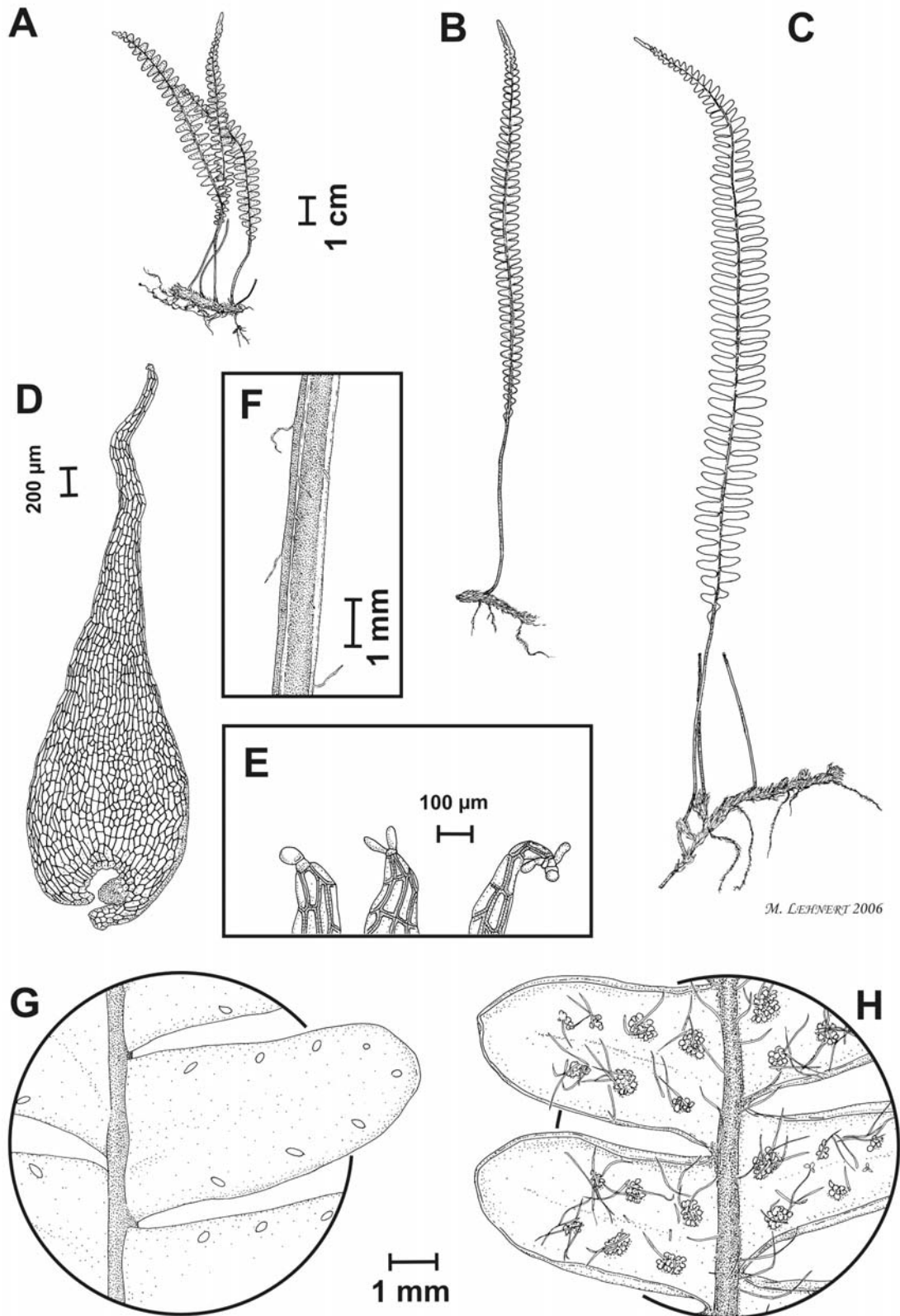


Fig. 13. *Melpomene flabelliformis*. A. habit, small African plant (*Hemp* 494, UBT); B. habit, medium sized Andean plant (*van der Werff* 10497, UC); C. habit, large Andean plant (*Young* 4423, USM); D. scale (*Lehnert* 955, GOET); E. detail of scale apex (*Lehnert* 955, GOET); F. petiole, central part (*Hemp* 494, UBT); G. segment and rachis adaxially (*Hemp* 494, UBT); H. fertile segments abaxially, sporangia immature (*van der Werff* 10497, UC).

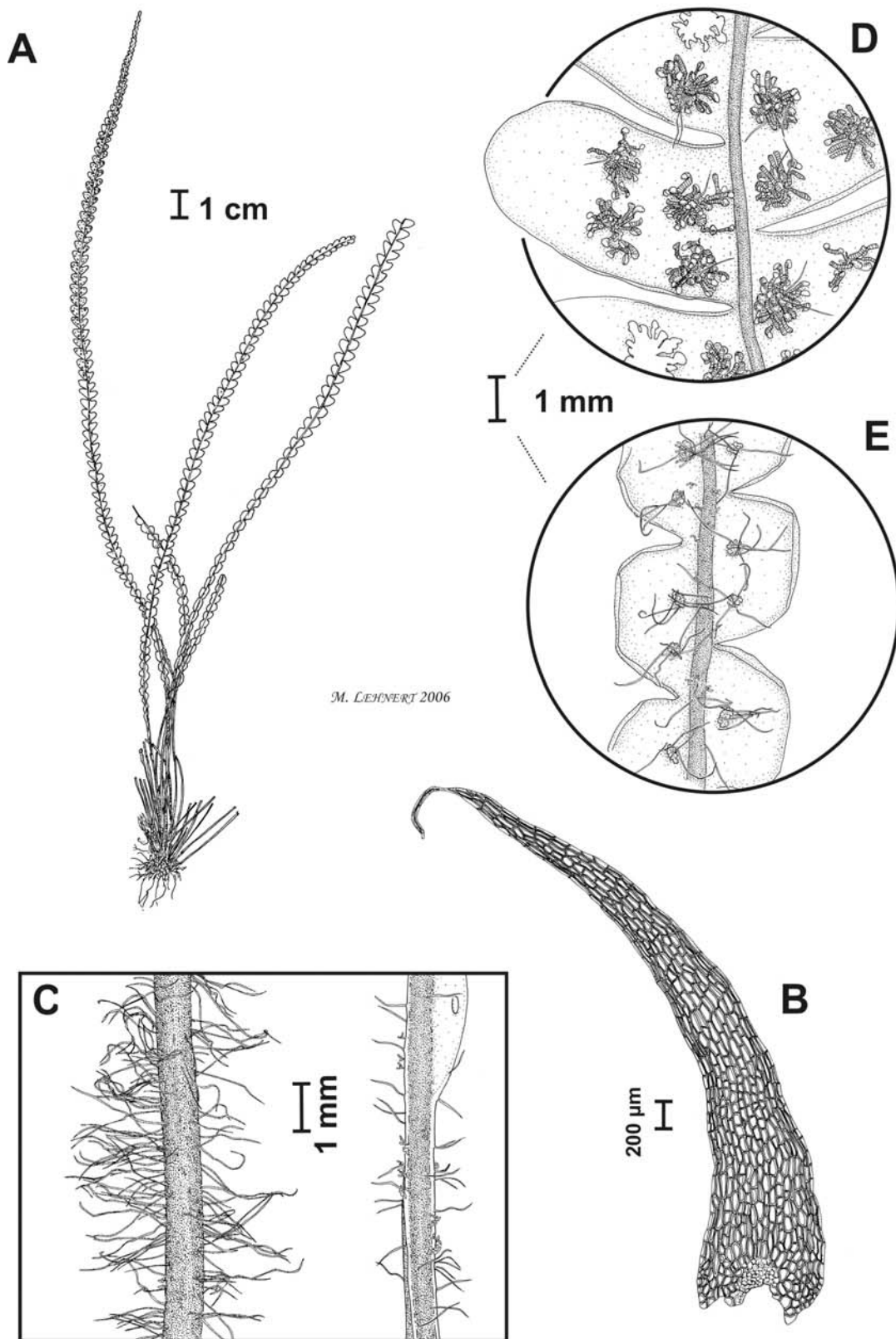


Fig. 14. *Melpomene flagellata*. A. habit (Kessler & Kelschbach 107, GOET); B. scale (Kessler & Kelschbach 107, GOET); C. petiole, left central part, right upper part (Lehnert 517, GOET); D. oblong segment abaxially, sporangia mature and open (Kessler et al. 7138, LPB); E. truncate segment abaxially, sporangia primordial (Kessler & Kelschbach 107, LPB).

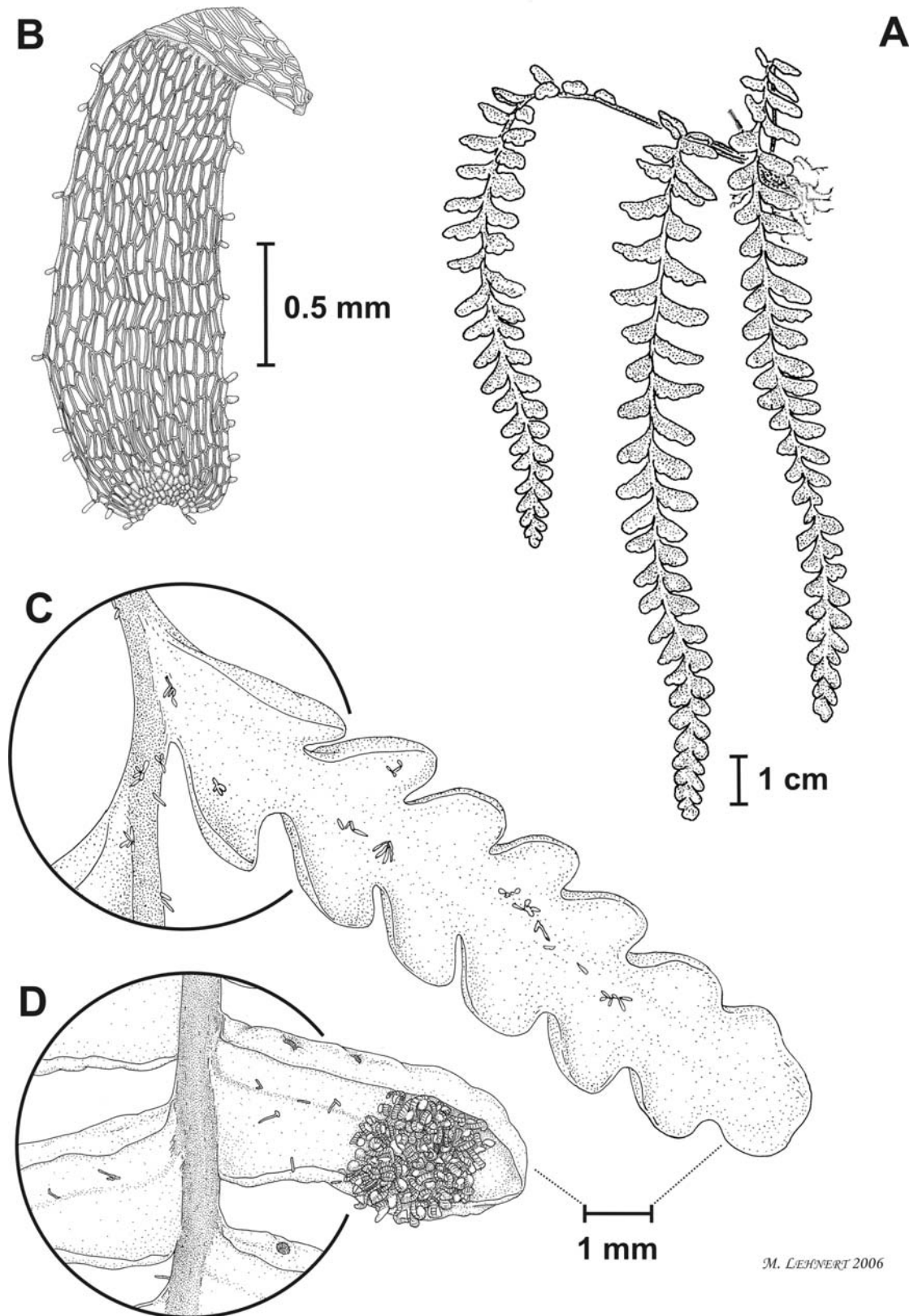


Fig. 15. *Melpomene gracilis*. A. habit; B. scale; C. sterile segment abaxially, large and deeply crenate to pinnatisect. D. fertile segment abaxially, small and margins entire.

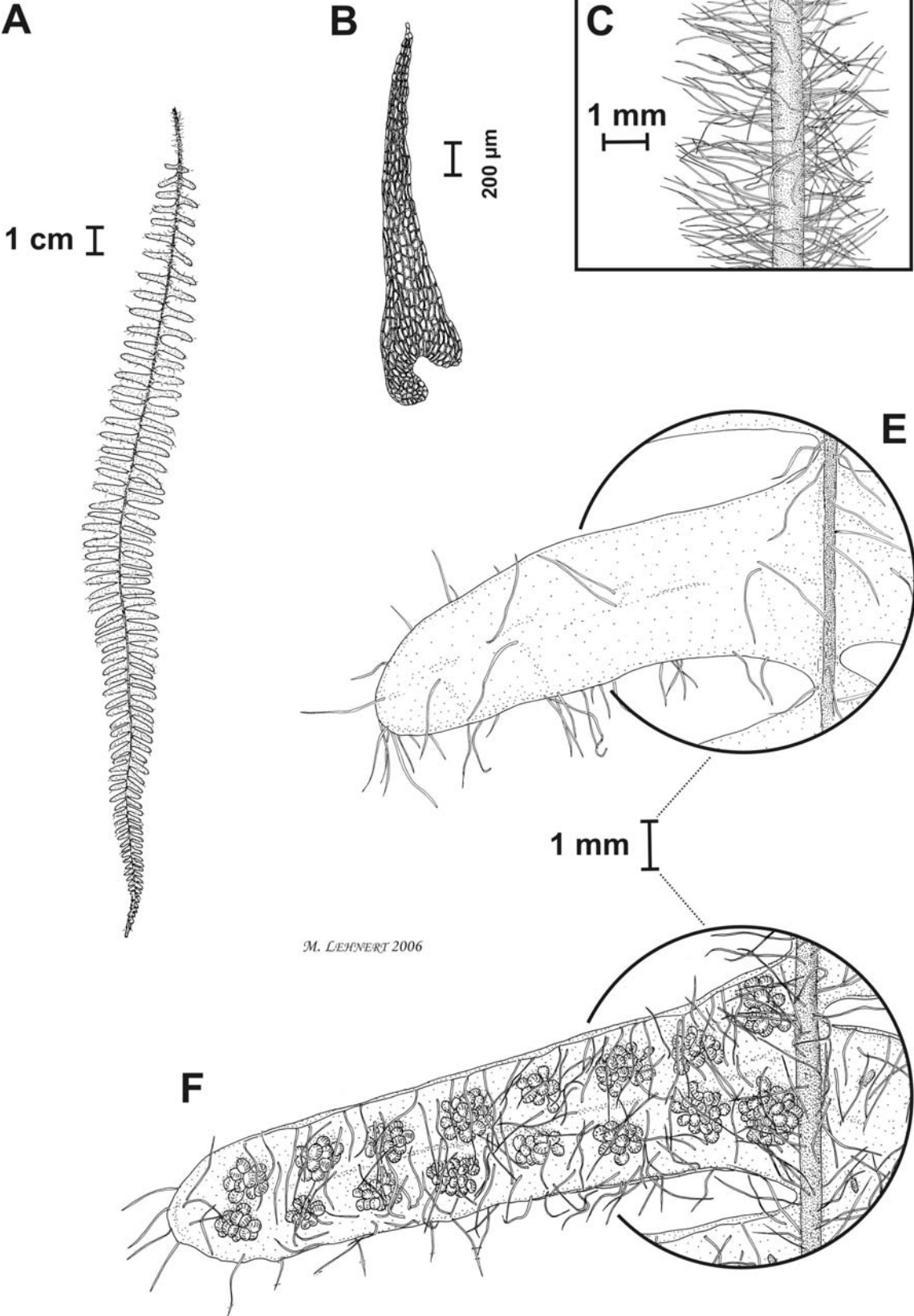


Fig. 16. *Melpomene huancabambensis*. A. frond; B. scale; C. petiole, central part; D. segment adaxially; E. segment abaxially, sporangia immature (all from van der Werff et al. 15353, UC).

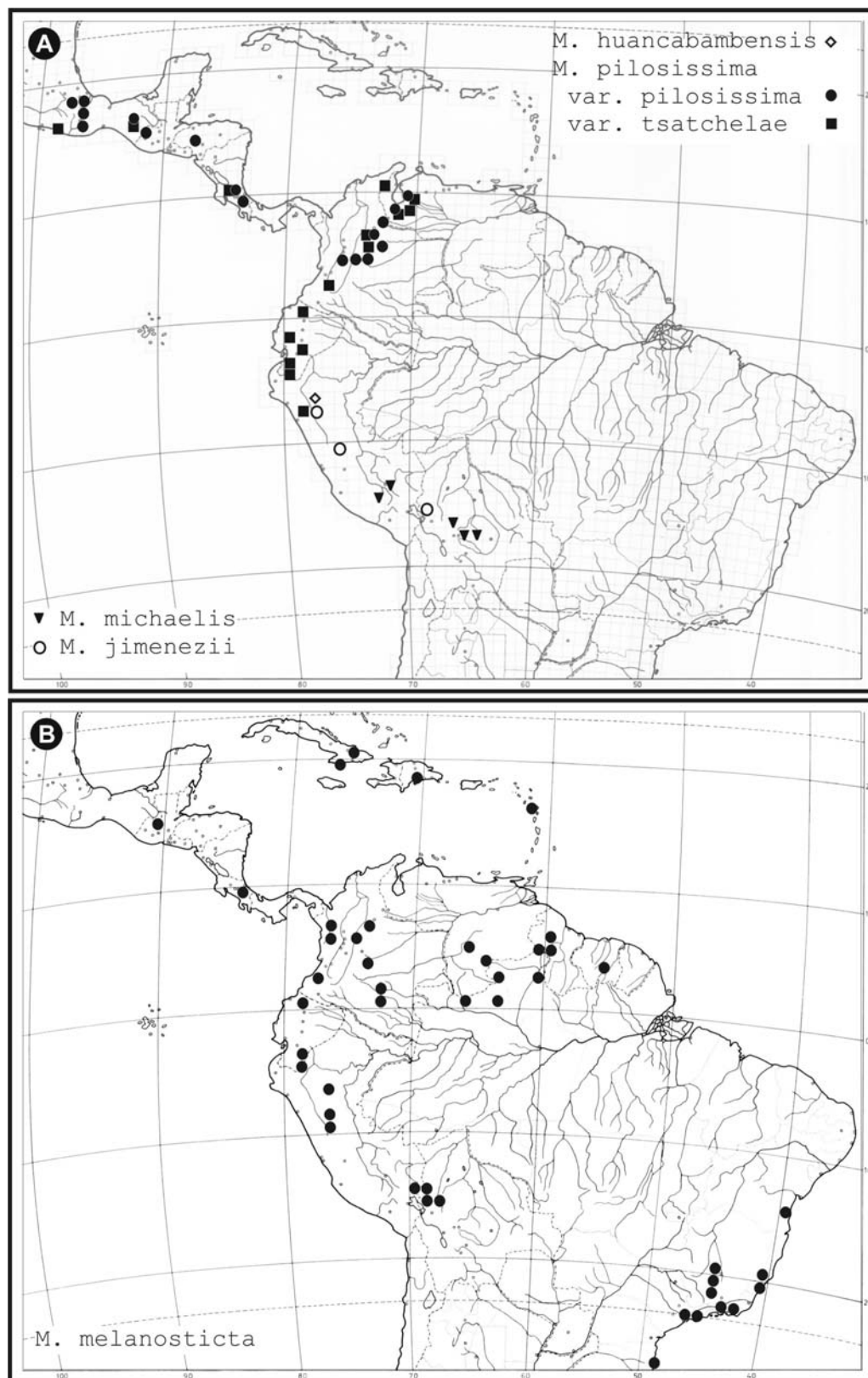


Fig. 17. Distribution maps. A. *Melpomene huancabambensis* (diamond); *M. jimenezii* (circles); *M. michaelis* (triangles); *M. pilosissima* var. *pilosissima* (dots), var. *tsatchelae* (squares); note the overlap of the varieties of *M. pilosissima*. B. *Melpomene melanosticta*.



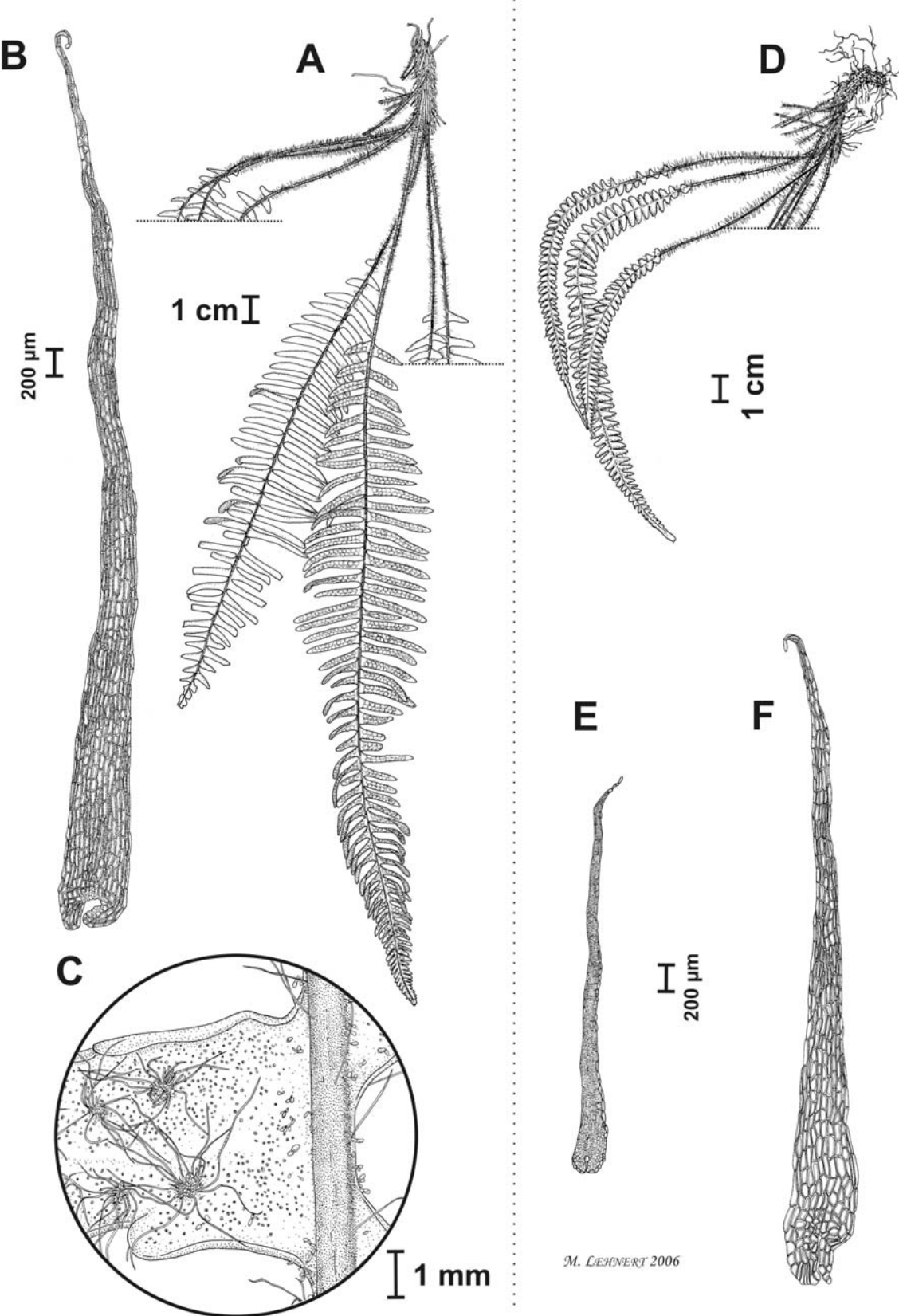
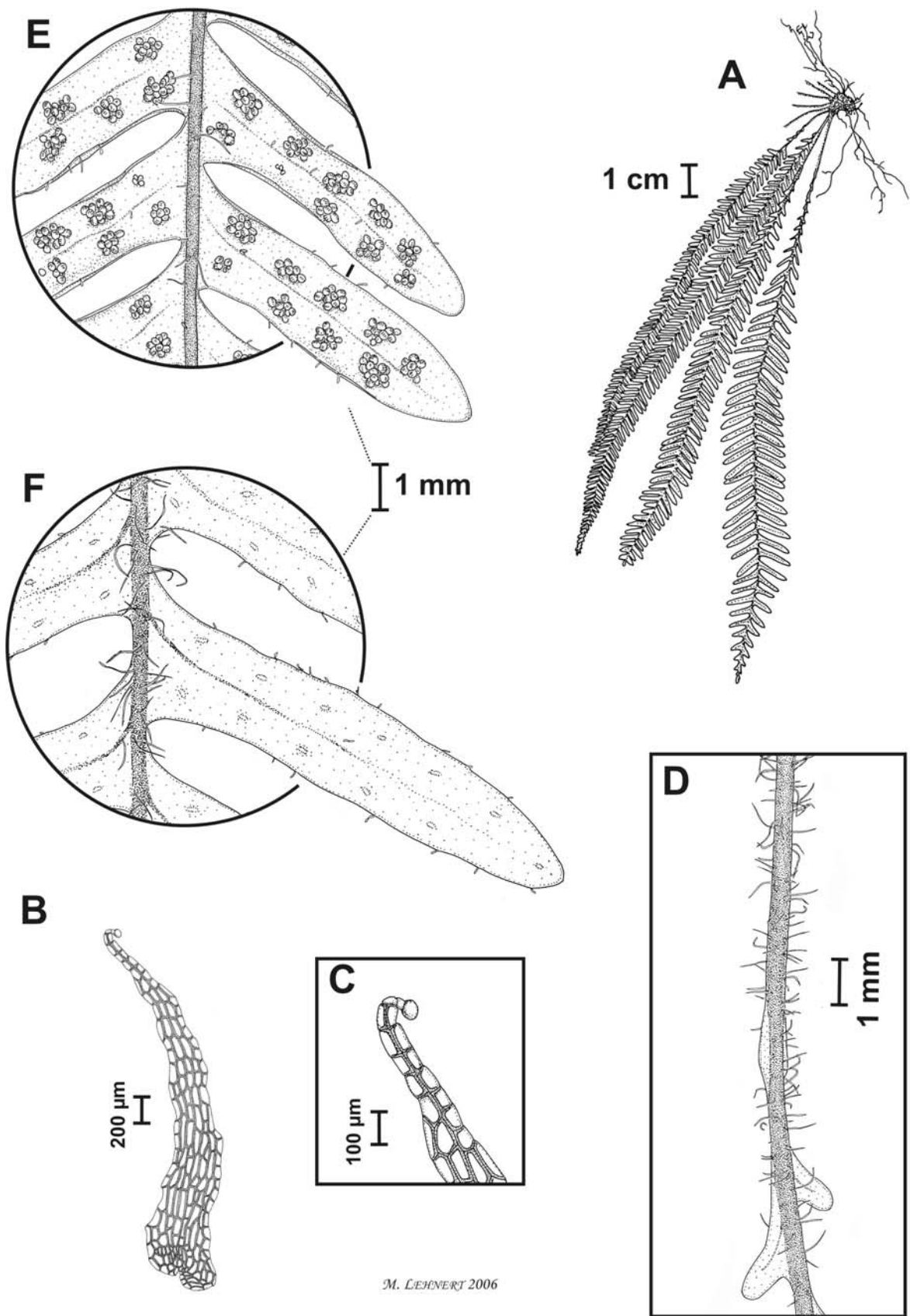


Fig. 18. A-C. *Melpomene jimenezii*. A. habit; B. scale; C. segment abaxially, sporangia removed (all from Jiménez 1859, GOET). D-F. *Melpomene michaelis*. D. habit (Lehnert 443, GOET); E. scale, with unexpanded cells (Lehnert 519, GOET); F. scale, typical (Lehnert 443, GOET).



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Fig. 19. *Melpomene leptostoma*. A. habit; B. scale; C. detail of scale apex; D. petiole, upper part; E. segment abaxially, sporangia immature; F. segment adaxially (all from *Kessler 13500*, GOET).

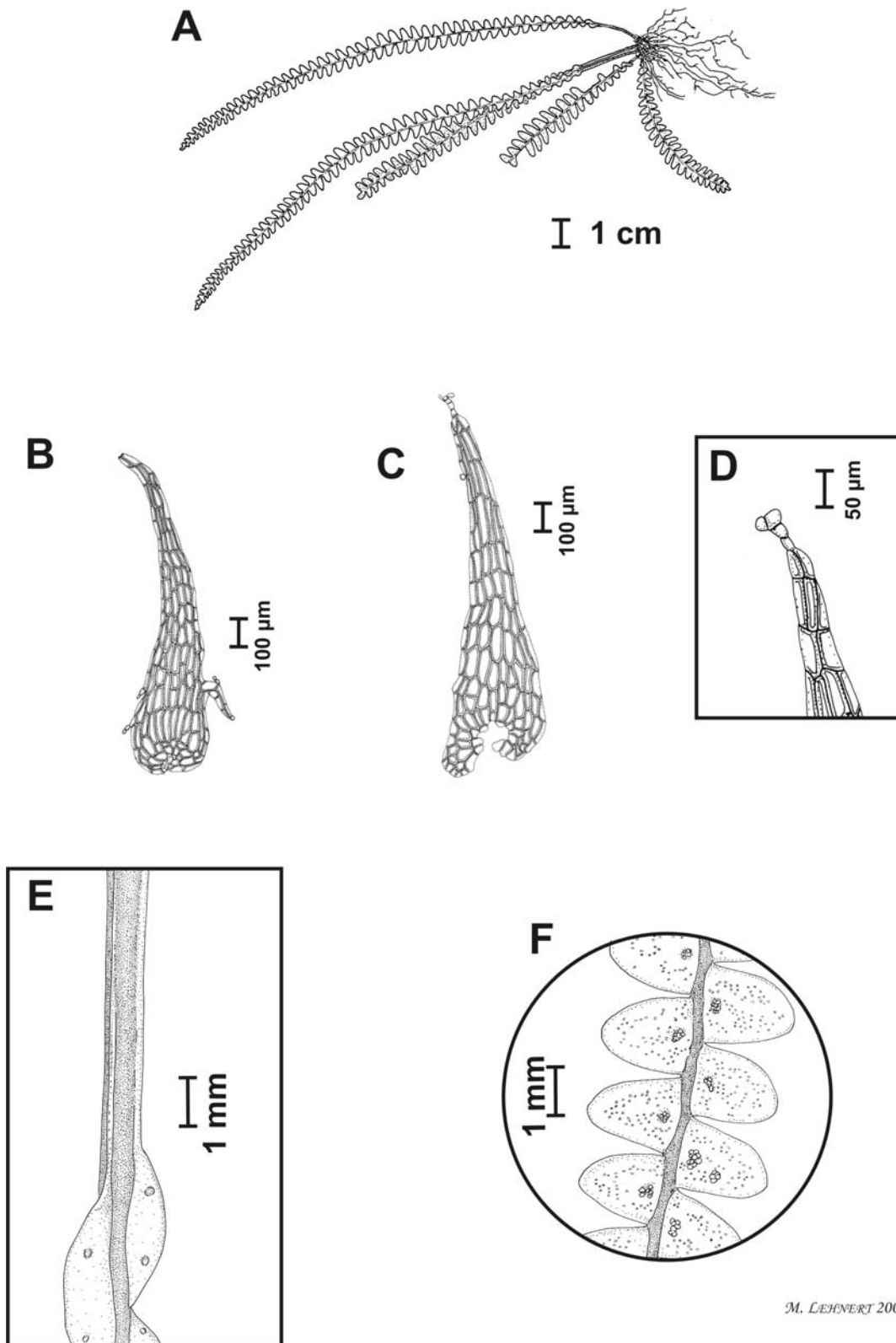


Fig. 20. *Melpomene melanosticta*. A. habit (Davidse & Huber 22756, UC); B. scale with large marginal secondary apex (Øllgaard et al. 979, AAU); C. typical scale (Fay & Fay 4180, UC); D. detail of scale apex (Fay & Fay 4180, UC); E. petiole, upper part (frond apex points down) (Øllgaard et al. 979, AAU); F. segment abaxially, sporangia primordial (Lehnert 1533, GOET).

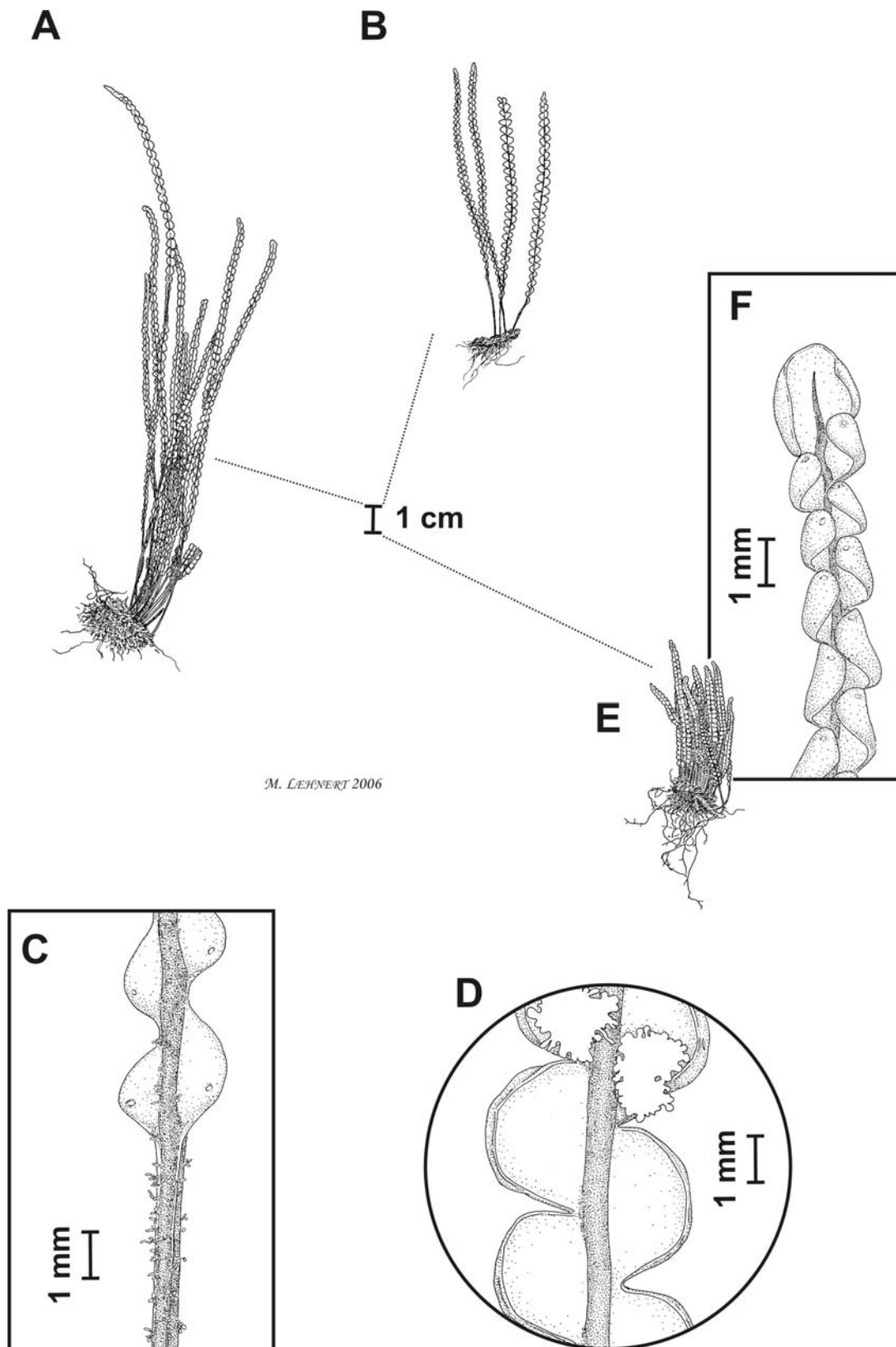


Fig 21. *Melpomene moniliformis*. A-D. var. *moniliformis*. A. habit of plant growing in cushions (ca. 1/6 of original cushion); B. habit of shaded plant; C. petiole (Lehnert 262, GOET); D. segments abaxially, sori shown as outline (Lehnert 262, GOET). E-F. var. *mina*. E. habit (Smith D. N. 7750, USM); F. distal frond part with imbricately grown segments (Lehnert 256, GOET).

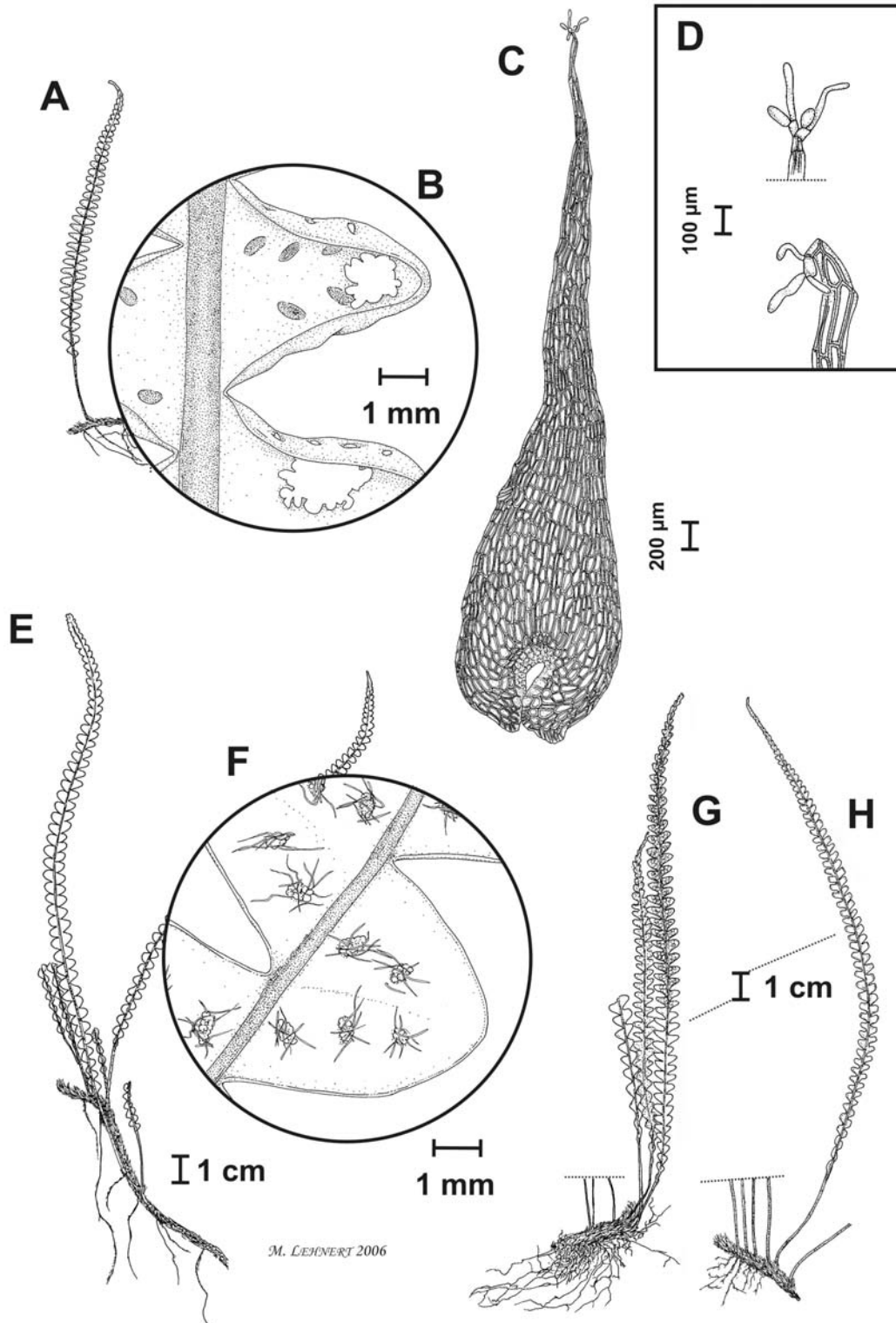


Fig. 22. *Melpomene moniliformis*, habit and characteristic features of the different varieties. A-D. var. *adnata*. A. habit (Lehnert 1576, GOET); B. fertile segment abaxially, present sporangia shown in outline (Lehnert 1576, GOET); C. scale (Lehnert 118, GOET); D. detail of scale apex (Lehnert 118, GOET). E-F. var. *paradoxa*. E. habit; F. fertile segments abaxially, sporangia primordial (all from Kessler 6663, UC). G. var. *tepuiensis*, habit (Liesner 23170, UC). H. var. *subdicarpon*, habit (Labiak 659, SP).

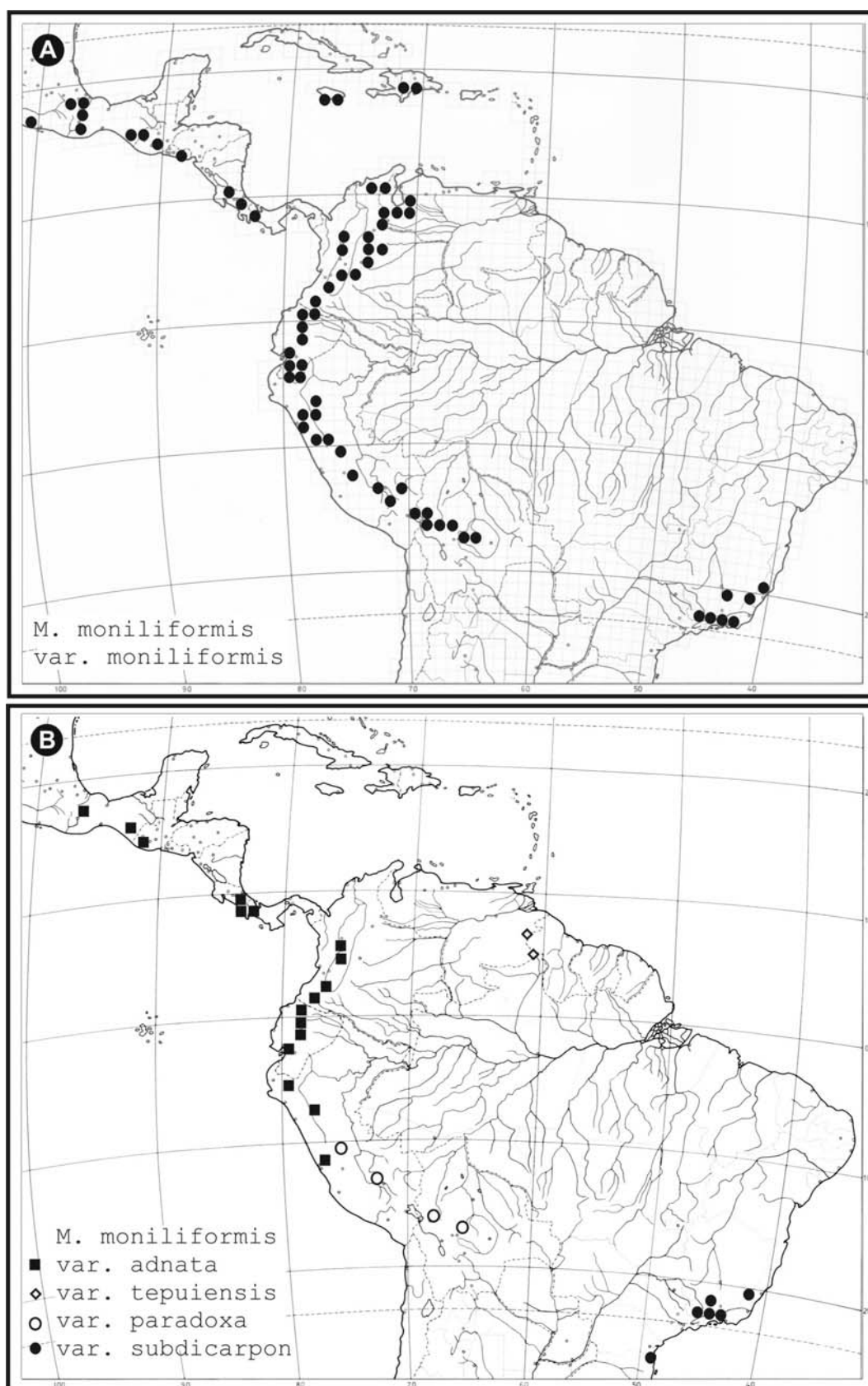


Fig. 23. Distribution maps. A. *Melpomene moniliformis* var. *moniliformis* (var. *mina* has a nearly identical distribution and is not shown here separately). B. *Melpomene moniliformis* var. *adnata* (squares); var. *tepuiensis* (diamonds); var. *paradoxa* (circles); var. *subdicarpon* (dots).

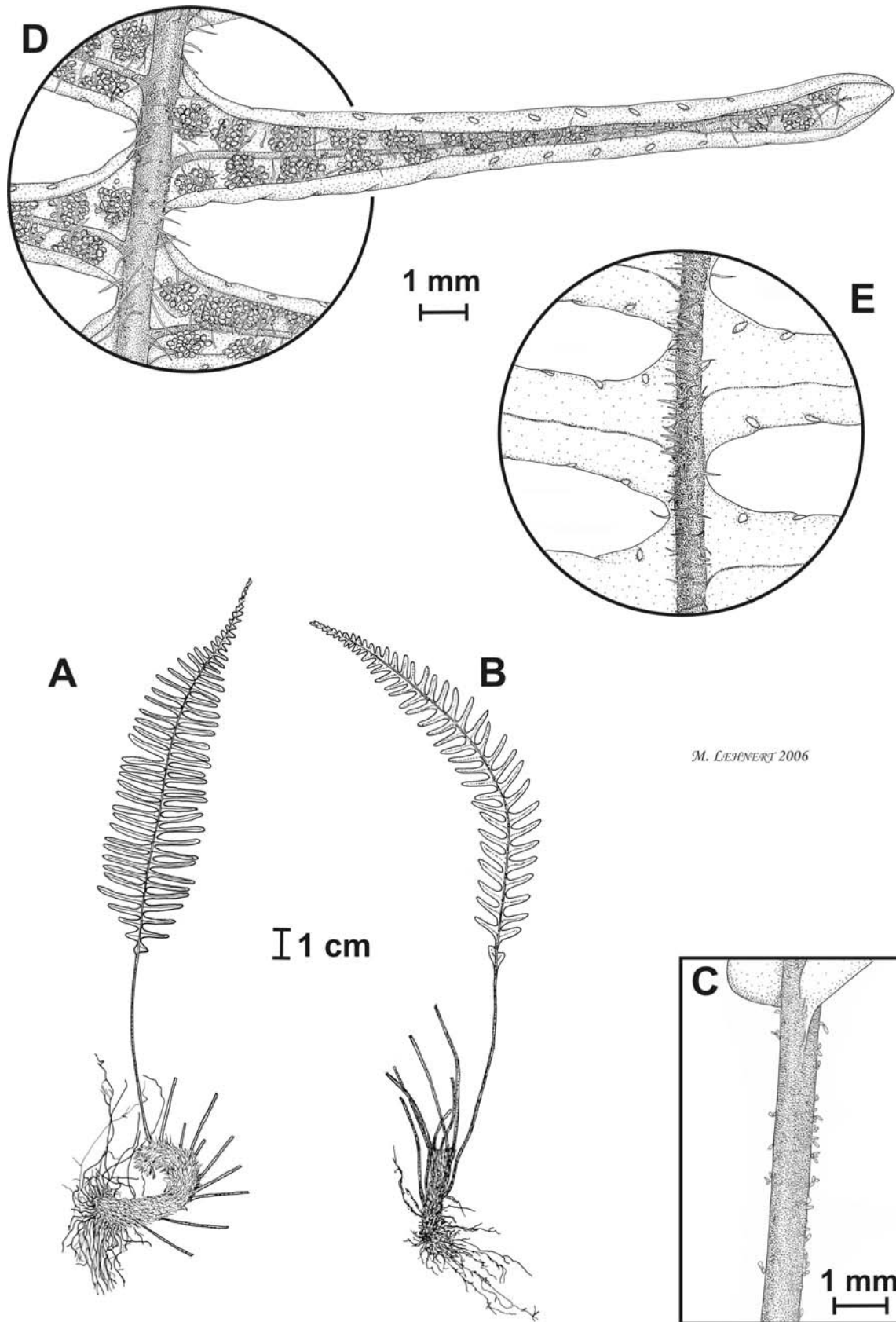


Fig. 24. *Melpomene occidentalis*. A. habit of plant with patent, linear pinnae (Lehnert 1343, GOET); B. habit of plant with weakly ascending, long deltate pinnae (Lehnert 1575, GOET); C. petiole, upper part (Lehnert 1343, GOET); D. fertile segment abaxially (Lehnert 1343, GOET); E. rhachis adaxially (Lehnert 1343, GOET).

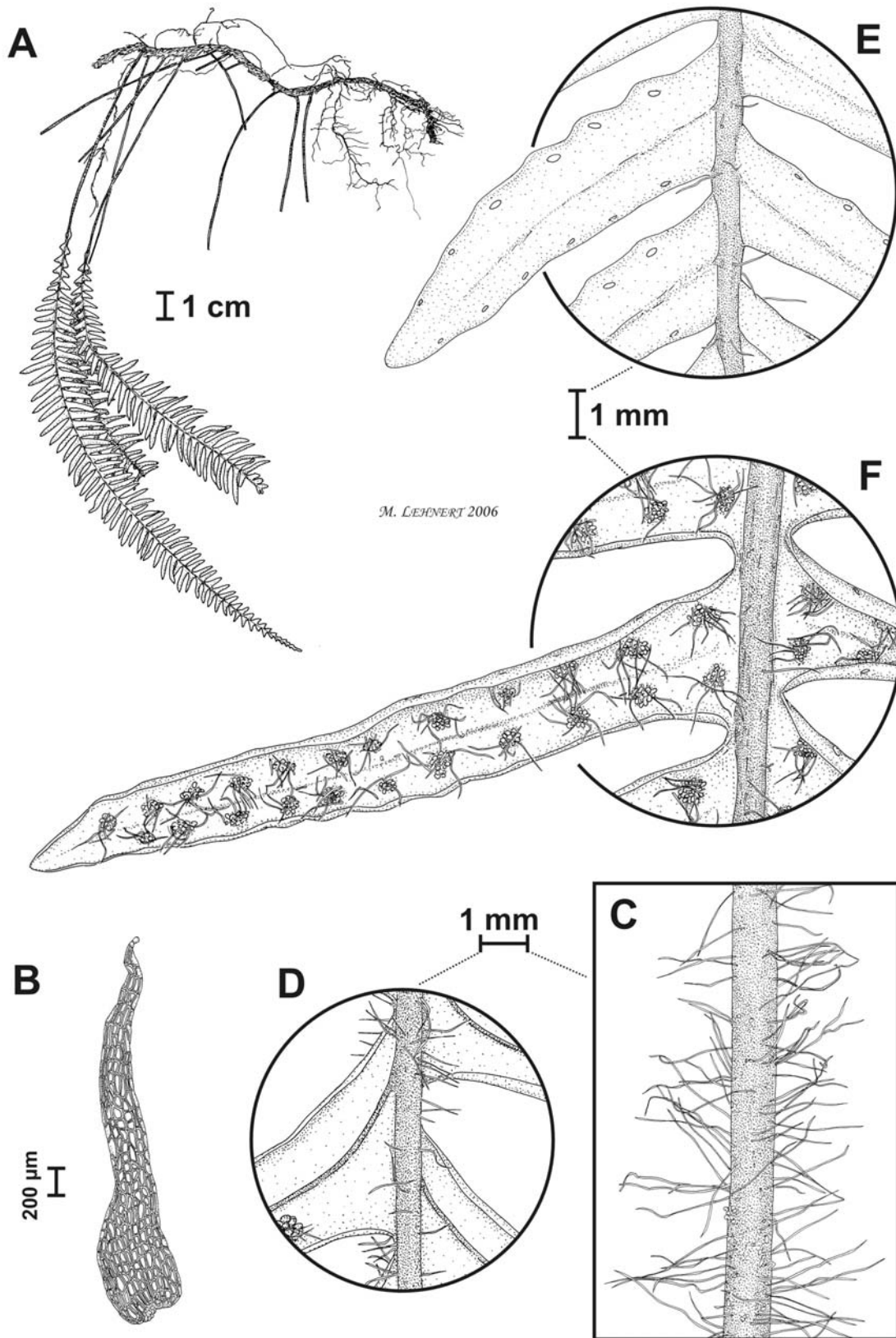


Fig. 25. *Melpomene personata*. A. habit (Lehnert 405, GOET); B. scale (Lehnert 145, GOET); C. petiole (Bach et al. 1080, GOET); D. rhachis and segments abaxially, costae clearly visible (Jiménez 1773, UC); E. segment adaxially, margins undulate (Kessler et al 7234, GOET); F. fertile segment abaxially, sporangia primordial, costae obscurely visible (Bach et al. 1080, UC).



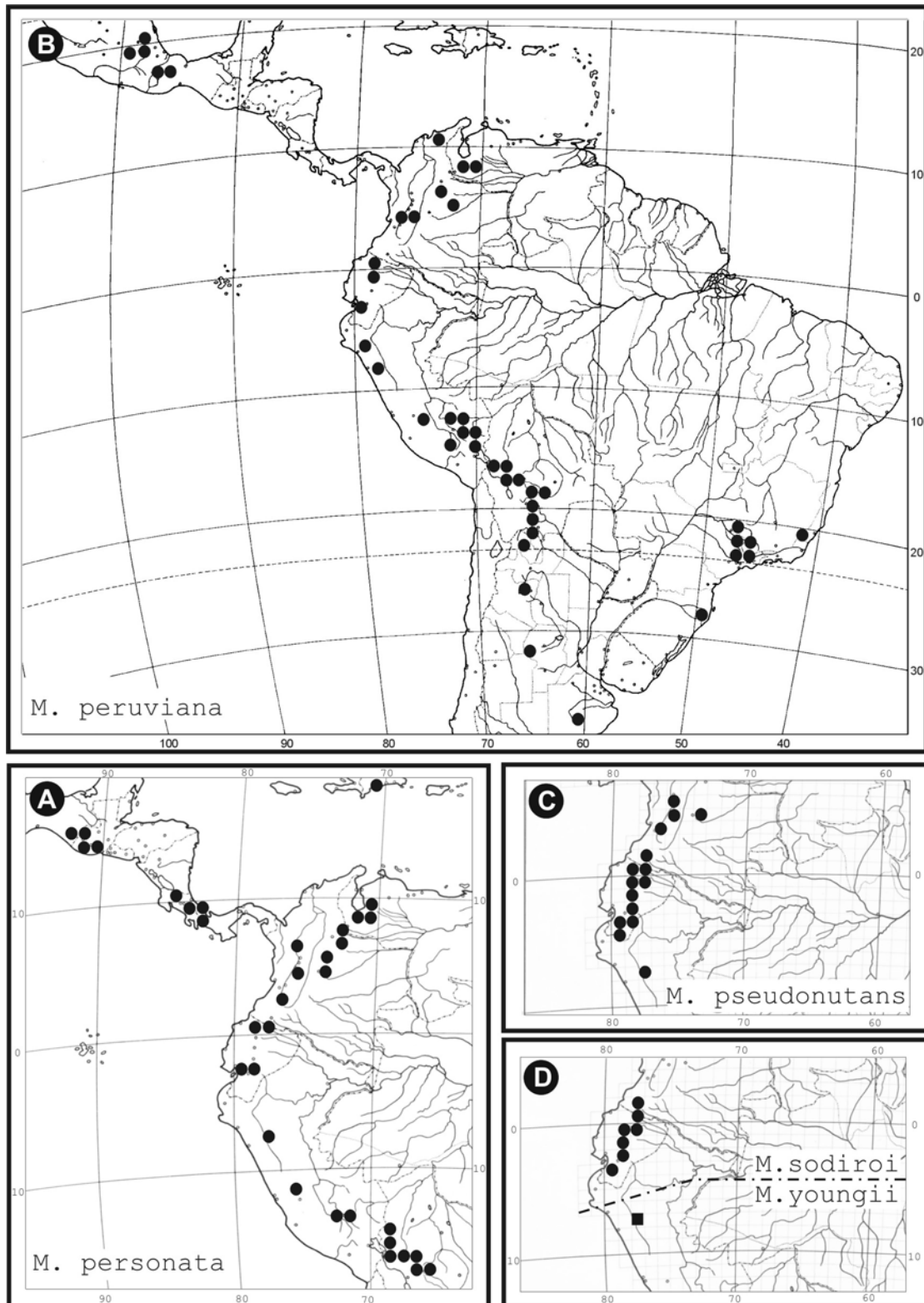


Fig. 26. Distribution maps. A. *Melpomene peruviana*. B. *Melpomene personata*. C. *Melpomene sklenarii*. D. *Melpomene sodiroi* (dots), *M. youngii* (squares).

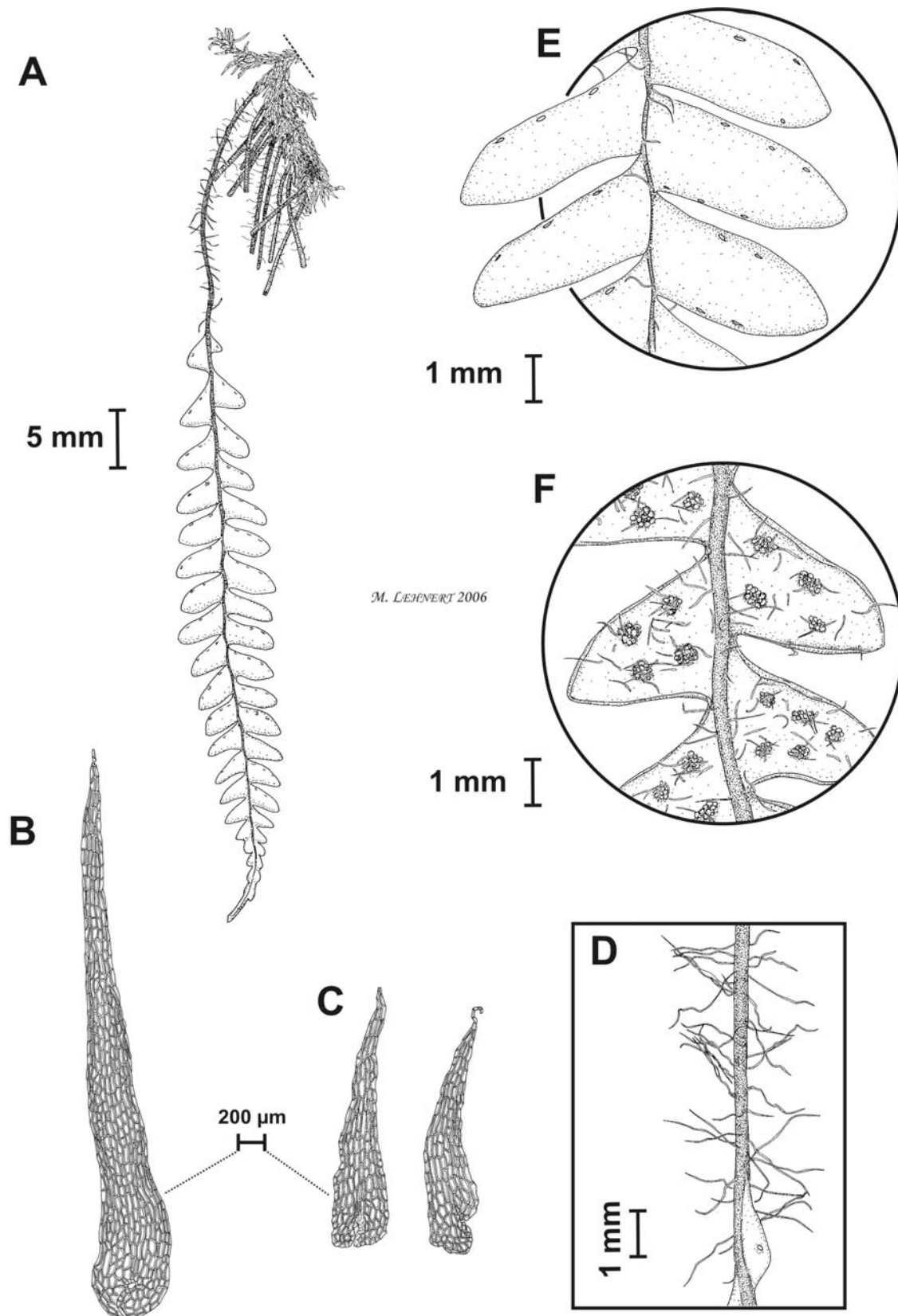


Fig. 27. *Melpomene peruviana*. A. habit (Lehnert 779, GOET); B. large scale (Lehnert 278, GOET); C. small scales (Lehnert 571, GOET); D. petiole (Lehnert 779, GOET); E. segment adaxially (Krapovickas & Schinini 38663, LPB); F. segments abaxially, sporangia immature (Lehnert 779, GOET).

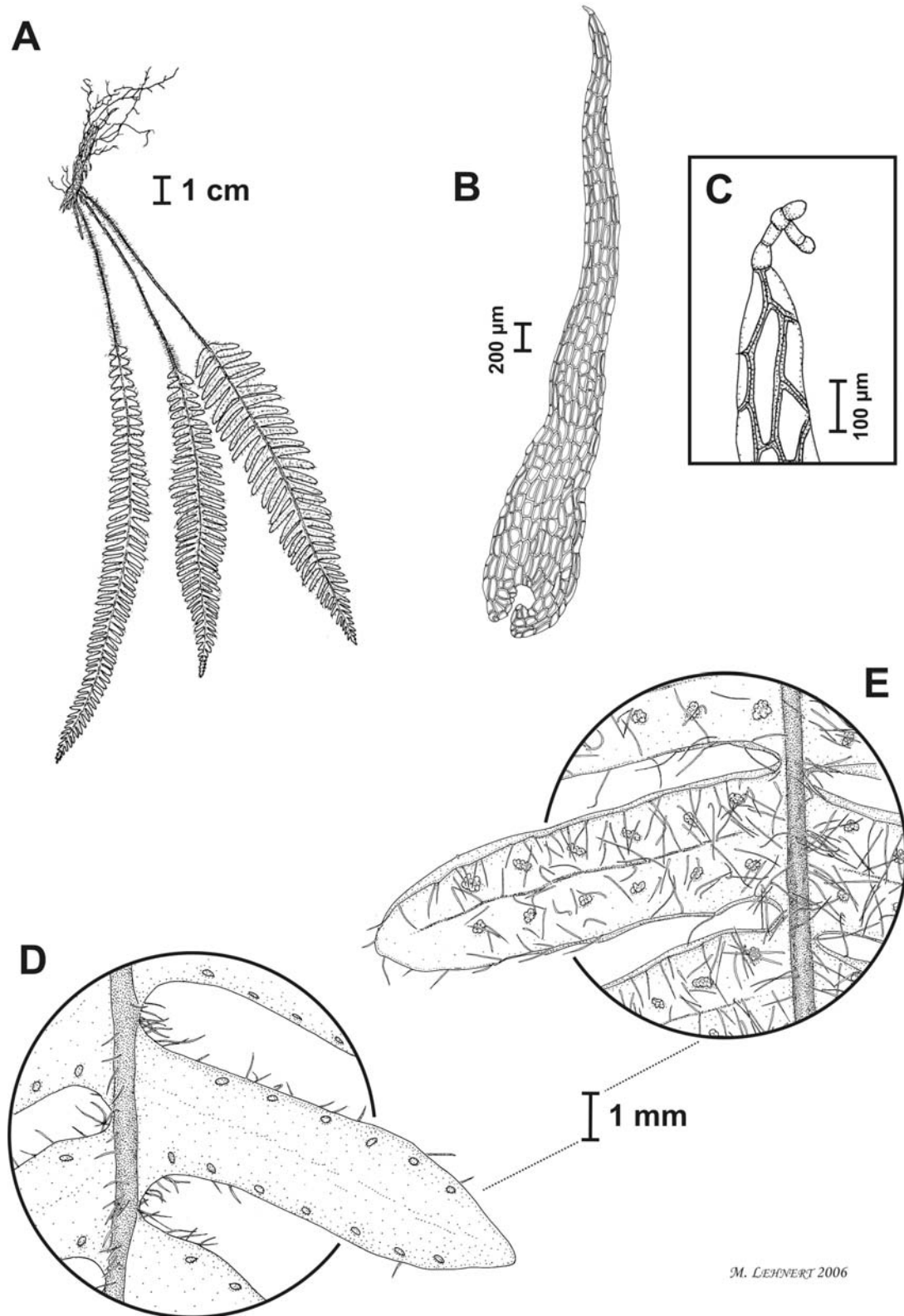


Fig. 28. *Melpomene pilosissima*. A. habit representative of both varieties, var. *pilosissima* (Kessler 13514, GOET). B-C. var. *pilosissima*. B. scale (Mickel 4960, UC); C. detail of scale apex (Mickel & Leonard 4960, UC). D-E. var. *tsatchelae*. D. segment adaxially; E. segment abaxially, sporangia primordia.

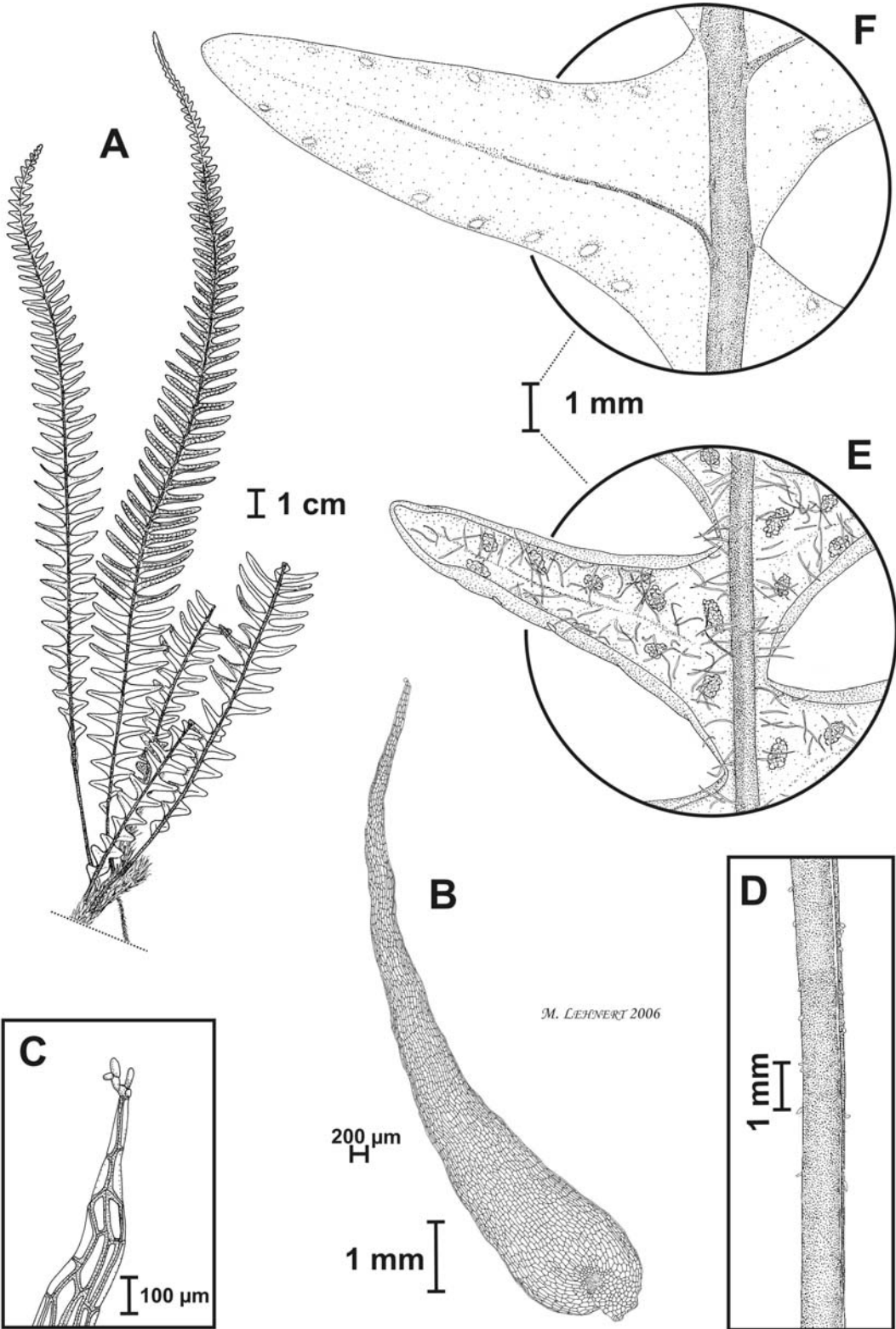


Fig. 29. *Melpomene pseudonutans*. A. habit; B. scale; C. detail of scale apex; D. petiole; E. segment abaxially, sporangia primordia; F. segment adaxially (all from *Laegaard 53349*, AAU).

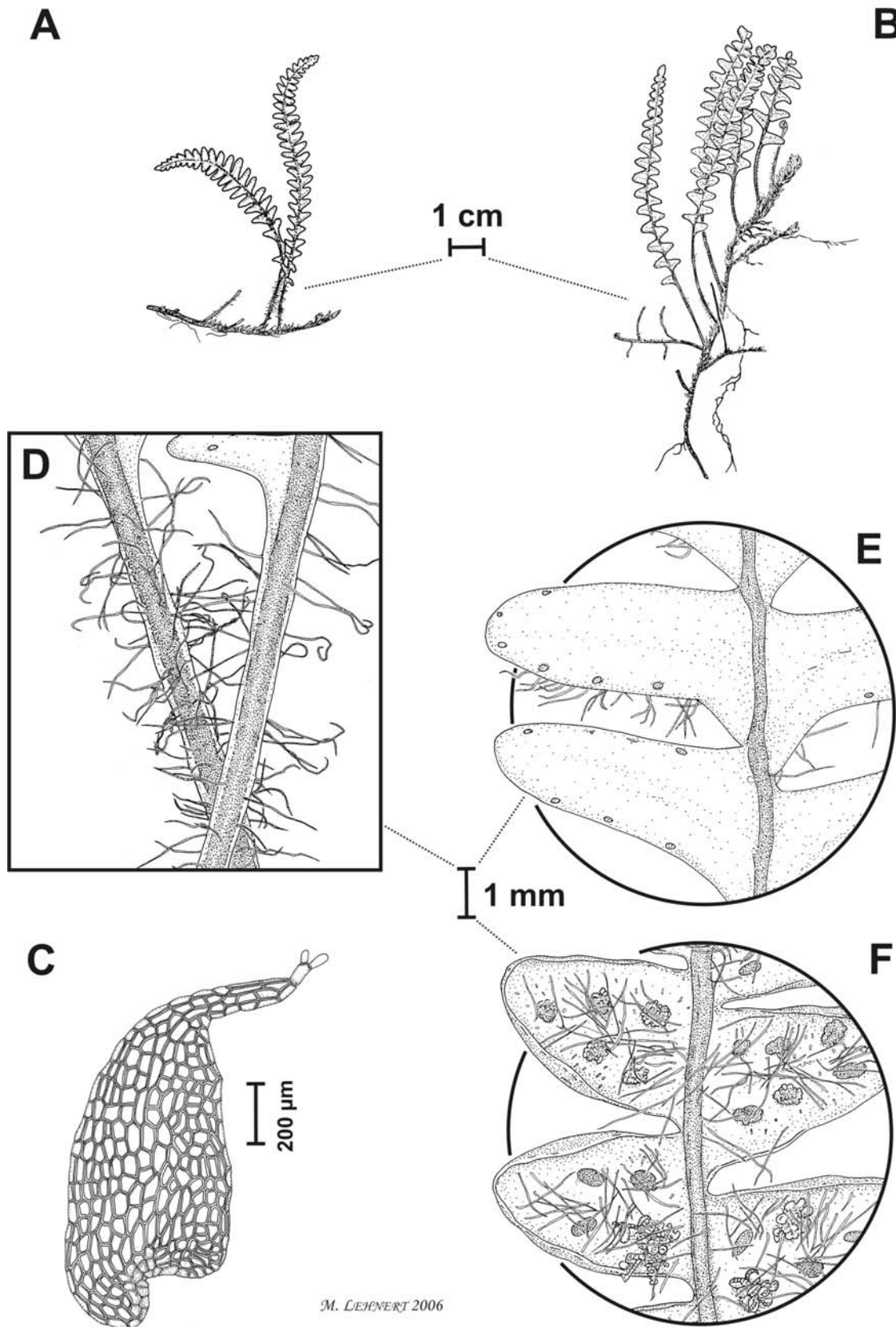


Fig. 30. *Melpomene sklenarii*. A. habit (Lehnert 156, GOET); B. habit (Lehnert 108, GOET); C. scale (Mille s.n., P); D. petiole (Lehnert 156, GOET); E. segment adaxially (Lehnert 156, GOET); F. segment abaxially, sporangia primordial to immature, partly removed (Lehnert 156, GOET).



Fig. 31. Distribution of *Melpomene sklenarii*.

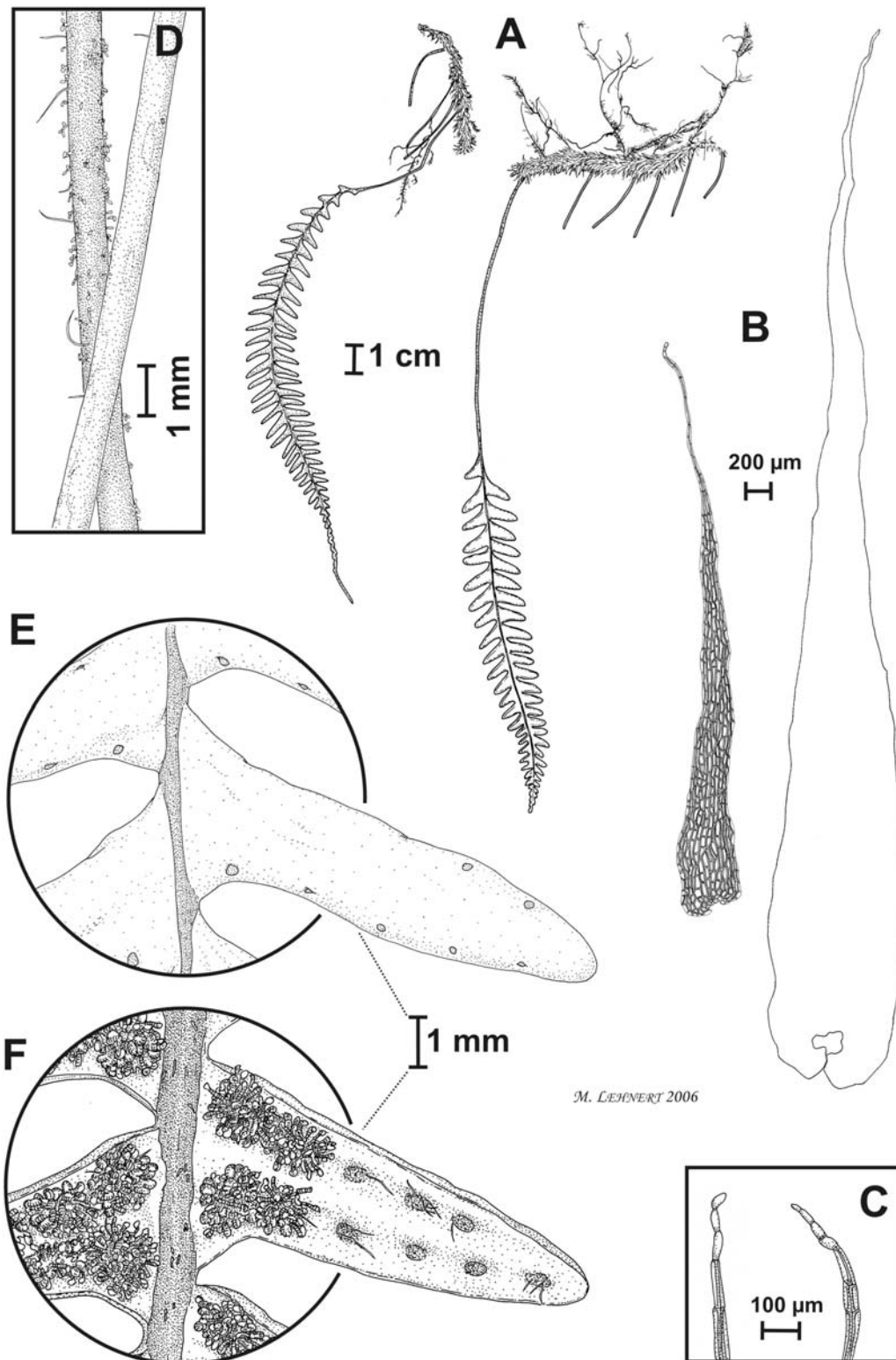


Fig. 32. *Melpomene sodiroi*. A. habit, right with wide pinnae and short frond apex (*Proctor 38737*, QCA), left with narrow pinnae and long tapering apex (*Lehnert 1106*, GOET); B. scales, small scale (*Lehnert 1106*, GOET) in detail, large scale shown as outline (*Laegaard 52141*, AAU); C. detail of scale apices (*Lehnert 1106*, GOET); D. petioles, hairy young one in the back, glabrous one in front (*Lehnert 1106*, GOET); E. segment adaxially (*Lehnert 1106*, GOET); F. segment abaxially, sporangia mature, partly removed (*Lehnert 1106*, GOET).

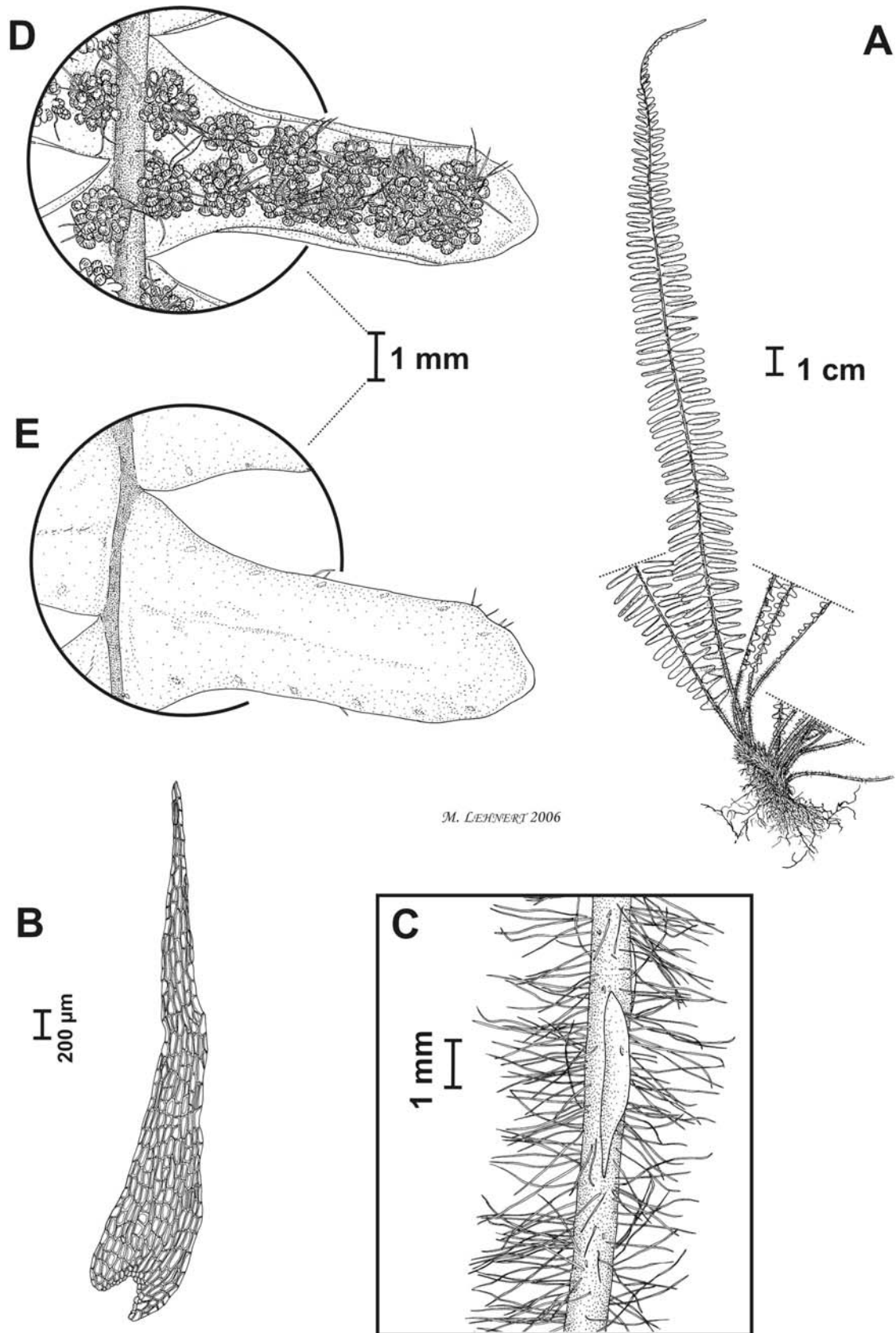


Fig. 33. *Melpomene vernicosa* A. habit (Holm-Nielsen 3315, AAU); B. scale (Lehnert 803, GOET); C. petiole (Lehnert 803, GOET); D. segment adaxially (Lehnert 803, GOET); E. segment abaxially, sporangia mature, closed (Lehnert 803, GOET).



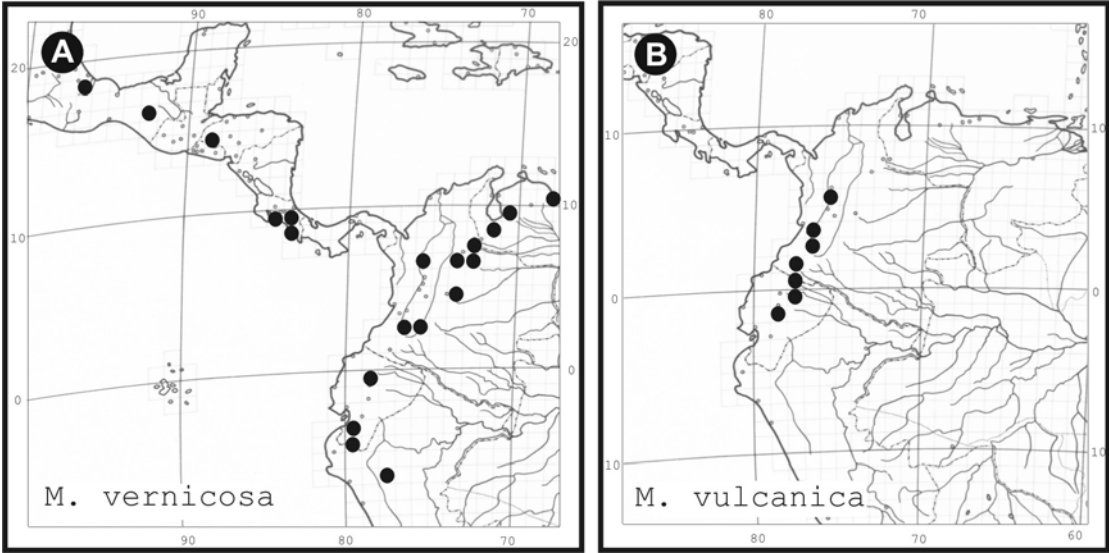


Fig. 34. Distribution maps. A. *Melpomene vernicosa*. B. *Melpomene vulcanica*.

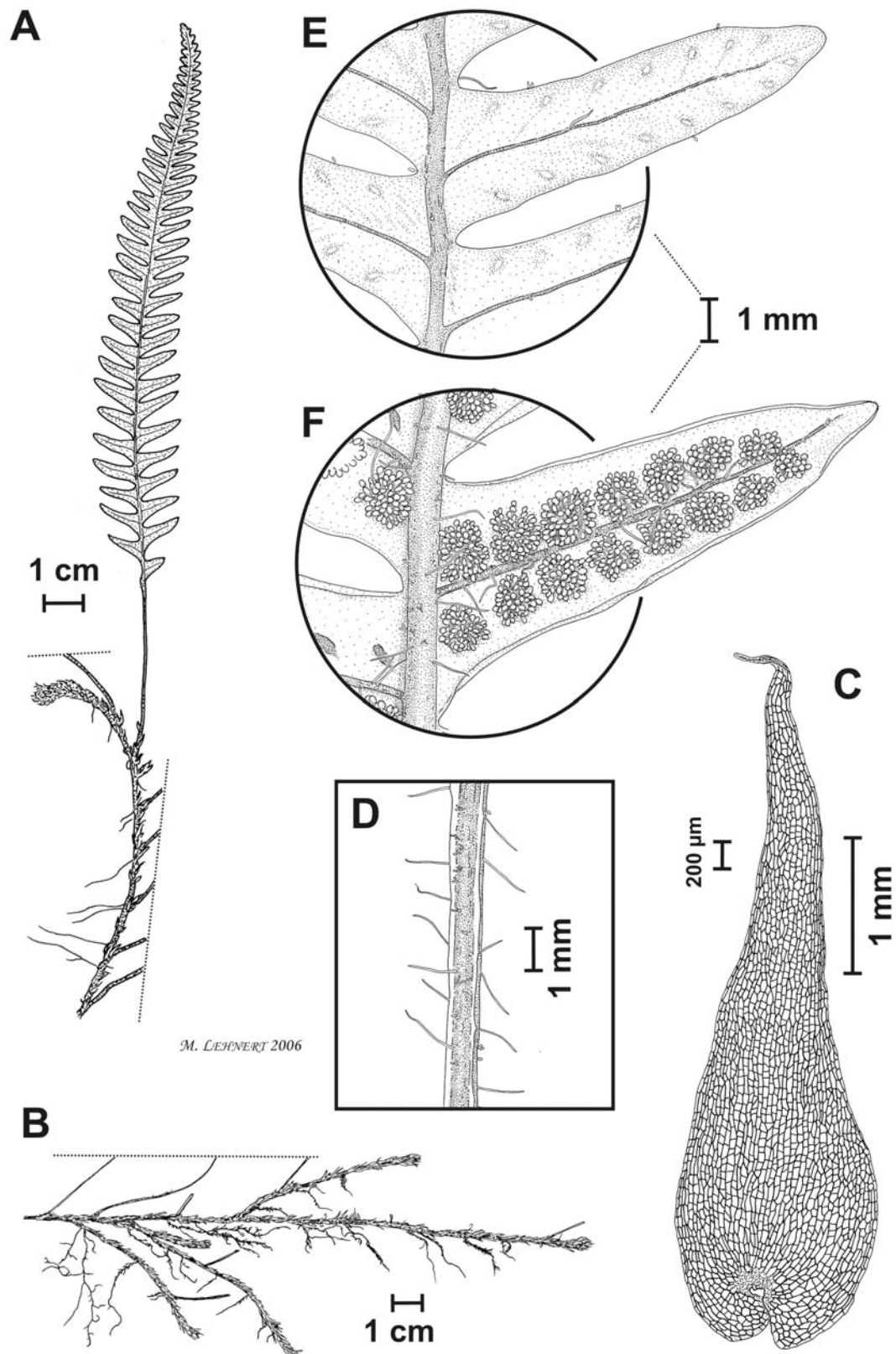


Fig. 35. *Melpomene vulcanica*. A. habit (*Øllgaard et al. 34159*, AAU); B. strongly branching rhizome, green fronds not shown; C. scale (*Holm-Nielsen et al. 17235*, AAU); D. petiole (*Holm-Nielsen et al. 17235*, AAU); E. segment adaxially (*Holm-Nielsen et al. 17235*, AAU); F. segment abaxially, sporangia immature (*Øllgaard et al. 34159*, AAU).

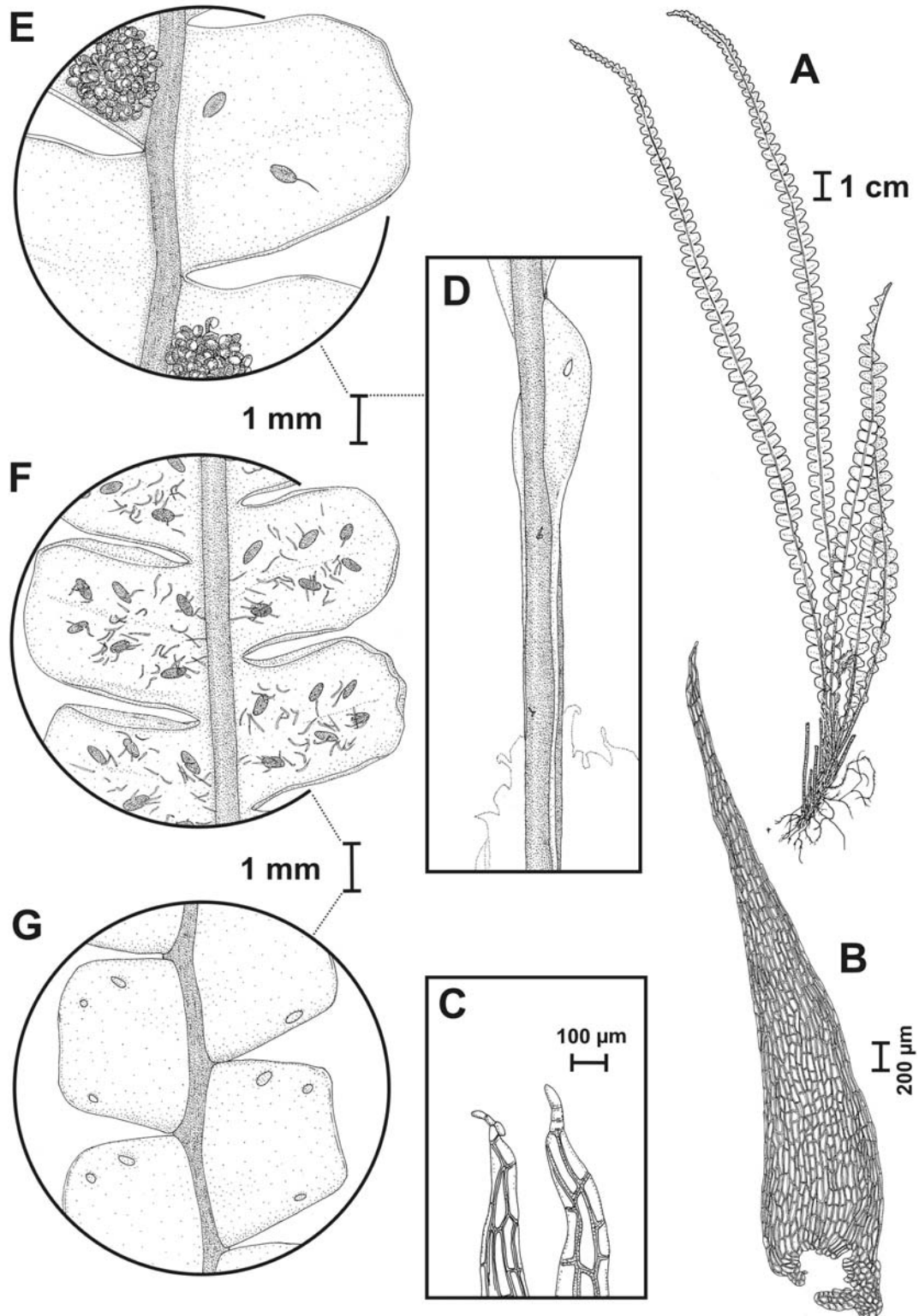


Fig. 36. *Melpomene wolfii*. A. habit (Lehnert 1427, GOET); B. scale (Lehnert 869, GOET); C. detail of scale apices (Lehnert 869, GOET); D. petiole (Lehnert 1427, GOET); E. segment abaxially, glabrous, sporangia partially removed (Lehnert 1427, GOET); F. segment abaxially, hairy, sporangia removed (Lehnert 1163, GOET); G. truncate segment adaxially (Lehnert 1427, GOET).

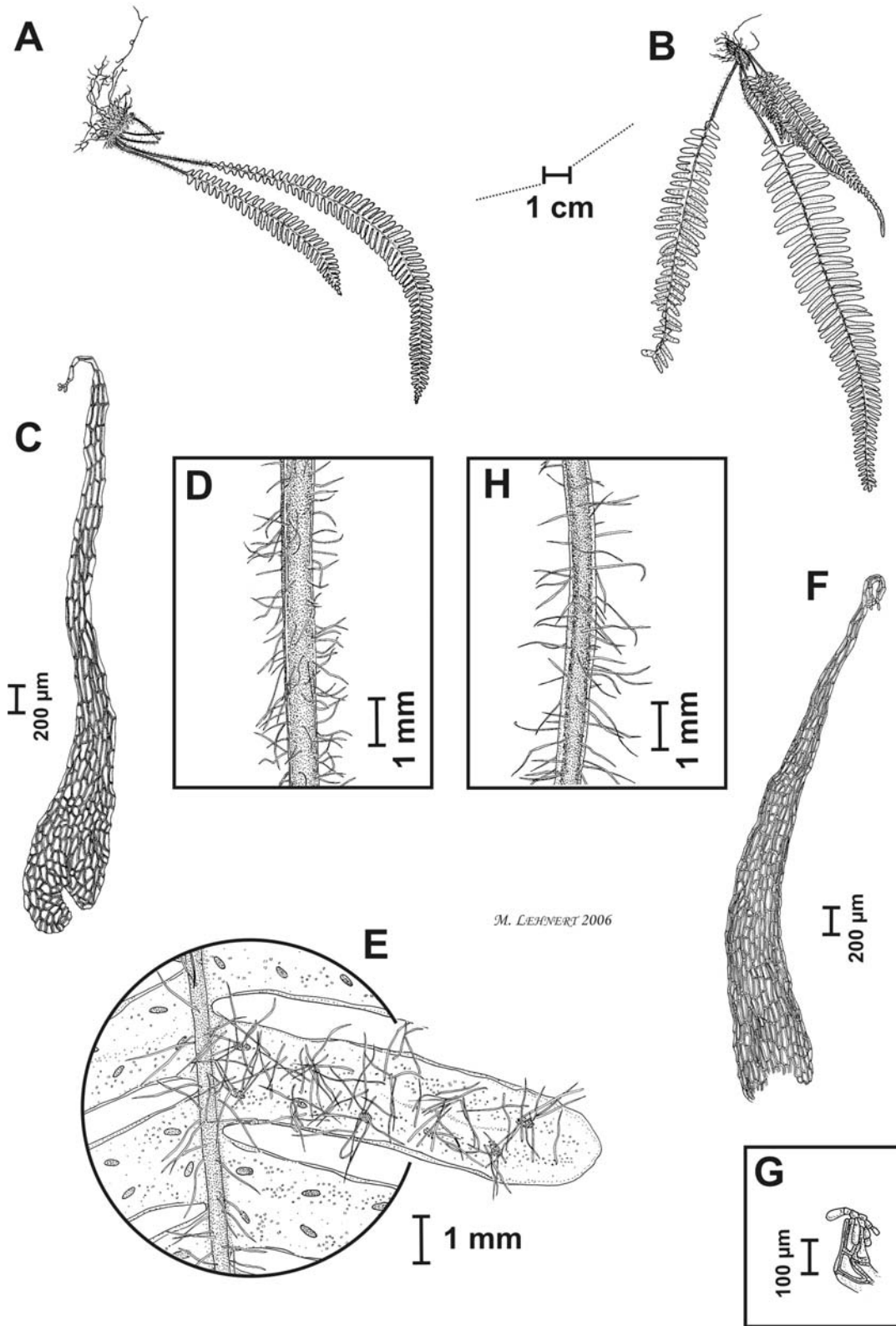


Fig. 37. *Melpomene xiphopteroides*. A. habit of var. *xiphopteroides* (Kessler 10232, UC); B. habit representative of both varieties; from var. *xiphopteroides* (Kessler 13484, GOET). C-E. var. *xiphopteroides*. C. scale (Mickel & Leonard 4723, UC); D. petiole adaxially, narrowly marginate; E. segment abaxially, sporangia removed (Kessler 10232, UC). F-G. var. *acrodontium*. F. scale; G. detail of scale tip; H. petiole abaxially, alate. (F-H. from Schwacke 10695, P)

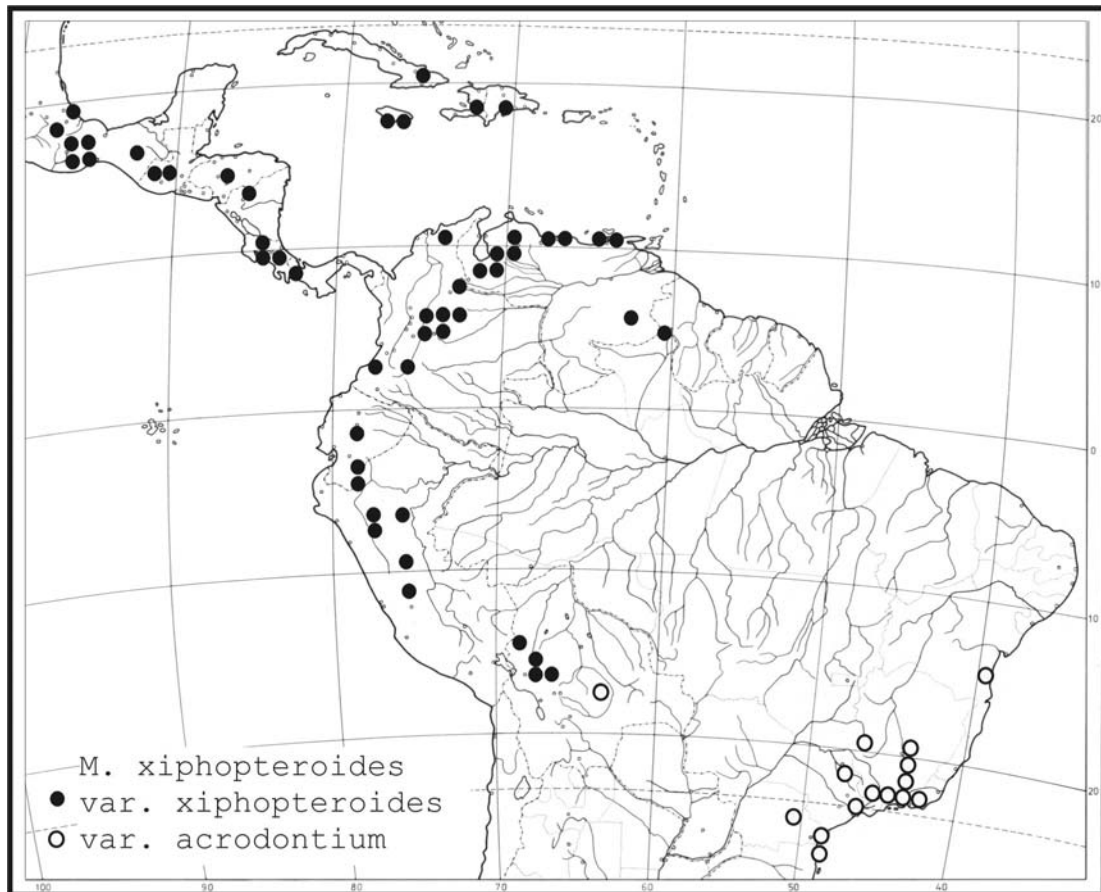


Fig. 38. Distribution map. *Melpomene xiphopteroides*; var. *xiphopteroides* (dots), var. *acrodontium* (circles).

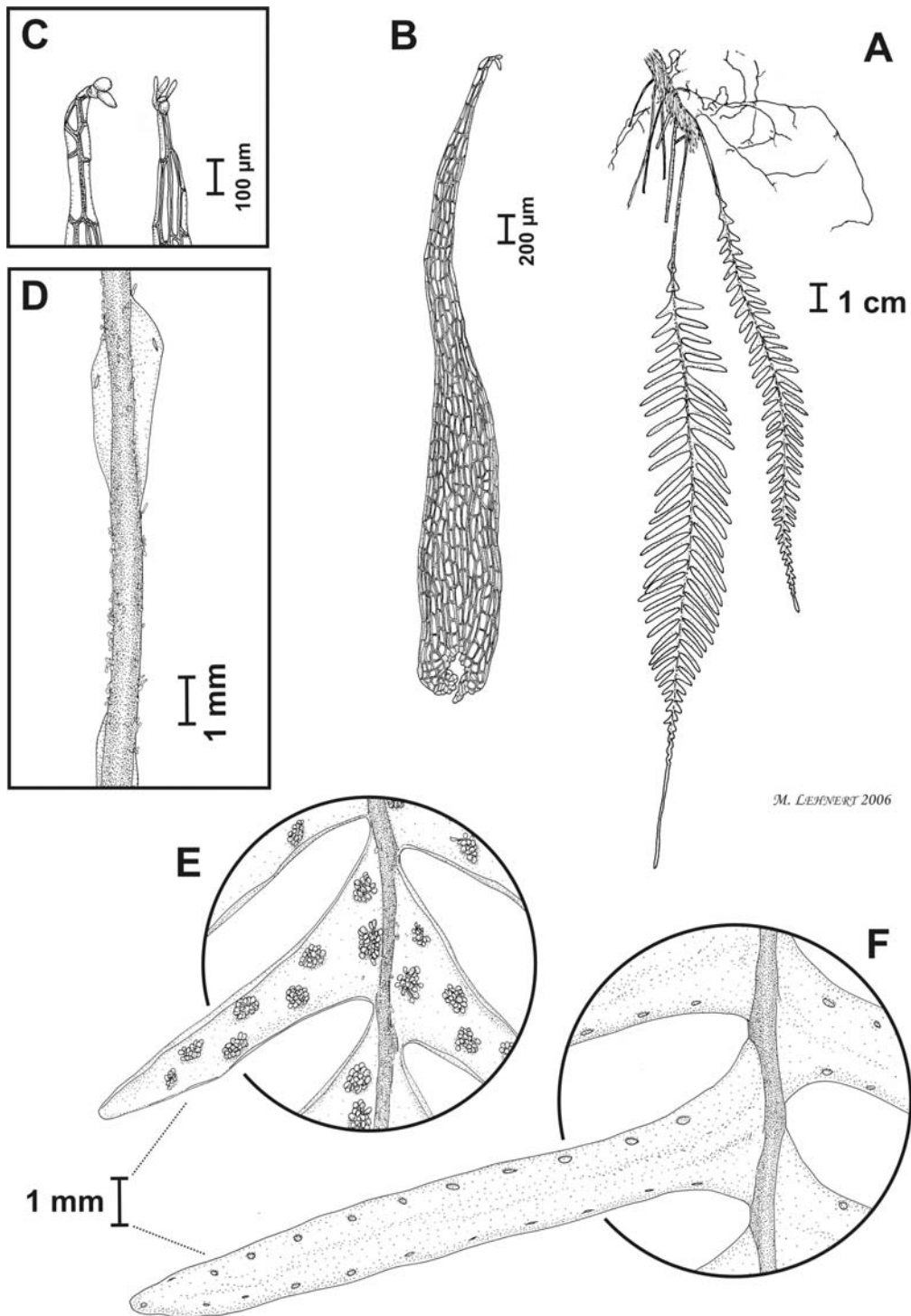


Fig. 39. *Melpomene youngii*. A. habit; B. scale; C. detail of scale tips (A-C. from León & Young 2052, USM); D. petiole (León & Young 4857, USM); E. segment adaxially, sporangia immature (Young 1620a, USM); F. segment adaxially (León & Young 2052, USM).

#### I.4. Phylogeny of the fern genus *Melpomene* (Polypodiaceae) inferred from morphology and chloroplast DNA analysis

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**Abstract.** In recent phylogenetic studies on the Polypodiaceae, the monophyly of the neotropical genus *Melpomene* was proposed. Since these studies included only few samples of morphologically similar and probably closely related species in a restricted sample size, these findings were put in doubt. Guided by systematic studies on the genus, we tested the monophyly involving 23 of the 27 recognized species, including the morphologically distinct *M. leptostoma* (Fée) R. C. Moran & A. R. Sm. and *M. gracilis* (Hook.) A. R. Sm. We analyzed sequences of cpDNA (*atpβ*, *rbcL*) and morphological characters. Each data set supported the monophyly of the genus and its placement as sister to the *Lellingeria apiculata* group as proposed in previous studies; the relationships within the genus, however, are only resolved and supported if the data sets are combined. While *M. leptostoma* and *M. gracilis* are basal lineages with large branch lengths, most of the core genus has very short branch lengths. This indicates a recent radiation of the genus in the northern Andes, its center of diversity, under the influence of the fast uplift of the mountain range and of glacial fluctuations of the vegetation zones, with subsequent dispersals to the Guyana Highlands, the Brazilian shield, and Africa.

Keywords. Andes, *atpβ*, Grammitidaceae, *Lellingeria*, *Melpomene*, monophyly, morphology, Polypodiaceae, *rbcL*.



### Introduction

The natural relationships among extant ferns have become more and more resolved thanks to extensive phylogenetic studies (Schneider et al. 2004; Ranker et al., 2004). Funding on these studies, Smith et al. (2006) proposed a new classification for extant ferns, which involves changes in nearly every fern family. The Polypodiaceae are among them, being again enriched by the species of the formerly separate family Grammitidaceae. In the past, the latter group has been recognized either as a family (Parris, 1990), as a subfamily (Presl, 1836), or just a group within the Polypodiaceae (Tryon & Tryon, 1982; Tryon & Stolze, 1993). The grammitid ferns, as which they are still referred to, are a monophylum of ca. 750 species nested within the neotropical members of the Polypodiaceae, from which they differ by many morphological traits (Paris, 1990) and a higher substitution rate in three chloroplast marker (Schneider et al., 2004). They are distributed throughout the tropics and the southern temperate region (Parris, 1990, 2003) but most diverse in South America, where their origin is assumed (Schneider et al., 2004). The clear delimitation as a discrete monophylum on morphological and molecular basis is contrasted by the long and confusing history of attempts to divide grammitid ferns into natural genera. The latest morphological concept (Bishop, 1974, 1977, 1978, 1988, 1989a, 1989b; Smith et al., 1991; Smith, 1992, 1993, 1995; Smith & Moran, 1992) is based on many previously neglected characters, like scales, hydathodes, and secondary metabolites notable as odors or waxy and calcareous deposits on the laminae. Although pragmatic and useful for determination, most of these characters turned out to be homoplastic in phylogenetic analysis (Ranker et al., 2004). Many of the genera have to be redefined or divided further in order to match the demands of a natural classification. One of the few genera that turned out to be monophyletic is *Melpomene*, a small genus of 27 species with ten varieties (Lehnert, submitted manuscript). Most of them have simply pinnate fronds, dark castaneous hairs, and have a characteristic aromatic odor. The species of this genus occur mainly in upper montane forests and páramo vegetation as epiphytes, less so also saxicolous or terrestrial. Endemic species are found only in the Andes, which is the center of diversity (26 of the 27 species occur here). The Guayana Highlands and the Brazilian shield, otherwise rich in endemic flora, have each only one endemic variety of widespread species. One species, *Melpomene flabelliformis* (Poir.) A. R. Sm. & R. C. Moran, has a disjunctive distribution in Africa, Madagascar,

and the Mascarene Islands; this is a distribution pattern found in many fern groups (Smith & Moran, 2001).

With our present study, we wanted to test the monophyly of *Melpomene*. The original sampling only included four species (Ranker et al., 2004), which belong to a morphologically tightly knit group easily recognized by large rhizome scales (Lehnert, submitted manuscript). If the scales, which bear the important characters, are small, the morphologically defined genera of grammitid ferns are sometimes troublesome to distinguish. Based on more thorough examination of their small rhizome scales, two species of the original set of species of *Melpomene* (Smith & Moran, 1992) were already transferred to other genera (Smith, 1995; León & Smith, 2004). It is possible that a broader sampling in the molecular analysis reveals that some species of *Melpomene* belong in other clades of grammitid ferns (Ranker et al., 2004).

Furthermore, we wanted to clarify the origin and status of the paleotropical population. Is the African *M. flabelliformis* really conspecific with the neotropical population? It is thinkable that *M. flabelliformis* has crossed the Atlantic several times, maybe even returning to South America after diverging in the African isolation. A paleotropical origin of the whole genus with *M. flabelliformis* as basal lineage and all the neotropical taxa as the result of an adaptive radiation is, judging from the diversity pattern and the young age of the whole family, unlikely but not impossible. The center of diversity of a group does not have to be the center of its origin, as shown for the complex of the neotropical genera *Eriosorus/Jamesonia* (Pteridaceae), which are most diverse in Andean páramo vegetation but originated on the Brazilian shield (Sánchez-Baracaldo, 2004).

## **Materials and Methods**

### Taxon sampling and DNA extraction

Outgroup taxa were chosen from the grammitid species used by Ranker et al. (2004), focusing on potential sister taxa. Sequences of 17 taxa were not processed but taken from Genbank. Samples of *Melpomene* were collected in the field by the first author in Ecuador, Peru, Bolivia, and Argentina during field trips from 2002 to 2004. Colleagues kindly provided additional samples from Mexico (Thorsten Krömer), Costa Rica (Jürgen Kluge, Ruth Kirkpatrick), Tanzania (Andreas Hemp), and

Madagascar (Thomas Janssen). The 52 samples of *Melpomene* used in our study cover 23 of the 27 species, but included only four of the ten recognized varieties (Lehnert, submitted manuscript). If possible, species were incorporated with two or more samples to test for intraspecific variability. Table 1 lists the voucher information, herbaria, and Genbank accession numbers of all species and sequences used in this study.

Most specimens were processed at the University of Colorado Boulder (Ranker Lab), USA (Tab. 1). DNA extraction followed Ranker et al. (2003, 2004). Sample DNA concentrations were standardized to 10 mg/ml with the aid of a mini-fluorometer. Additional specimens (Tab.1) were processed at the “Experimentelle Phykologie und

Sammlung von Algenkulturen” (SAG), A.-v.-Haller Institute for Plant Sciences, Georg-August-University Göttingen, Germany, using a Qiagen DNEasy Kit (QIAGEN GmbH – Germany, 40724 Hilden). We followed the manufacturer’s protocol, including the optional RNase step.

#### PCR and sequencing

We amplified and sequenced two loci of the chloroplast genome: a 1311 bp fragment of the *rbcL* gene and a 1266 bp fragment of the *atpβ* gene. Methods followed largely Ranker et al. (2003, 2004) for PCR amplification. For the additional specimens processed at Göttingen, only *rbcL* gene sequences were obtained using the primer combination cited in Korall et al. (2006; Schuettpelz, unpubl.). For sequencing, we used the service of Macrogen Inc., South Korea ([www.macrogen.com](http://www.macrogen.com)).

#### Phylogenetic analysis of molecular data

Sequences were visually edited using SeqAssem (Hepperle, 2004); consensus sequences were aligned with BioEdit (Hall, 1997). For *Melpomene*, we obtained a 1299 bp block of the *rbcL* gene for 52 samples and a 1206 bp block of the *atpβ* gene for 43 samples.

Phylogenetic analyses were conducted at the Mishler Lab, Dept. of Integrative Biology, University of California, Berkeley, using *PAUP\* 4.0b10* for MAC (Swofford, 2002). All characters were treated as unordered and equally weighed.

The *rbcL* and *atpb* data sets were submitted to a partition homogeneity test, using parsimony informative characters only. Rearrangements were limited to

1,000,000 per partition subset replicate. We performed maximum parsimony (MP) searches for each molecular data set separately and with both combined. In each approach we analyzed the dataset with uninformative characters excluded.

#### Phylogenetic analysis of morphological data

We coded 42 morphological characters, focusing on differences within the genus *Melpomene* (Tab. 2). Encoding of the character states was orientated on Ranker et al. (2004). We conducted maximum parsimony phylogenetic analyses in PAUP\* 4.0b10 (Swofford, 1998) of the morphological dataset. All characters were unordered and equally weighted. We performed a heuristic search with 100 random addition sequence replicates and with MulTrees activated, TBR branch swapping, and ACCTRAN character-state optimization. The morphomatrix is available in App. 2.

#### Phylogenetic analysis of combined morphological and molecular datasets

All characters were treated as unordered and equally weighted. In a first approach, we performed a heuristic search in MP with a MaxTrees increase of 100 and ACCTRAN character-state optimization. A restriction to 1,000,000 rearrangements per step in TBR mode was necessary to terminate the calculations.

In a second approach, we used the trees gained from the first analysis as starting seed in a MP analysis with automatic MaxTrees increase by 100 in TBR mode; rearrangements were not restricted. Bootstrap analyses were carried out in TBR branch swapping algorithm with 100 random addition sequence replicates, with MulTrees activated, 1,000,000 rearrangements per replicate, and ACCTRAN character state optimization.

## **Results**

### *Sequence variation*

Of the sequenced 1207 bp of the *atpβ* marker, 981 characters are constant; 102 variable characters were parsimony-uninformative, and 124 variable sites were parsimony informative. Of the 1299 bp of the *rbcL* gene sequenced, 1059 characters are constant; 123 variable characters were parsimony-uninformative, 117 variable sites were parsimony informative. The partition homogeneity test for both molecular data sets resulted in  $p = 0.2$ . Sum of tree length varied between 513 and 523, with ten

replicates for the original partition (517). Among the morphological characters chosen, all 42 were variable but only 40 were parsimony informative. Of all 2548 characters, 2040 were constant; 227 variable characters were parsimony uninformative and 281 were parsimony informative.

#### Molecular data

##### *atpβ*

The analysis resulted in 37038 equally parsimonious trees with L= 265, CI= 0.5509, and RI= 0.7586. Bootstrap analysis was omitted for this dataset. The strict consensus tree (Fig. 1A) shows no resolution as expected from the previous analysis (Ranker et al., 2004), except for weakly supported cluster of some conspecific samples.

##### *rbcL*

The analysis resulted in 21 equally parsimonious trees with L= 252, CI= 0.5476, and RI= 0.7472. Bootstrap analysis was omitted for this dataset. The strict consensus tree supports *Melpomene* as monophyletic with *M. gracilis* and *M. leptostoma* resolved as basal paraphylum to the remainder of the genus (Fig. 1B), which is referred to as the core group in the following.

##### *atpβ* and *rbcL* combined

The analysis of the combined molecular data set resulted in 619 equally parsimonious trees with L= 524, CI= 0.5420, and RI= 0.7458. Bootstrap analysis was omitted for this dataset. The resolution of the strict consensus tree (Fig. 1C) does not vary greatly from that of the *rbcL* data set: *Melpomene* is monophyletic with *M. leptostoma* and *M. gracilis* as basal paraphylum to the remainder of the genus.

#### Morphological data

Of the 42 chosen variable character sets, 40 were parsimonious informative for the ingroup species. Heuristic MP analysis found 108 equally parsimonious trees with L= 262, CI= 0.2786, and RI= 0.7523 (Fig. 1D). The outgroup is differently resolved as compared to the genetic data; well supported are the monophyly of *Melpomene* and the basal position of *M. leptostoma* and *M. gracilis* (Fig. 1D).

#### Combined morphological and molecular datasets

The combined analysis of the morphological and molecular datasets resulted in the first approach in 328 most parsimonious trees with L= 846, CI= 0.4220, and RI= 0.7135 (Fig. 2). The strict consensus tree shows again the monophyly of the genus *Melpomene* with *M. leptostoma* and *M. gracilis* as basal paraphylum. The resolution within the core group is different than in the previous approaches, most noticeably the basal position of *M. sodiroi* and the basal paraphylum including *M. xiphopteroides* and *M. pilosissima*.

The second approach with the 328 trees from the first approach as starting seed and unrestricted rearrangements per step resulted in 52670 most parsimonious trees with L= 843, CI= 0.4235, and RI= 0.7153 (Fig. 3). The majority consensus tree shows a different topology of the core group than the trees of the previous approach, with *M. sodiroi* being located near the outer branches and the clades including *M. pilosissima* and *M. xiphopteroides* placed in an unresolved polytomy.

### Discussion

Like in previous studies (Ranker, 2004), the species of *Melpomene* form a monophyletic clade, which is sister to the *Lellingeria apiculata* group (Smith et al., 1991; Ranker et al., 2004). Shared morphological traits between these two groups are clathrate rhizome scales (i.e., showing a lattice pattern) with marginal cellular appendages and laminar hydathodes. In *Melpomene*, the marginal appendages are reduced to small, unicellular to multicellular hairs with presumed glandular properties (Lehnert, submitted manuscript). In *Lellingeria*, the marginal appendages are large unicellular setae. Both the marginal appendages and the hydathodes may be reduced or missing in species of both groups. Such species are hard to place confidently into a morphologically defined genus. New interpretation of the morphology revealed that some of the species originally included in the genus *Melpomene* (Smith & Moran, 1992) belong to other genera: *Melpomene dissimulans* (Maxon) A. R. Sm. & R. C. Moran, which has been transferred into *Lellingeria* (Smith, 1995), is not included in our analysis; *Melpomene anfractuosa* (Desv.) A. R. Sm. & R. C. Moran was transferred to *Terpsichore* (León & Smith, 2004), which was confirmed by molecular data (Ranker et al., 2004). In our amplified dataset, *Terpsichore anfractuosa* remains well outside the *Melpomene/Lellingeria* clade, underlining the ambiguity of many morphological characters within the grammitid ferns (Ranker et al., 2004). Evidently

all species currently treated as *Melpomene* are one natural group, although some of them have ambiguous characters. The three basal species *M. leptostoma*, *M. gracilis*, and *M. allosuroides* (not included in analysis), stand out as small plants with several characters that are in part more reminiscent of other grammitid groups (e.g., rather thin petioles and small, ovate petiole scales with weakly cordate bases) than the core group of *Melpomene*. The peculiarity of *M. leptostoma* was already recognized by Smith and Moran (1992), with laxly pendent fronds and only short, rather pale uniseriate hairs (vs. petioles and rhachises stiff, and hairs dark castaneous to reddish brown in the core group of *Melpomene*). The status of *Melpomene gracilis* and *M. allosuroides* as sister taxa is based on morphology only (Lehnert, submitted manuscript), because we were not able to obtain a genetic sample of the latter species. However, unique characters that are not found in any other *Melpomene* species, such as cuneate (i.e., wedge-shaped) segment bases, gibbose segments, and lack of uniseriate hairs, tie them together as closest relatives. Their rhizome scales also have marginal glands, which presumably represent the ancestral state in the genus and may be homologous with the marginal hairs usually present in *Lellingeria* scales. *Melpomene leptostoma* and *M. gracilis* appear as a paraphylum with large branch lengths in the phylogram (Fig. 4), indicating a relatively early divergence from the remaining species of *Melpomene*.

The core group of *Melpomene* is highly supported in the MP analysis but with weak additional support (bootstrap; Fig. 3). Comparing the different trees, we note that some species like *M. sodiroi* and *M. vulcanica* are found in quite different places. Conflicting results between chloroplast marker and nucleus marker may indicate hybridizations among species, because the chloroplasts are inherited in direct line from the female parent whereas the nucleus contains genetic information of both parents. We only have the morphology as proxy for the nucleic encoded characters. Because the morphological characters have only a narrow variation among the species of *Melpomene* (Lehnert, submitted manuscript), hybrids with intermediate morphology are almost impossible to point out. Thus we refrain from making any implications about the possible hybrid status of certain species at this point.

Despite often weakly supported in the phylogenetic analysis, there are some reoccurring clusters within the core group of *Melpomene* that we believe to reflect natural alliances. The clade containing *M. firma* and *M. occidentalis* is found in the strict consensus analysis of all datasets except for *atpβ*, with high support in the

combined analysis (MP 100, bootstrap 94; Fig. 3). Morphologically, they share marginal glands on the rhizome scales, a character found with such regularity only in the basal clade of *M. gracilis*. Another group is formed by *M. pseudonutans* and *M. wolfii*, which are characterized by stiffly erect fronds on stout, shortly creeping, and usually ascending rhizomes with relatively wide diameter and large scales. This group is found in the combined dataset with quite high support (Fig. 3). Morphological and ecological similarities suggest that *M. erecta* should be included in here, although we have no support from our phylogenetic analysis (Fig. 1, 2, 3).

*Melpomene melanosticta* is an interesting species because it is one of the most widespread of the genus and the only one adapted to premontane to lowland forests. Morphologically, it is hard to distinguish from almost equally distributed *M. xiphopteroides*, with which it has a small elevational overlap (Lehnert, submitted manuscript). Unfortunately, we could only include one sample of *M. melanosticta* in our analysis; its position is unresolved in the strict consensus trees of the separate analyses (Fig. 1) and contradictory in the majority rule trees (not shown). Only in the MP analysis of the combined dataset, *M. melanosticta* appears basal in the sister clade to the monophyletic *M. xiphopteroides*, but with low MP support (Fig. 3).

Although the resolution in the main clade of *Melpomene* is weakly supported (Fig. 3), it still indicates that morphologically similar species are not necessarily related. For example, *M. wolfii* (as *Ctenopteris assurgens* (Maxon) Copel.) was described as a “glorified” *Melpomene moniliformis* “that merits distinction” (Copeland, 1955), suggesting a close relationship. Both species are superficially similar, but the molecular data shows that *Melpomene wolfii* is more closely related to *M. pseudonutans*, which itself resembles other, not closely related species, like *M. vulcanica*.

The partition in the total evidence majority rule consensus tree (Fig. 3) reflects the general split in the core group of *Melpomene* between species with rather short-creeping, erect or ascending rhizomes, appressed petioles, and narrowly lanceolate rhizome scales, and those with horizontally creeping rhizomes, spreading petioles, and a tendency towards wide rhizome scales (Fig. 3). The first one is referred to as the *M. pilosissima* group and is morphologically quite homogenous (Lehnert, submitted manuscript); the second one is called here *M. moniliformis* group and shows a greater morphological variability but with a tendency towards broadly ovate-lanceolate



rhizome scales and deltate or short-oblong segments of the fronds (vs. mainly narrowly lanceolate scales and linear-oblong segments in the *M. pilosissima* group).

The core group of *Melpomene* is characterized by relatively short branch-lengths in the phylogram (Fig. 4), indicating a rapid evolution with relatively few changes. A similar phenomenon is observed in the high elevations inhabiting genus *Lupinus* (Fabaceae; Hughes & Eastwood, 2007). In both cases, the rapid uplift of the Andes, especially of the northern parts, is suspected to have triggered this radiation. The young high montane habitat was subsequently divided by altitudinal shifts of the vegetation zones during the ice ages (Hooghiemstra & van der Hammen, 2004). This development of insular distributed vegetation types may have favored the evolution of ecological similar, closely related species with notable morphological differences (Vuillemeur, 1970; Hughes & Eastwood, 2007).

#### Biogeographical implications

Among the species of *Melpomene*, *M. leptostoma* is the only one restricted to northern Mesoamerica (Mexico, Guatemala). Its well-supported basal position (Fig. 3) and large branch length (Fig. 4) indicate an early long distance dispersal event from the Andean main stock, probably leading to isolation before a permanent land bridge between North and South America was established. After the closure of the Panamanian isthmus, plant migration was facilitated and several, more derived species of *Melpomene* invaded the area, differing greatly in morphology from *M. leptostoma*.

The distribution of the widespread *Melpomene melanosticta* shows no historically retraceable pattern. Its preferred habitat is the premontane and lowland forests, which have a more or less continuous distribution in space and time in South America in the Cenozoic (Willis & McElwain, 2003). This prevents making an assumption about when and where the species descended from its high montane ancestor. The continuity of its habitat probably facilitated the dispersal of the species and the eventual recolonization after local extinctions (e.g., during glacial periods) as well as maintaining a homogenous morphology throughout its vast range (Lehnert, submitted manuscript).

The other species are either restricted to or centering in the Andes. The groups of *M. pseudonutans* and *M. firma*, which are morphologically distinct subsets of the *M. moniliformis* group and *M. pilosissima* group, respectively, are restricted to the Andes. One exception is *M. firma*, which also occurs in Mesoamerica, the Caribbean,

and the Guayana Highland, but is absent in southeastern Brazil. The *M. moniliformis* group contains the species with the largest disjunctions in the distribution. *Melpomene flabelliformis* can be found in all humid tropical mountain ranges in South America as well as in Africa, Madagascar, and the Mascarene Islands (Lehnert, submitted manuscript). Our data neither support nor deny a single long distance dispersal event to the Paleotropics. This species appears as an unresolved paraphylum basal to the *M. pseudonutans* group (Fig. 3). Among the few pairings are combinations of paleotropical samples (Madagascar, *TJ 2927*; Tanzania, *AF2*) with neotropical samples (Bolivia, *IJ 1874*; Colombia, *AY 460656, CO 5*). The results of the analysis at least exclude an origin of the genus in the Paleotropics.

Another species with disjunctive distribution is *M. peruviana*, which is rather frequent in the central Andes, Brazil, and Argentina, rare in the northern Andes, absent in Central America but present in southern Mexico. This distribution pattern coincides with the occurrence of tree-less, often dry high montane vegetation in Mesoamerica and the Andean Cordillera (Ibisch et al., 1999; Hughes & Eastwood, 2007), and reflects the adaptation of *M. peruviana* to the drier climates of high elevations and semi-deserts. Often confused as a small form of *M. flabelliformis* (Tryon & Stolze, 1993), a recent morphological study confirmed its distinctness and suggested a closer relationship with *M. personata* (Lehnert, submitted manuscript). The differences between the two species are mainly the preferred habitats and their size; *M. personata* is usually an epiphyte 5-10 times bigger than the predominantly terrestrial *M. peruviana*. For this reason we trust the resolution in the total evidence tree (Fig. 3) to reflect the natural relationship between the two species despite the low support (MP 81; bootstrap 51). It does not appear that both species are mere ecotypes of the same species because *M. peruviana* does not reach the same dimensions and proportions of *M. personata* in the rare cases when it grows epiphytically (northern Argentina, southeastern Brazil; Lehnert, submitted manuscript). *Melpomene personata* does not occur in the southeastern range of *M. peruviana*, but is otherwise sympatric and also is common in the Central American gap in the distribution of *M. peruviana* (Lehnert, submitted manuscript). If *M. peruviana* has descended from *M. personata*, the Mexican population of *M. peruviana* may represent a different, but morphologically not separable species that has evolved from *M. personata* in a homologous procedure.

### Conclusions

*Melpomene* is a monophyletic genus whose evolution and diversification has been driven most likely by the uplift of the northern Andes. The radiation of the crown group is young and appears largely unresolved in the analysis of chloroplast markers (*atpβ* and *rbcL*). Future studies should include faster evolving sequences and/or whole genome approaches (RFLP, AFLP) in order to elucidate the true relationships within this genus.

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**Figure captions**

Fig. 1. Strict consensus trees. A. *atpβ* data; B. *rbcL* data; C. combined *atpβ* and *rbcL* data; D. morphological data. Abbreviations: L. = *Lellingeria*; M. = *Melpomene*; Mi. = *Micropolypodium*; T. = *Terpsichore*. Numbers in brackets are laboratory numbers used in this study; numbers without brackets are GenBank accession numbers.

Fig. 2. Total evidence strict consensus tree. Heuristic search run with MaxTrees set to automatic increase and with maximum rearrangements per step restrained to 1,000,000. For explanations of abbreviations see Fig. 1.

Fig. 3. Total evidence 50% majority rule consensus tree. Numbers above branches are Maximum Parsimony support/bootstrap values. This is a second approach with the 328 equally parsimonious trees from the first step used as starting points in a heuristic search with unlimited rearrangements per step (see Materials & Methods). For explanations of abbreviations see Fig. 1.

Fig. 4. Total evidence phylogram. For explanations of abbreviations see Fig. 1.

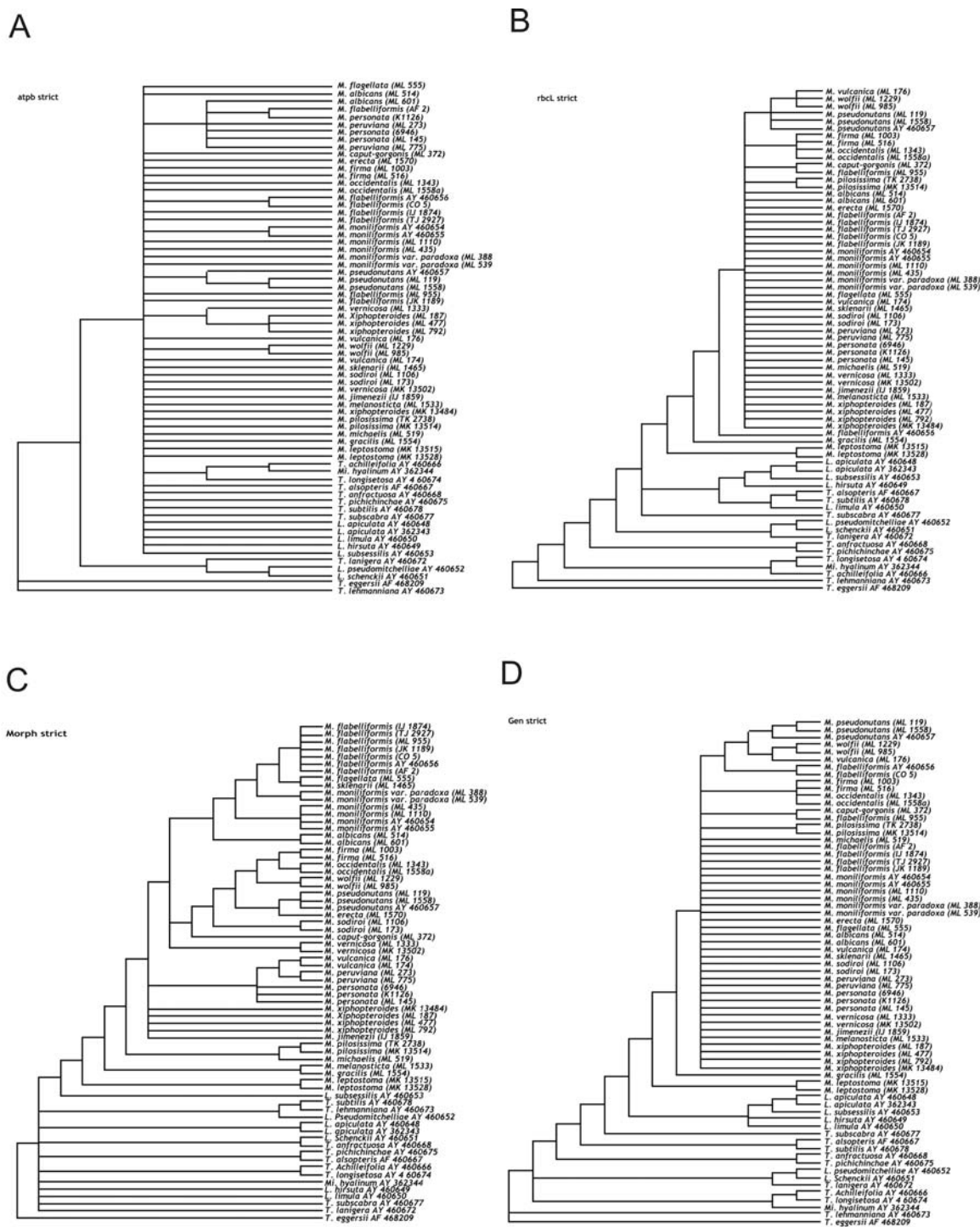


Fig. 1. Strict consensus trees. A. *atpβ* data; B. *rbcL* data; C. combined *atpβ* and *rbcL* data; D. morphological data. Abbreviations: L. = *Lellingeria*; M. = *Melpomene*; Mi. = *Micropolypodium*; T. = *Terpsichore*. Numbers in brackets are laboratory numbers used in this study; numbers without brackets are GenBank accession numbers.

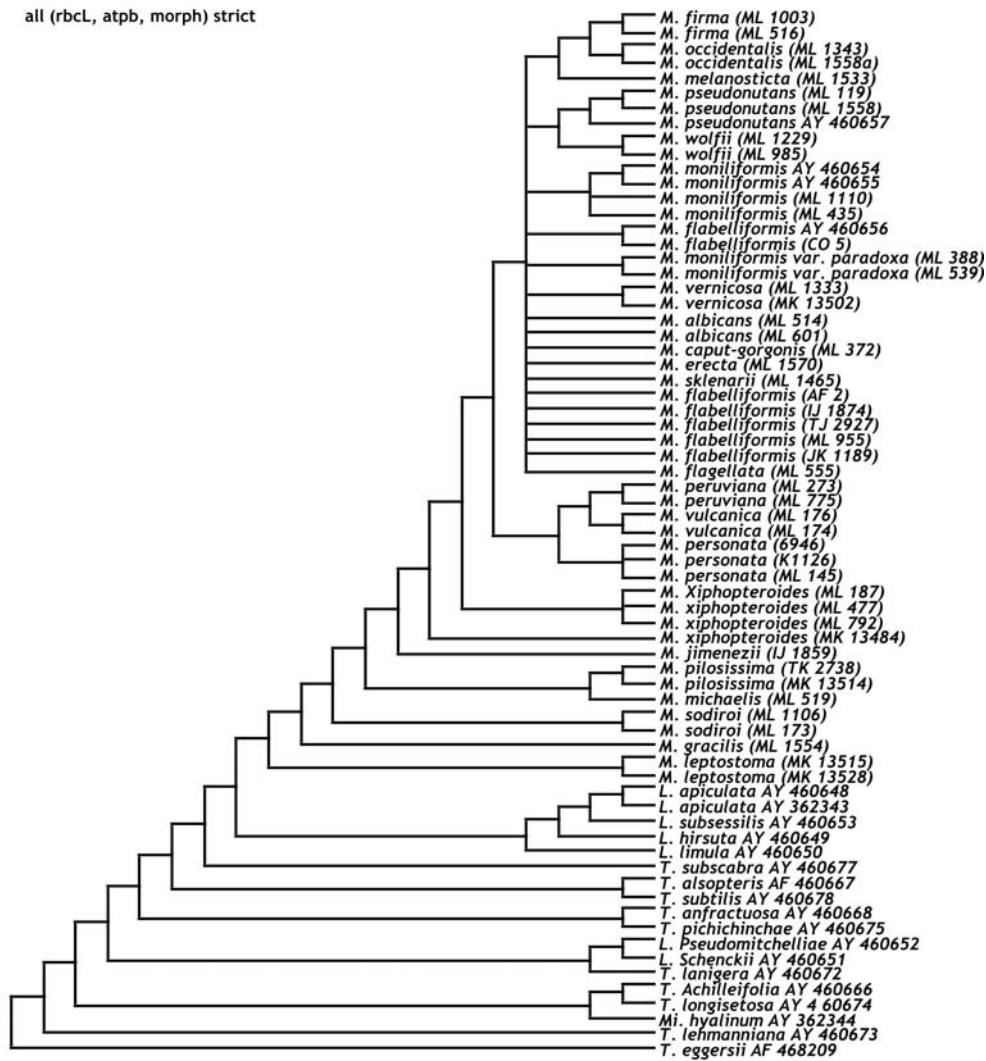


Fig. 2. Total evidence strict consensus tree of 328 equally parsimonious trees. Heuristic search run with MaxTrees set to automatic increase and with maximum rearrangements per step restrained to 1,000,000. For explanations of abbreviations see Fig. 1.



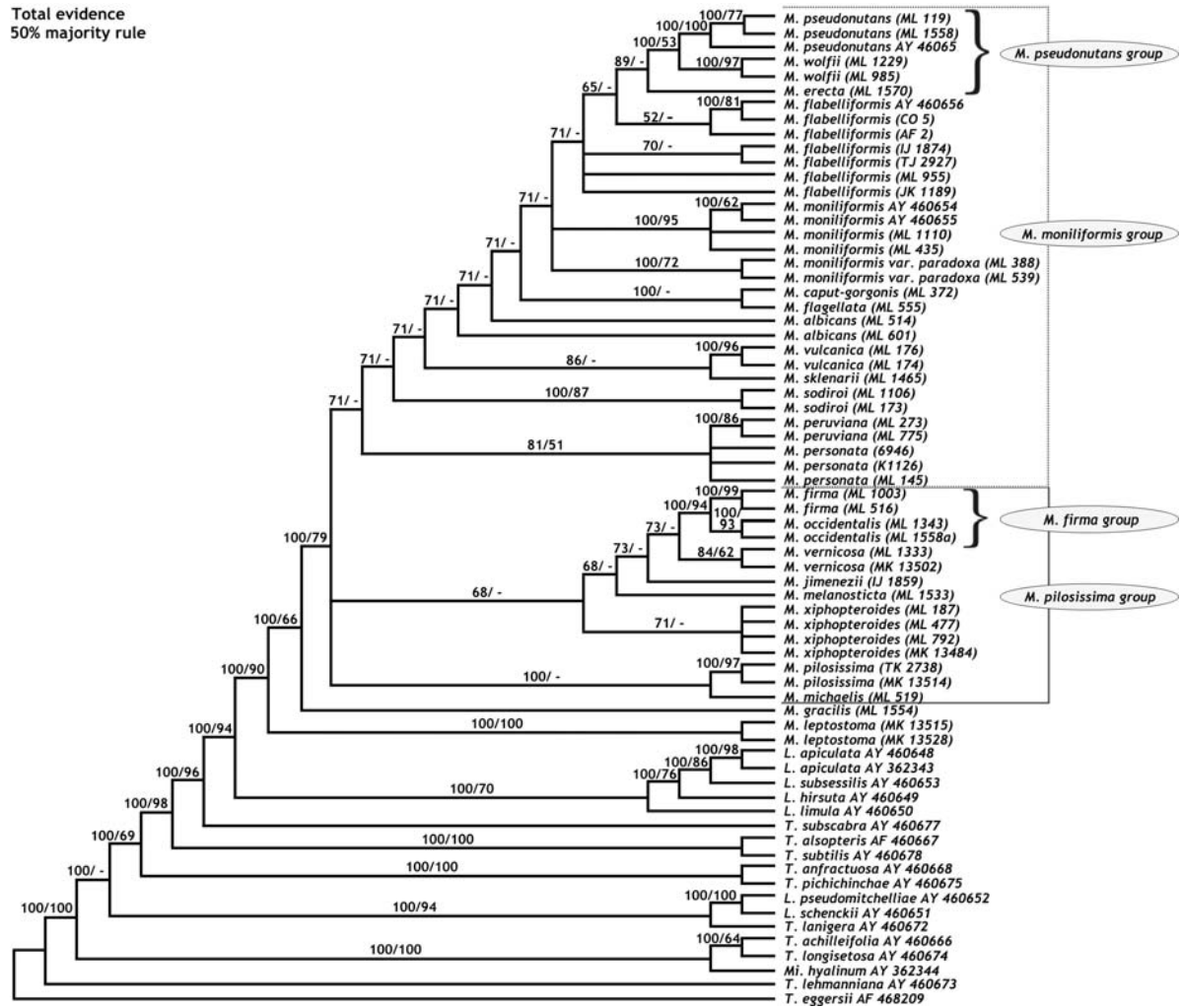


Fig. 3. Total evidence 50% majority rule consensus tree. Numbers above branches are Maximum Parsimony support/bootstrap values. This is a second approach with the 328 equally parsimonious trees from the first approach (Fig. 2) used as starting points in a heuristic search with unlimited rearrangements per step (see Materials & Methods). For explanations of abbreviations see Fig. 1.

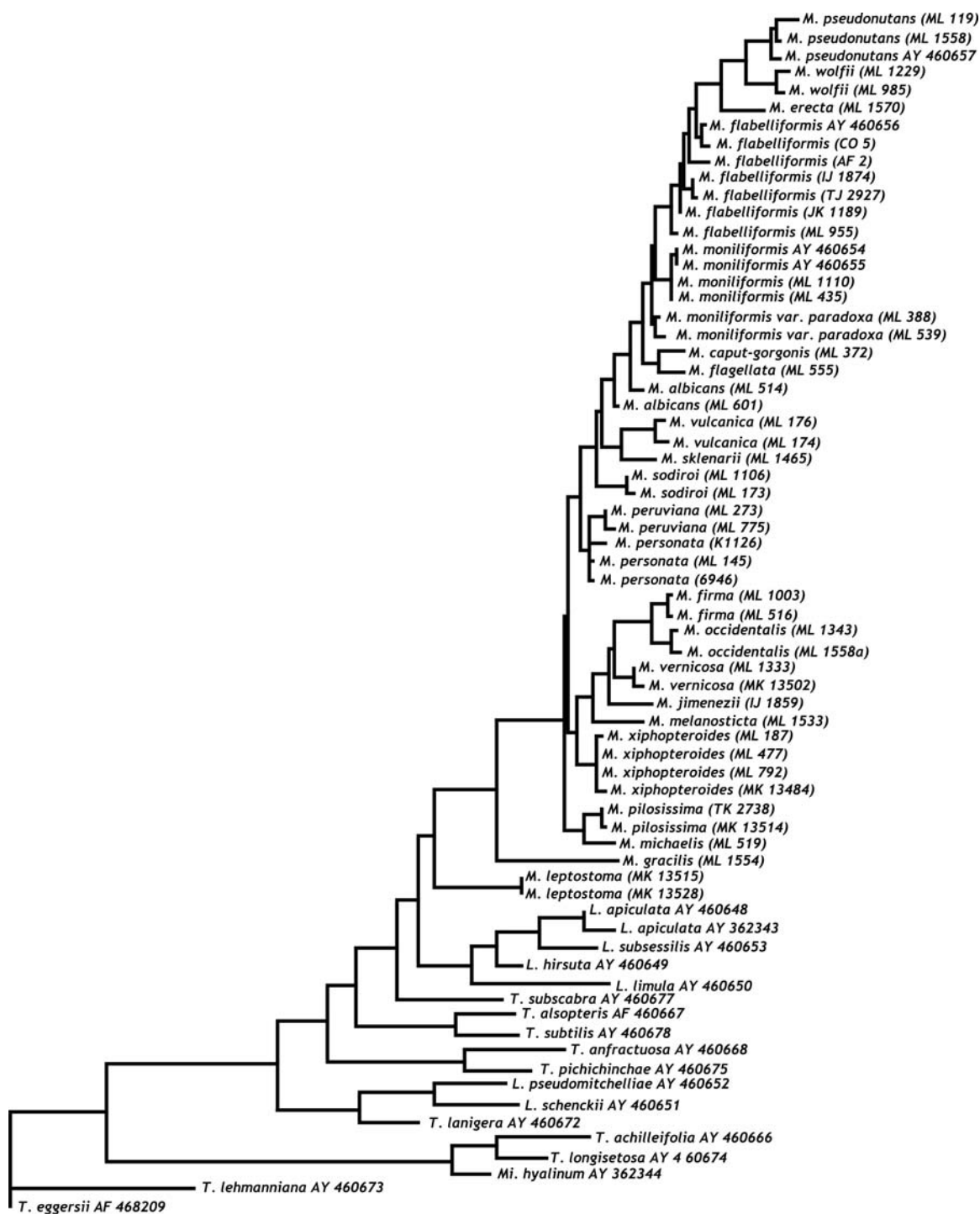


Fig. 4. Total evidence (*atpβ*, *rbcL*, morphology) phylogram; one of 52670 most parsimonious trees found in the second approach (see Materials & Methods). For explanations of abbreviations see Fig. 1.

Tab. 1. Sampled taxa; asterisks mark samples processed at Göttingen University.

Abbreviation	Species	Origin	Voucher	Herbarium	<i>rbcL</i>	<i>atpβ</i>
AY460648	<i>Lellingeria apiculata</i> (Kunze ex Klotzsch) A. R. Sm. & R. C. Moran	Costa Rica	Rojas A. et al. 3298	UC	AY460648	AY459481
AY362343	<i>Lellingeria apiculata</i> (Kunze ex Klotzsch) A. R. Sm. & R. C. Moran	Brazil	Salino 3009	UC	AY362343	AY459480
AY460649	<i>Lellingeria hirsuta</i> A. R. Sm. & R. C. Moran	Costa Rica	Rojas A. & E. Fletes 3145	UC	AY460649	AY459482
AY460650	<i>Lellingeria limula</i> (Christ) A. R. Sm. & R. C. Moran	Costa Rica	Moraga A. & A. Rojas 501	UC	AY460650	AY459523
AY460652	<i>Lellingeria pseudomitchelliae</i> (Lellinger) A. R. Sm. & R. C. Moran	Costa Rica	Rojas A. 3005	MO	AY460652	AY459484
AY460651	<i>Lellingeria schenckii</i> (Hieron.) A. R. Sm. & R. C. Moran	Brazil	Salino 4538	BHCB, UC	AY460651	AY459483
AY460653	<i>Lellingeria subsessilis</i> (Baker) A. R. Sm. & R. C. Moran	Costa Rica	Rojas A. 3022 & M. Mata	UC	AY460653	AY459485
ML 514	<i>Melpomene albicans</i> Lehnert	Bolivia	Lehnert M. 514	GOET, LPB, UC	+	+
ML 601	<i>Melpomene albicans</i> Lehnert	Bolivia	Lehnert M. 601	GOET, LPB, UC	+	+
ML 372	<i>Melpomene caput-gorgonis</i> Lehnert	Bolivia	Lehnert M. 372	GOET, LPB, UC	+	+
ML 1570	<i>Melpomene erecta</i> (C. V. Morton) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 1570	GOET, QCA, UC	+	+
ML 1003	<i>Melpomene firma</i> (J. Sm.) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 1003	GOET, QCA, UC	+	+
ML 516	<i>Melpomene firma</i> (J. Sm.) A. R. Sm. & R. C. Moran	Bolivia	Lehnert M. 516	GOET, LPB, UC	+	+
CO 5	<i>Melpomene flabelliformis</i> (Poir.) A. R. Sm. & R. C. Moran	Colombia	Dassler C. 94-7-14-2	UC	+	+
AF 2	<i>Melpomene flabelliformis</i> (Poir.) A. R. Sm. & R. C. Moran	Tanzania	Hemp A. s.n.	UBT	+	+
TJ 2927*	<i>Melpomene flabelliformis</i> (Poir.) A. R. Sm. & R. C. Moran	Madagascar	Janßen T. 2927	GOET	+	-

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IJ 1874*	<i>Melpomene flabelliformis</i> (Poir.) A. R. Sm. & R. C. Moran	Bolivia	Jimenez I. 1874	GOET, LPB, UC	+	-
JK 1189*	<i>Melpomene flabelliformis</i> (Poir.) A. R. Sm. & R. C. Moran	Costa Rica	Kluge J. 1189	GOET	+	-
ML 955	<i>Melpomene flabelliformis</i> (Poir.) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 955	GOET, QCA, UC	+	+
AY460656	<i>Melpomene flabelliformis</i> (Poir.) A. R. Sm. & R. C. Moran	Colombia	Sanchez-B. P. 183	UC	AY460656	AY459488
ML 555*	<i>Melpomene flagellata</i> Lehnert	Bolivia	Lehnert M. 555	GOET, LPB, UC	+	-
ML 1554	<i>Melpomene gracilis</i> (Hooker) A.R. Sm. & R.C. Moran	Ecuador	Lehnert M. 1554	GOET, QCA, UC	+	+
IJ 1859*	<i>Melpomene jimenezii</i> Lehnert	Bolivia	Jiménez I. 1859	GOET, LPB, UC	+	-
MK 13515	<i>Melpomene leptostoma</i> (Fée) A. R. Sm. & R. C. Moran	Mexico	Kessler M. 13515	GOET	+	-
MK 13528	<i>Melpomene leptostoma</i> (Fée) A. R. Sm. & R. C. Moran	Mexico	Kessler M. 13528	GOET	+	-
ML 1533	<i>Melpomene melanosicta</i> (Kunze) A.R. Sm. & R.C. Moran	Ecuador	Lehnert M. 1533	GOET, QCA, UC	+	+
ML 519*	<i>Melpomene michaelis</i> Lehnert	Bolivia	Lehnert M. 519	GOET, LPB, UC	+	-
AY460655	<i>Melpomene moniliformis</i> (Lagasca ex Sw.) A. R. Sm. & R. C. Moran	Mexico	Farrar D. 94-9-21-1	no voucher	AY460655	AY459487
ML 388	<i>Melpomene moniliformis</i> (Lagasca ex Sw.) A. R. Sm. & R. C. Moran var. <i>paradoxa</i> Lehnert	Bolivia	Lehnert M. 388	GOET, LPB, UC	+	+
ML 435	<i>Melpomene moniliformis</i> (Lagasca ex Sw.) A. R. Sm. & R. C. Moran	Peru	Lehnert M. 435	GOET	+	+
ML 539	<i>Melpomene moniliformis</i> (Lagasca ex Sw.) A. R. Sm. & R. C. Moran var. <i>paradoxa</i> Lehnert	Bolivia	Lehnert M. 539	GOET, LPB, UC	+	+
ML 1110	<i>Melpomene moniliformis</i> (Lagasca ex Sw.) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 1110	GOET	+	+
AY460654	<i>Melpomene moniliformis</i> (Lagasca ex Sw.) A. R. Sm. & R. C. Moran	Costa Rica	Moraga A. & A. Rojas 446	INB	AY460654	AY459486
ML 1343	<i>Melpomene occidentalis</i> Lehnert	Ecuador	Lehnert M. 1343	GOET, QCA, UC	+	+

ML 1558a	<i>Melpomene occidentalis</i> Lehnert	Ecuador	Lehnert M. 1558a	GOET, QCA, UC	+	+
JK 6946	<i>Melpomene personata</i> Lehnert	Costa Rica	Kluge J. 6946	GOET	+	+
ML 145	<i>Melpomene personata</i> Lehnert	Ecuador	Lehnert M. 145	GOET, QCA, UC	+	+
ML 775	<i>Melpomene peruviana</i> (Desv.) A. R. Sm. & R. C. Moran	Bolivia	Lehnert M. 775	GOET, LPB, UC	+	+
ML 273	<i>Melpomene peruviana</i> (Desv.) A. R. Sm. & R. C. Moran	Peru	Lehnert M. 273	GOET	+	+
MK 13514	<i>Melpomene pilosissima</i> (M. Mart. & Gal.) A. R. Sm. & R. C. Moran	Mexico	Kessler M. 13514	GOET	+	-
TK 2738	<i>Melpomene pilosissima</i> (M. Mart. & Gal.) A. R. Sm. & R. C. Moran	Mexico	Krömer T. 2738	GOET	+	-
ML 119	<i>Melpomene pseudonutans</i> (Rosenst. & Christ) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 119	GOET, QCA, UC	+	+
ML 1558	<i>Melpomene pseudonutans</i> (Rosenst. & Christ) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 1558	GOET, QCA, UC	+	+
AY460657	<i>Melpomene pseudonutans</i> (Rosenst. & Christ) A. R. Sm. & R. C. Moran	Ecuador	Wilson K. A. 2806	UC	AY460657	AY459489
ML 1465	<i>Melpomene sklenarii</i> Lehnert	Ecuador	Lehnert M. 1465	GOET, QCA, UC	+	+
ML 1106	<i>Melpomene sodiroi</i> (Rosenst. & Christ) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 1106	GOET, QCA, UC	+	+
ML 173*	<i>Melpomene sodiroi</i> (Rosenst. & Christ) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 173	GOET, QCA, UC	+	-
MK 13502*	<i>Melpomene vernicosa</i> (Copel.) A. R. Sm. & R. C. Moran	Mexico	Kessler M. 13502	GOET	+	-
ML 1333	<i>Melpomene vernicosa</i> (Copel.) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 1333	GOET, QCA, UC	+	+
ML 174*	<i>Melpomene vulcanica</i> Lehnert	Ecuador	Lehnert M. 174	GOET, QCA, UC	+	-
ML 176	<i>Melpomene vulcanica</i> Lehnert	Ecuador	Lehnert M. 176	GOET, QCA, UC	+	+
ML 985	<i>Melpomene wolfii</i> (Hieron.) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 985	GOET, QCA, UC	+	+
ML 1229	<i>Melpomene wolfii</i> (Hieron.) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. & M. Kessler 1229	GOET, QCA, UC	+	+

MK 13484*	<i>Melpomene xiphopteroides</i> (Liebm.) A. R. Sm. & R. C. Moran	Mexico	Kessler 13484	M.	GOET	+	-
K 1126	<i>Melpomene xiphopteroides</i> (Liebm.) A. R. Sm. & R. C. Moran	Costa Rica	Kirkpatrick 1126	R.	UC	+	+
ML 187	<i>Melpomene xiphopteroides</i> (Liebm.) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 187		GOET, QCA, UC	+	+
ML 477	<i>Melpomene xiphopteroides</i> (Liebm.) A. R. Sm. & R. C. Moran	Bolivia	Lehnert M. 477		GOET, LPB, UC	+	+
ML 792	<i>Melpomene xiphopteroides</i> (Liebm.) A. R. Sm. & R. C. Moran	Ecuador	Lehnert M. 792		GOET, QCA, UC	+	+
AY362344	<i>Micropolypodium hyalinum</i> (Maxon) A. R. Sm.	Costa Rica	Rojas A. et al. 3210	et al.	CR, INB, MO, UC	AY362344	AY459490
AY460666	<i>Terpsichore achilleifolia</i> (Kaulf.) A. R. Sm.	Brazil	Cordeiro J. & O. Ribas 1398	&	UC	AY460666	AY459499
AY460667	<i>Terpsichore alsopertis</i> (C. V. Morton) A. R. Sm.	Ecuador	Wilson K. A. 2609a	A.	UC	AY460667	AY459500
AY460668	<i>Terpsichore anfractuosa</i> (Kunze ex Klotzsch) B. León & A. R. Sm.	Costa Rica	Rojas A. et al. 3321	et al.	INB	AY460668	AY459501
AF468209	<i>Terpsichore eggersii</i> (Baker ex Hook.) A. R. Sm.	Dominican Republic	Hill S. R. 29109		UC	AF468209	AF469785
AY460672	<i>Terpsichore lanigera</i> (Desv.) A. R. Sm.	Peru	Leon B. 3647		UC, USM	AY460672	AY459505
AY460673	<i>Terpsichore lehmanniana</i> (Hieron.) A. R. Sm.	Ecuador	Wilson K. A. 2589	A.	UC	AY460673	AY459506
AY460674	<i>Terpsichore longisetosa</i> (Hook.) A. R. Sm.	Costa Rica	Rojas A. et al. 3209	et al.	CR, INB, MO, UC	AY460674	AY459507
AY460675	<i>Terpsichore pichincha</i> (Sodiro) A. R. Sm.	Colombia	Dassler 94-7-13-1		ILLS	AY460675	AY459508
AY460677	<i>Terpsichore subscabra</i> (Klotzsch) B. León & A. R. Sm.	Costa Rica	Rojas A. et al. 3211	et al.	UC, CR, INB, MO	AY460677	AY459511
AY460678	<i>Terpsichore subtilis</i> (Kunze ex Klotzsch) A. R. Sm.	Costa Rica	Moraga M. & A. Rojas 505	& A.	INB	AY460678	AY459512

Tab. 2. Morphological characters used in phylogenetic analysis.

**Habit**

1. Plants: 1. terrestrial (rooting in soil), 0. not.
2. Plants: 1. epilithic/saxicolous; 0. not.
3. Plants: 1. epiphytic, 0. not.

**Rhizomes**

4. Rhizome diameter: 0. < 1.5 mm; 1. >1.5 mm.
5. Rhizomes: 0. erect; 1. horizontally creeping.
6. Rhizomes: 0. not ascending/decumbent, 1. ascending/decumbent.
7. Rhizomes branching: 0. not or rarely; 1. regularly.
8. Rhizomes; indument: 0. glabrous; 1. hairs only; 2. scales (additionally or solely).

**Scales**

9. Insertion: [? scales absent/not applicable;]; 1. basifix; 2. pseudopeltate.
10. Scales clathrate: ? scales absent/not applicable; 0. not: 1. weakly/occluded; 2. strongly.
11. Scales iridescent: ? scales absent/not applicable; 0. not; 1. weakly; 2. strongly.
12. Scales: ? absent; 0. without hair-like marginal ciliae; 1. with marginal ciliae
13. Scales: ? absent; 0. without marginal glandular hairs; 1. with marginal glandular hairs all along the margin; 2. glandular hairs restricted to tips, with narrow insertion; 3. glandular hairs restricted to tip, on wide insertion.
14. Scales; apical glands: ? scales absent/not applicable; 0. absent; 1. linear (incl. single cells); 2. palmately; 3. clustered.
15. Scales; width in cells across bases: ? scales absent/not applicable; 1. (<14); 2. (14<20); 3. (20-35). 4. (>35-60).
16. Scales: length: ? scales absent/not applicable; 1. [to 1.5 mm]; 2. [to 3.5 mm]; 3. [to 5 mm]; 4. [to 7 mm or more].

**Fronds**

17. Fronds arranged along rhizomes: 0. closely, < 5 mm apart; 1. widely, > 6 mm apart.
18. Fronds arranged towards axis of rhizome: 0. fasciculate, appressed to rhizomes; 1. spreading to patent.
19. Fronds arranged to substrate: 0. pendent; 1. patent; 2. erect.
20. Fronds growing: 0. indeterminate; 1. determinate.
21. Petioles; maximum diameter in average: 0. to 0.4 mm; 1. to 0.7 mm; 2. to 0.9 mm; 3. to 1.0 mm or more.
22. Petioles; indument: 0. without glandular hairs; 1. with glandular hairs.
23. petioles 0. without septate, uniseriate hairs; 1. with uniseriate hairs.
24. Petioles; uniseriate hairs: ? absent 1. (<1.5 mm); 2. (>1.5 mm).
25. Petioles: 0. terete; 1. decurrently marginate; 2. alate throughout. ordered
26. Laminae: 0. entire; 1. pinnatifid to simply pinnate; 2. pinnate-pinnatifid or more.
27. Laminae; segments: 0. entire; 1. subentire to shallowly crenate; 2. deeply crenate to pinnatifid.
28. Laminae; hydathodes: 0. absent; 1. partially absent or irregularly present; 2. always present.
29. Laminae; shape: 0. linear; 1. elliptic (widest in the middle); 2. lanceolate (widest below the middle); 3. oblanceolate incl. obovate (widest above the middle).

30. Laminae; uniseriate hairs: 0. absent; 1. only in sori; 2. only abaxially; 3. on both sides.
31. Laminae; uniseriate hairs in sori: ?. not applicable; 0. absent; 1. clustered; 2. evenly distributed.
32. Rhachises; middle parts: 0. glabrous; 1. hairy adaxially; 2. hairy on both sides; 3. hairy abaxially.
33. Segments; shape: 0. oblong; 1. linear; 2. deltate; 3. round.
34. Segments; orientation in middle section of laminae; 0. patent; 1. ascending; 2. reflexed.
35. Segments; tips: 0. straight; 1. falcate.
36. Segments; tips: 0. round; 1. obtuse; 2. acute; 3. truncate to emarginate.
37. Segments; 0. simply adnate; 1. basiscopically decurrent; 2. acroscopically decurrent, basiscopically auriculate.
38. Segments; margins: 0. flat; 1. revolute.
39. Segments; thickness: 0. flat, thin; 1. flat, thick; 2. gibbose; 3. carinate (weakly so).

**Miscellaneous**

40. proliferous roots: 0. absent; 1. present.
41. lime dots on hydathodes: 0. absent; 1. present.
42. black clavate fungal fruiting bodies: 0. absent; 1. present.



Appendix 1: Morphomatrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	40	41	42
MgraciML1554	0	1	0	0	{0,1}	0	0	2	{1,2}	2	0	0	1	1	2	1	0	0	0	1	1	0	0
MalbiML514	0	1	1	0	1	0	0	2	2	2	2	0	{0,1}	1	0	{0,1}	1	1	2	0	0	0	0
MalbiML601	0	1	3	1	1	1	0	2	2	1	1	2	{0,2}	{2,3}	0	{1,2}	0	0	{1,2}	1	0	0	0
McapuML372	0	1	3	1	1	1	0	2	2	1	1	2	{0,2}	{2,3}	0	{1,2}	0	0	{1,2}	1	0	0	0
MerecML1570	0	0	1	1	1	1	0	2	{0,1}	2	2	0	3	1	0	1	{0,1}	0	1	0	0	0	0
MfirmaML1003	2	1	1	0	2	1	1	2	2	2	1	0	2	3	4	4	1	1	1	1	1	1	0
MfirmML516	2	3	1	{0,1}	2	1	0	2	2	2	2	0	1	{1,3}	2	4	0	0	2	1	1	0	0
MfishML1343	1	1	1	{0,1}	0	1	0	2	{1,3}	2	2	0	1	{0,1}	2	4	0	0	0	1	1	1	0
MfishML1558a	2	3	1	1	2	1	0	2	{1,3}	2	1	1	0	{0,1}	0	1	2	0	0	1	0	0	0
MfiabAF2	0	0	0	1	0	1	0	2	{1,2}	2	2	1	1	{1,3}	2	4	0	0	0	1	1	1	0
MfiabAY460656	2	{0,1}	1	0	0	1	0	2	2	2	2	0	1	{1,3}	2	4	{0,2}	0	0	1	1	0	0
MfiabCO5	2	3	1	0	1	0	1	2	{1,2}	2	2	1	2	0	0	4	{0,2}	0	0	1	0	0	0
MfiabML955	1	1	1	0	1	0	1	2	2	2	2	0	2	3	2	3	1	1	2	1	1	1	0
MmetaML1533	2	3	1	0	{0,1}	1	0	2	2	2	2	0	2	3	2	{1,2}	{0,1}	0	1	2	1	0	0
MmoniiAY460654	0	1	0	0	0	0	0	2	{0,1}	2	1	0	2	3	1	2	0	0	1	1	1	0	0
MmoniiAY460655	1	1	1	1	1	0	1	2	2	2	2	0	3	2	2	3	0	1	1	2	1	0	0
MmoniiML1110	1	3	1	1	{1,2}	1	0	2	0	1	2	0	3	0	2	{0,1}	0	1	1	2	1	0	0
MperuML273	1	3	1	1	{1,2}	1	0	2	2	2	2	0	3	0	2	{0,1}	0	1	1	2	1	0	0
MmoniiML435	1	1	1	0	1	0	1	2	{0,2}	2	1	1	2	{2,3}	1	{1,2}	1	{0,1}	0	1	0	0	0
MmoparML388	1	1	1	0	1	0	1	2	2	2	2	0	2	2	2	3	0	1	2	1	2	1	0
MmoparML539	0	0	1	0	{1,2}	1	0	2	2	2	2	0	3	2	2	{0,1}	0	1	1	2	1	0	0
Mperso6946	1	3	1	1	1	1	0	2	{0,1}	2	1	0	2	2	2	{0,1}	1	1	2	1	2	1	0
	0	1	1	0	1	0	1	2	{0,1}	2	1	0	2	{1,2}	1	3	0	1	0	1	0	0	0



MpiloTK2738	1	1	0	0	2	2	2	2	0	2	2	2	0	2	2	0	3	1	1	{1,2}	3	{0,1}	0	0	1	1	0	0
MpiloMK13514	0	1	1	0	2	2	2	3	0	2	2	2	3	0	2	3	1	0	1	{1,2}	3	{0,1}	0	0	1	0	0	0
MsodiML173	1	1	1	0	2	2	2	2	0	2	2	2	0	2	2	0	4	2	1	{0,1}	4	{0,1}	1	0	1	1	0	0
MvernMK13502	0	1	1	1	2	2	2	2	0	2	2	2	0	2	2	0	4	2	1	{2,3}	4	0	0	1	1	0	0	0
MxiphMK13484	0	1	1	0	2	2	2	2	0	2	2	2	0	2	2	0	1	2	1	{0,1}	1	0	0	1	1	0	0	0
TachilAY460666	1	0	1	1	2	2	2	2	0	2	2	2	0	2	2	0	1	2	1	{0,1}	2	1	0	1	1	0	0	0
TalsopAF460667	0	1	1	1	2	2	2	2	0	2	2	2	0	2	2	0	2	1	0	{0,1}	2	1	1	1	1	0	0	0
TanfraAY460668	3	2	0	1	2	2	2	2	0	2	2	2	0	2	2	0	2	0	0	{0,1}	2	{0,1}	0	0	0	0	1	0
TeggerAF468209	0	2	0	1	2	2	2	2	0	2	2	2	0	2	2	0	3	1	1	{0,1}	3	0	0	1	1	1	1	1
TlanigAY460672	0	1	1	0	2	2	2	2	0	2	2	2	0	2	2	0	2	2	0	{0,2}	2	{0,1}	0	0	0	0	0	0
TliehmaAY460673	0	0	1	0	2	2	2	2	0	2	2	2	0	2	2	0	2	2	1	{0,1}	2	1	0	0	0	0	0	0
TlongiAY460674	3	2	0	1	2	2	2	2	0	2	2	2	0	2	2	0	2	2	1	{0,1}	2	1	0	0	0	0	0	0
TpichiAY460675	1	3	1	1	2	2	2	2	0	2	2	2	0	2	2	0	2	2	1	{1,2}	2	1	0	0	1	1	0	0
TsubitiAY460678	2	2	0	1	2	2	2	2	0	2	2	2	0	2	2	0	2	2	0	{0,2}	2	0	1	0	0	0	1	1
TsubscAY460677	0	0	2	0	2	2	2	2	0	2	2	2	0	2	2	0	2	2	0	0	0	1	0	0	0	0	0	0
LapicAY460648	0	1	1	0	2	2	2	2	0	2	2	2	0	2	2	0	2	2	1	{0,1}	2	1	0	0	0	0	0	0
LapicAY362343	2	2	1	0	2	2	2	2	0	2	2	2	0	2	2	0	2	2	0	{0,1}	2	1	0	0	0	0	0	0
LlimulAY460650	2	2	1	0	2	2	2	2	0	2	2	2	0	2	2	0	2	2	0	{0,1}	2	1	0	0	0	0	0	0
LhirsuAY460649	0	3	1	1	2	2	2	2	0	2	2	2	0	2	2	0	3	2	1	0	1	0	0	0	0	0	0	0
LpseumAY460652	0	0	1	0	2	2	2	2	0	2	2	2	0	2	2	0	2	2	0	{1,2}	2	1	0	0	0	0	0	0
LschenAY460651	0	0	2	1	2	2	2	2	0	2	2	2	0	2	2	0	2	2	1	{0,1}	2	1	0	0	0	0	0	0
LsubsAY460653	0	0	1	0	2	2	2	2	0	2	2	2	0	2	2	0	2	2	1	0	1	0	0	0	0	0	0	0
MihyalAY362344	1	0	1	0	2	2	2	2	0	2	2	2	0	2	2	0	2	2	1	{1,3}	2	1	0	0	0	0	0	0

Chapter II

**Ferns as populations: floristics and biogeography**

“The most exciting phrase to hear in science, the one that heralds new discoveries, is not 'Eureka!' but 'That's funny...!' “

*Isaac Asimov*

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**P**lants are not distributed randomly on earth. They follow specific patterns determined by their ecological preferences (e.g., climate, soil) and geological changes through time (continental drift, mountain uplift; Gaston, 1998). One of the most species rich areas in the world is the Andean range. This mountain ridge forms the only strong continuous barrier for winds in the southern hemisphere (Gregory-Wodzicki, 2000), and receives heavy precipitation in many parts, which supports a diverse flora. As ferns – like cryptogams in general – rely on humidity for fulfilling their life cycles, it is no wonder that they are especially diverse here.

The Neotropics contain several distinct subunits that are generally recognized but often differently delimited. Basically, the western mountain ranges of North and South America form today a continuous pathway for species (plants and animals) that prefer moderate temperatures (Burnham & Graham, 1999). There are examples of typical northern temperate angiosperm genera that are common in the Andes (e.g., *Alnus* [Betulaceae]; *Thalictrum*, *Clematis*, *Ranunculus/Krapfia* [Ranunculaceae]; *Viola* [Violaceae]); in the case of *Quercus* (Fagaceae), the arrival to the Andes has been in the geologically young past (Hooghiemstra & van der Hammen, 2001). Relatively few South American genera have spread north, usually finding their limit in southern Mexico (Burnham & Graham, 1999). There are some examples from the species groups chosen for this study (*Melpomene*, Cyatheaceae) that also indicate several waves of northward range extension prior to the closure of the Mesoamerican land bridge. Among *Melpomene*, *M. leptostoma* is the only Mexican-Guatemalan endemic. Its basal phylogenetic position (chapter I.4) indicates an early disjunction from the primordial gene pool in the Andes and subsequent differentiation due to longer isolation. Other species of *Melpomene* reaching into Mexico are widely distributed in South America (chapter I.3). Within the Cyatheaceae, there are several species restricted to Mexico-Guatemala with strong affinities to widely distributed Andean species. This region was proposed to be recognized in phytogeography as “Megamexico” (Islebe & Velasquez, 1994). Noteworthy from this area are *Alsophila salvinii* Hook. and *Sphaeropteris horrida* (Liebm.) R. M. Tryon, which belong to groups more diverse in the Paleotropics of SE Asia and may be (like the genus *Cibotium* [Cibotiaceae]) indicators of a prehistoric boreotropical belt that connected both areas (as discussed by Moran & Smith, 2001). To the south, Costa Rica is a region with its own endemic element, but which like the rest of the Costa Rican flora

shows a strong Andean/South American affinity. The change towards the Chocó region that stretches from Panama along the western escarpment of the Colombian Andes to northern Ecuador (here often referred to as Esmeraldas region) lies mainly in the lack of higher elevations and the presence of very high precipitations (Rangel-Ch., 2004). The Chocó elements are adapted to high temperatures and thus restricted to lower elevations. They are substituted at higher elevations by more common Andean species, which are adapted to more temperate conditions. Typical Chocó elements are *Alsophila esmeraldensis* R. C. Moran, *Cyathea decorata* (Hieron.) Domin, and *C. planadae* N. C. Arens & A. R. Sm. Some species are distributed in all before mentioned regions: we find *Alsophila firma* (C. Chr.) D. S. Conant, *Melpomene pilosissima* (Mart. & Gal.) A. R. Sm. & R. C. Moran, and *M. vernicosa* (Copel.) A. R. Sm. & R. C. Moran from Mexico south over the northern Andes to southern Ecuador; *Sphaeropteris brunei* (C. Chr.) R. M. Tryon reaches from Costa Rica to southern Ecuador.

The Andes are roughly divided in three parts, the northern, central, and southern Andes (Simpson, 1975; Gregory-Wodzicki, 2000). The northern Andes consist of three distinct cordilleras (the lowest one, the Cordillera Occidental, belongs to the humid Chocó region). They are further characterized by high precipitations on both west and east flanks (Killeen et al., 2007). Species endemic to the northern Andes are usually páramo elements (Luteyn, 1999); from the example groups, *Melpomene sodiroi* (C. Chr. & Rosenst.) A. R. Sm. & R. C. Moran, *M. sklenarii* M. Lehnert, and *M. vulcanica* M. Lehnert belong to this group. Between the Northern and Central Andes lies a depression, the so-called Amotape-Huancabamba zone (Molau, 1988; Weigend, 2002). Here, the areas above 3000 m are not connected and trade winds may locally pass through the Andes unhindered (chapter II.4), but are otherwise slowed down and deprived of humidity by the foothills of this area. All this results in a patchy distribution of moist forest, semideciduous forest, and shallow interandean dry valley. This pattern benefited the development of a diverse endemic element (*M. huancabambensis* M. Lehnert, *Cyathea concordia* B. León & R. C. Moran, *C. palaciosii* R. C. Moran, *C. phegopteroides* Hieron., *C. thelypteroides* A. R. Sm., *C. windischiana* A. R. Sm., to name just a few) and forms a barrier for many species distributed south and north of it (Ibisch et al., 1999; Weigend, 2002; Lunde & Pacheco, 2003; Andersson, 2006). Some species apparently have colonized this region without being able to traverse it, like *Alsophila mostellaria* M. Lehnert coming from

the south, and *Melpomene pseudonutans* (H. Christ & Rosenst.) A. R. Sm. & R. C. Moran coming from the north. The central Andes reach to central Bolivia, where a deflection in the Cordillera marks the transition from perhumid montane forests to semideciduous forests (Ibisch, 1999; Killeen et al, 2007). Here, only the east facing slopes receive moisture by the trade winds while the western slopes towards the Pacific Ocean are dry, bordering to the Atacama Desert. Consequently, only the eastern Andean slopes support tropical forests with high fern diversity. Typical of this region are *C. ruiziana* Klotzsch, *C. herzogii* Rosenst., *C. austropallescens* Lehnert sp. nov. ined., and several *Melpomene* species, e.g., *M. jimenezii* Lehnert, sp. nov. ined., and *M. caput-gorgonis* Lehnert, sp. nov. ined.

The southern Andes comprise two well-separated centers of fern diversity. The northern Bolivian-Tucuman region is adjacent to the Central Andean region. From the example groups, *Alsophila odonelliana* is the only Cyatheaceae that occurs here and also is restricted to this area. The wide spread *Melpomene peruviana* (Desv.) A. R. Sm. & R. C. Moran is the only species of the genus to be found in this region. The southern region in central Chile and Argentina, which is characterized by a cool temperate climate, shows more affinities its species composition to the Circum-Antarctic Flora shared with New Zealand, Australia, and the Subantarctic islands than with the rest of the Andes (Ponce et al., 2002; Sanmartín & Ronquist, 2004). There are only few species shared with the tropical Andean region, and no member of the example groups is found there.

The Brazilian shield and the Guayana shield belong to the same ancient geological formation and are separated just by the mouth of the Amazon. However, the areas of high fern diversity, i.e., the tepuis and the Mata Atlântica, are well separated; a previous connection of both biomes in earth's history cannot be proven. Supposedly they harbored the ancestors of many Andean fern taxa (e.g., *Jamesonia/Eriosorus* [Pteridaceae]; Sánchez-Baracaldo, 2004). In the case of the tree ferns, the high percentage of endemic species with often uncertain affinities to Andean taxa indicate a long evolutionary history. The genus *Melpomene*, however, is only present with taxa which occur also in the Andes or which can only be separated from Andean species as varieties. One of the few fern species to be found in both the Brazilian and Guayana shield areas is *Cyathea villosa* Humb. & Bonpl. ex. Willd., which also has small outlying populations in the Andes. An often observed pattern is a disjunction of taxa typical of the Guyanas to the Amotape-Huancabamba region (as

defined by Weigend, 2002) and the foothills of the northern Andes (*Purdiaea nutans* Planch. [Cyrillaceae/Angiospermae], *Pterozonium* [Pteridaceae], *Cyathea aterrima* (Hook.) Domin, and *C. macrocarpa* (C. Presl) Domin [Cyatheaceae]).

Regional surveys of plant diversity are prerequisites for biogeographical studies. Checklists and inventories (chapters II.1, 2) give insight not only about the area the species occupy but also about the elevational distribution. Many attempts have been undertaken in the past to describe the reoccurring changes in plant communities but regional peculiarities often distort the limits within which plants are distributed (chapter II.3). In the altitudinal zonation of vegetation, concordance has not been found for the absolute heights in which the zones are changing; a universal vegetation zonation can evidently only work on a relative scale (chapter II.4).

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## II.1. The Cyatheaceae and Dicksoniaceae (Pteridophyta) of Bolivia

Brittonia 58: 229-244. 2006.

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**Abstract:** In total two species of Dicksoniaceae (*Culcita* 1 sp., *Dicksonia* 1 sp.) and 34 species of Cyatheaceae (*Sphaeropteris* 1 sp., *Alsophila* 5 spp., *Cyathea* 26 spp., *Cnemidaria* 2 spp.) are known. One hybrid in *Cyathea* is recognized. The endemic ***Cyathea dintelmannii*** is newly described, and *Cyathea herzogii* from Bolivia and Peru is separated from *Cyathea caracasana* var. *boliviana*. Both species are illustrated. An artificial key to the Bolivian species of Cyatheaceae is provided.

**Key words:** Andes, Bolivia, *Cyathea dintelmannii*, *Cyathea herzogii*, Cyatheaceae, Dicksoniaceae, endemism, hybrid.

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## **II.2. Checklist to the pteridophytes of the Reserva Biológica San Francisco**

**(RBSF, Prov. Zamora-Chinchipec, Ecuador)**

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**Abstract:** 248 species of pteridophytes (ferns and lycophytes) are reported for the Reserva Biológica San Francisco in southern Ecuador, Prov. Zamora-Chinchipec.

### Introduction

A total of 248 species of pteridophytes are recorded for the Reserva Biológica San Francisco (RBSF), including five newly described species from the vicinity of Podocarpus National Park (Lehnert 2006a, b). Covered here is the RBSF from 1800-3140 m a.s.l. where ca. 380 collections of ferns and fern allies have been gathered by the first author for the DFG project “Cryptogamic plant diversity of the *Purdiaea nutans* forest in southern Ecuador and its relationship to soil, climate, and vegetation structure”. The frequently used comparative study site Bombuscaro near Zamora is not included here because the authors did no extensive collections there. As our focus lay on the *Purdiaea nutans* forest which covers the ridges between 2000 m and 2600 m a.s.l. in the RBSF, our list for that area is fairly complete and well supported by collections. Less investigated are the quebradas and the subpáramo zone of the reserve. Thus, future collections will increase the total number of Pteridophyte species known from the RBSF.

The mayor reference for this study was the checklist of Ecuador (Jørgensen & León-Yáñez, 1999), which lists more than 1300 species of ferns and fern allies for the country; 177 are considered as endemics for Ecuador (Valencia et al., 2000)

### Voucher information

Collectors: ML = Marcus Lehnert, FW = Florian Werner. Voucher specimens have been deposited in Quito (QCA), Loja (LOJA), Göttingen (GOET), and Berkeley (UC), unless otherwise mentioned.

### Abbreviations

Life form: e = epiphyte; t = terrestrial; r = saxicolous (rocks). Aquatics have not been found.

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	Locality	Elevation (range in m)	Vegetation type	Frequency	Range	Degree of novelty	Voucher	Chorotype
<b>Aspleniaceae</b>								
<i>Asplenium hallii</i> Hook.	A	2500-2550	III	++	Am-S	-	ML 1395	t
<i>Asplenium tricholepis</i> Rosenst.	A	1800-2000	II	++	A-s	-	FW 465	t
<i>Asplenium cf. hastatum</i> Klotzsch ex Kunze	A	2500-2550	III	++	A	-	ML 1393	e
<i>Asplenium cristatum</i> Lam.	A	1800-2000	II	++	Am-C, S	-	FW 619	e
<i>Asplenium harpeodes</i> Kunze	A	1800-2000	II	++	Am-C, S	-	FW 742	e
<i>Asplenium juglandifolium</i> Lam.	A	2050	II	++	Am-C, S	-	ML 838	e
<i>Asplenium laetum</i> Lam., vel aff.	A	1800-1900	II	++	Am-C, S	-	ML 1096	e
<i>Asplenium macrurum</i> Mickel & Stolze	A	1800-2000	II	++	A	-	FW 1386	e
<i>Asplenium radianum</i> Gaudich	A	1800-2000	II	++	Am-S	-	FW 1030	e
<i>Asplenium</i> sp. 1	A	1950	II	++	End	-	ML 959	e
<i>Asplenium</i> sp. 2	A	1950	II	++	End	-	ML 962	e
<i>Asplenium alatum</i> Willd.	A	2050	II	++	Am-C, A	-	ML 836	e, t
<i>Asplenium auritum</i> Sw.	A	2660	III	++	Am-C, S	-	ML 1473	e, t
<i>Asplenium cf. cuspidatum</i> Lam.	A	1800-2660	II	++	Am-C, S	-	ML 1016	e, t
<i>Asplenium serra</i> Langsd. & Fisch., vel aff.	A	2500-2550	III	++	Am-C, S	-	ML 1394	e, t
<b>Blechnaceae</b>								
<i>Blechnum acutum</i> (Desv.) Mett.	A	1800-2000	II	++	Am-C, S	-	FW 1375	t
<i>Blechnum columbiense</i> Hieron.	C	2750	III	++	A-n	-	ML 833	t
<i>Blechnum cordatum</i> (Desv.) Hieron.	A	2600	III	++	A	-	ML 986	t
<i>Blechnum divergens</i> (Kze.) Mett., vel aff.	A	2640	III	++	Am-C, S	-	ML 1022	t
<i>Blechnum ensiforme</i> (Liebm.) C. Chr.	A	2530	III	+++	Am-C, S	-	ML 942	e, t
<i>Blechnum fragile</i> (Liebm.) Morton & D.B. Lellinger	A	2500-2640	III	+++	Am-C, S	-	ML 1025	e, t
<i>Blechnum schomburgkii</i> (Klotzsch) C. Chr.	A	2400-2600	III	+++	A-n	-	ML 1363	t
<i>Blechnum</i> sp. 1	A	2400	III	++	End	-	ML 1440	t

	Locality	Elevation (range in m)	Vegetation type	Frequency	Range	Degree of novelty	Voucher	Chorotype
<i>Blechnum stipellatum</i> (Sodirol) C. Chr.	A	2500-2660	III	+++	A-n	-	ML 1361	t
<b>Culcitaceae</b>								
<i>Culcita conifolia</i> (Hook.) Maxon	A	2900	III	++	Am-C, S	-	ML 799	t
<b>Cyatheaceae</b>								
<i>Alsophila conantiana</i> M. Lehnert, spec. nov. ined.	A	2500-2600	III	+	EC	nS	ML 1415	t
<i>Alsophila engelii</i> R.M.Tryon	A	2560-2645	III	++	A	-	ML 1040	t
<i>Alsophila erinacea</i> (H. Karst.) D.S. Conant	A	2050	II	+++	A	-	ML 840	t
<i>Alsophila mostellaria</i> M. Lehnert	A	1800-1900	II	+++	A	nE	ML 1099	t
<i>Cyathea atahualpa</i> (R.M. Tryon) Lellinger	A, C	2500-2730	III	++	A-n	-	ML 1573	t
<i>Cyathea bipinnatifida</i> (Baker) Domin	A	2050-2550	III	+++	A	-	ML 1400	t
<i>Cyathea brevistipes</i> R. C. Moran	C	3050 m	IV	+	A-s	-	ML 828	t
<i>Cyathea cf. frigida</i> (H. Karst.) Domin	A	2500-3000	III	+	A-n	-	ML 1344	t
<i>Cyathea cf. nigripes</i> (C. Chr.) Domin	A	1800-1900	II	++	A-n	-	ML 1098	t
<i>Cyathea chimborazensis</i> Hook. var. <i>boreopallescens</i> M. Lehnert, var. nov. ined.	A	2420-2600	III	+	End	-	ML 1500	t
<i>Cyathea conjugata</i> (Hook.) Domin	A	1800-2500	II-III	+++	A	-	ML 1002	t
<i>Cyathea dudleyi</i> R. M. Tryon	A	2400	III	++	A-n	-	ML 1550	t
<i>Cyathea ebenina</i> H. Karst.	A	2550	III	++	A-n	-	ML 937	t
<i>Cyathea frondosa</i> H. Karst.	A	2500	III	+	A-n	-	ML 1572	t
<i>Cyathea heliophila</i> R. M. Tryon	A	2530-2840	III	++	A-n	-	ML 821	t
<i>Cyathea meridensis</i> H. Karst.	A	2500-2800	III	++	A-n	-	ML 1430	t
<i>Cyathea moranii</i> M. Lehnert, sp. nov. ined.	A	2400-2600	III	++	End	nS	ML 1380	t
<i>Cyathea obnoxia</i> M. Lehnert, sp. nov.	A	2530-2630	III	++	End	-	ML 943	t
<i>Cyathea patens</i> H. Karst.	A	3000	III-IV	++	A-n	-	ML 797	t
<i>Cyathea peladensis</i> (Hieron.) Domin	A	2300-2490	III	+++	A-n	-	ML 801	t

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<i>Cyathea plicata</i> M. Lehnert, sp. nov.	A	2200-2630	III	++	End	nS	ML 844	t
<i>Cyathea poeppigii</i> (Hook.) Domin	A	1800-1900	II	+	Am-S	-	ML 1100	t
<i>Cyathea</i> sp., hybrid	A	2400-2500	III	+	End	-	ML 1434	t
<i>Cyathea squamipes</i> H. Karst.	A	1800-2550	II-III	++	A	-	ML 1091	t
<i>Cyathea tungurahuae</i> Sodiro	C	2600-2700	III	+	A-n	-	ML 1504	t
<i>Cyathea xenoxyla</i> M. Lehnert	A	1950	II	++	A	-	ML 960	t
<i>Sphaeropteris quindiuensis</i> (H. Karst.) R.M. Tryon	A	1800-2400	II-III	++	A	-	ML 999	t
<b>Dennstaedtiaceae</b>								
<i>Blotiella lindeniana</i> (Hook.) R.M. Tryon	A	2200	II	+	Am-C, S	-	Øllgaard B. 74926 (AAU, QCA)	t
<i>Dennstaedtia arcuata</i> Maxon	A	1200-2400		++	A-n	-	ML 841	t
<i>Dennstaedtia cornuta</i> (Kaulf.) Mett.	A	600-2550	I-III	+	A	-	ML 837	t
<i>Dennstaedtia globulifera</i> (Poiret) Hieron.	A	2400	III	++	Am-C, S	-	ML 1489	t
<i>Dennstaedtia macrosora</i> H. Navarrete & B. Øllg.	A, T	2100-3000	III	+	End	-	Madsen J.E. 86995 (AAU, LOJA, QCA)	t
<i>Dennstaedtia matthewsii</i> (Hook.) C. Chr.	A, T	1200	I	++	A-s	-	Navarrete H. 266 (AAU, QCA, QCNE)	t
<i>Histiopteris incisa</i> (Thunb.) J. Sm.	A	2660	III	++	Am-C, S	-	ML 1008	t
<i>Hypolepis bogotensis</i> H. Karst.	A	2645	III	++	Am-C, A	-	ML 1039	t
<i>Hypolepis stuebelii</i> Hieron.	A, T	2400	III	+	A	-	Holm-Nielsen L. et al. 3619 (AAU)	t
<i>Paesia glandulosa</i> (Sw.) Kuhn	A	2460-2600	III	++	Am-C, S	-	ML 896	t
<b>Dicksoniaceae</b>								
<i>Dicksonia sellowiana</i> Hook.	A	1800-2700	II-III	++	Am-C, S	-	ML 957	t
<i>Lophosoria quadripinnata</i> (Gmel.) C. Chr.	A	2500-2600	III	++	Am-C, S	-	ML 1417	t



	Locality	Elevation (range in m)	Vegetation type	Frequency	Range	Degree of novelty	Voucher	Chorotype
<i>Lophosoria</i> sp. 1	A	2500-2600	III	++	Am-C, S	-	ML 1416	t
<b>Dryopteridaceae</b>								
<i>Arachniodes denticulata</i> (Sw.) Ching	A	1800-2600	II-III	++	Am-C, S	-	ML 1377	t
<i>Diplazium moritzianum</i> Stolze	A	2520	II	++	Am-S	-	ML 1056	t
<i>Elaphoglossum acutifolium</i> Rosenst.	A	2600	III	+	A-s	-	ML 1340	t
<i>Elaphoglossum andicola</i> (Fée) T. Moore	A	2400-2600	III	+++	A	-	ML 889	e, t
<i>Elaphoglossum antisanae</i> (Sodirot) H. Christ	A	2400-2600	III	++	End	-	ML 858	e
<i>Elaphoglossum argyrophyllum</i> (Sodirot) R. C. Moran, comb. ined.	A	2400	III	+	End	-	ML 1490	e
<i>Elaphoglossum burchellii</i> (Baker) C. Chr.	A	2500-2650	III	++	Am-C, S	-	ML 1338	t
<i>Elaphoglossum</i> cf. <i>eggersii</i> (Baker) H. Christ	A	2660	III	++	Am-C, S	-	ML 916	e
<i>Elaphoglossum</i> cf. <i>floccosum</i> Mickel	A	2500-2600	III	+	A-n	-	ML 1366	e
<i>Elaphoglossum</i> cf. <i>guamanianum</i> (Sodirot) C. Chr.	A	2400	III	+	A-n	-	ML 1493	e
<i>Elaphoglossum</i> cf. <i>latevagans</i> Mickel	A	2500-2550	III	++	A-n	-	ML 1390	t
<i>Elaphoglossum</i> cf. <i>latifolium</i> (Sw.) J. Sm.	A	2400	III	++	Am-C, S	-	ML 1492	e
<i>Elaphoglossum</i> cf. <i>squarrosus</i> (Klotzsch) T. Moore	A	2400	III	+	A	-	ML 1488	t
<i>Elaphoglossum concinnum</i> Mickel	A	2500-2600	III	+	A-n	-	ML 1409	e
<i>Elaphoglossum crassipes</i> (Hieron.) Diels	A	1800-1900	II	++	A	-	ML 1371	s
<i>Elaphoglossum erinaceum</i> (Fée) T. Moore	A	2500-2550	III	++	Am-C, S	-	ML 1387	t
<i>Elaphoglossum eximium</i> (Mett.) H. Christ	A	2500-2550	III	++	Am-C, S	-	ML 1388	t
<i>Elaphoglossum gayanum</i> (Fée) T. Moore, vel aff.	A	2530	III	+	A	-	ML 938	e
<i>Elaphoglossum glossophyllum</i> Hieron.	A	2400-2550	III	+++	A-n	-	ML 930	e
<i>Elaphoglossum killipii</i> Mickel	A	1800-1900	II	++	A-n	-	ML 1374	s
<i>Elaphoglossum lingua</i> (Raddi) Brack.	A	1800-2640	II-III	+	Am-C, S	-	ML 1370	e
<i>Elaphoglossum lloense</i> (Hooker) T. Moore	A	2400-2860	III	++	A	-	ML 1491	e

	Locality	Elevation (range in m)	Vegetation type	Frequency	Range	Degree of novelty	Voucher	Chorotype
<i>Elaphoglossum molle</i> (Sodirol) H. Christ	A	2500-2660	III	++	A	-	ML 1364	e
<i>Elaphoglossum notatum</i> (Fée) T. Moore	A	2660-2860	III	++	A	-	ML 817	e
<i>Elaphoglossum pachyphyllum</i> (Kunze) C. Chr.	A	2550-2660	III	+	A-n	-	ML 936	e
<i>Elaphoglossum papillosum</i> (Baker) H. Christ	A	2630	III	++	A	-	ML 1472	t
<i>Elaphoglossum petiolosum</i> (Desv.) T. Moore	A	2500-2600	III	++	A	-	ML 1441	e
<i>Elaphoglossum productum</i> Rosenst.	A	2400-2470	III	++	A	-	ML 1553	e
<i>Elaphoglossum</i> sp. 1	A	2500-2600	III	+	End	-	ML 1418	e
<i>Elaphoglossum</i> sp. 2	A	1800-1900	II	+	End	-	ML 1372	s
<i>Elaphoglossum</i> sp. 3	A	2500-2600	III	+	End	-	ML 1357	e
<i>Elaphoglossum</i> sp. 4	A	1800-1900	II	+	End	-	ML 1375	s
<i>Elaphoglossum</i> sp. 5	A	2400-2550	III	+++	End	-	ML 1486	e
<i>Elaphoglossum</i> sp. 6	A	2500-2600	III	+	End	-	ML 1425	T
<i>Elaphoglossum</i> sp. 7	A	2470 m	III	+	End	-	ML 872	e
<i>Elaphoglossum</i> sp. 8	A	2480 m	III	+	End	-	ML 882	e
<i>Elaphoglossum</i> sp. 9	A	2460-2470	III	+	End	-	ML 899	e
<i>Elaphoglossum stenophyllum</i> (Sodirol) Diels	A	2500-2600	III	++	A-n	-	ML 1365	e
<i>Elaphoglossum tenuiculium</i> (Fée) Baker	A	1800-1900	II	++	Am-C, S	-	ML 1373	s
<i>Elaphoglossum trivittatum</i> (Sodirol) H. Christ	A	2550-2660	III	++	End	-	ML 920	e
<i>Elaphoglossum vulcanicum</i> H. Christ	A	2640-2660	III	++	A	-	ML 1475	e
<i>Lastreopsis kilippii</i> (Maxon) Tindale	A	2600	II	++	A	-	ML 980	t
<i>Olfersia cervina</i> (L.) Kunze	A	1950	II	++	Am-C, S	-	ML 961	e, t
<i>Polybotrya appressa</i> R.C. Moran	A	1800-2000	II	++	A-n	-	FW 545	e, t
<i>Polybotrya crassirhizoma</i> D.B. Lellinger	A	2050	II	++	Am-S	-	ML 839	e, t
<i>Polybotrya osmundacea</i> Humb. & Bonpl. ex Willd.	A	1800-2000	II	++	Am-C, S	-	FW 1268	e, t
<i>Polystichum dicyophyllum</i> C. Chr.	A	1800-1900	II	++	End	-	ML 1369	t

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<i>Polystichum platyphyllum</i> (Willd.) C. Presl	A	2500-2600	III	++	Am-C, S	-	ML 1412	t
<i>Polystichum</i> sp. 1	A	1800-1900	II	++	End	-	ML 1376	t
<i>Polystichum</i> sp. 2	a	2500-2600	III	++	End	-	ML 1411	t
<i>Rumohra adiantifolia</i> Hook.	A	1800-2000	II	+	Am-Afr	-	Photo FW	e
<b>Equisetaceae</b>								
<i>Equisetum bogotense</i> Kunth	A, T	1800-2500	II-III	++	Am-C, S	-	Croat T.B. 92120 (MO)	
<b>Gleicheniaceae</b>								
<i>Diplazium bancroftii</i> (Hook.) A.R. Sm.	A	1800-2520	II-III	++	Am-C, S	-	ML 1097	t
<i>Sticherus arachnoideus</i> Østergaard & B. Øllg.	A	1900-2550	II-III	++	Am-C, A-n	-	ML 1090	t
<i>Sticherus brevitomentosus</i> Østergaard & B. Øllg.	A	2300-2600	III	++	A	-	ML 1088	t
<i>Sticherus lechleri</i> (Mett. ex Kuhn) Nakai	A	2500-2600	III	++	A	-	ML 1359	t
<i>Sticherus melanoblastus</i> Østergaard & B. Øllg.	A	2600-2700	III	++	A-n	-	ML 1549	t
<i>Sticherus remotus</i> (Kaulf.) Chrysler	A, B	1500-1800	II	++	Am-C, S	-	ML 796	t
<i>Sticherus revolutus</i> (Kunth) Ching	A	2300-2860	III	+++	Am-S	-	ML 814	t
<i>Sticherus rubignosus</i> (Mett.) Nakai	A	2600	III	++	Am-C, S	-	ML 1478	t
<i>Sticherus</i> sp. 1	A	2600	III	++	End	-	ML 1479	t
<i>Sticherus tomentosus</i> (Cav. ex Sw.) A.R. Sm.	A	2600	III	++	A	-	ML 1477	t
<b>Hymenophyllaceae</b>								
<i>Trichomanes cf. rigidum</i> Sw.	A	2650	III	++	Am-Afr	-	ML 1047	t
<i>Trichomanes dactylites</i> Sodiro	A	2420-2500	III	++	A	-	ML 1501	t
<i>Hymenophyllum cristatum</i> Hooker & Grev.	A	2100-2470	III	++	A-s	-	ML 1547	e
<i>Hymenophyllum fragile</i> (Hedw.) C.V. Morton	A	2520-2660	III	++	Am-C, S	-	ML 1013	e
<i>Hymenophyllum fucoides</i> (Sw.) Sw.	A	2500-2600	III	+++	Am-C, S	-	ML 1444	e
<i>Hymenophyllum jamesonii</i> Hook.	A	2600	III	++	A-n	-	ML 975	e

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<i>Hymenophyllum lobatolatum</i> Klotzsch	A	1800-2600	II-III	++	A-n	-	FW 651	e
<i>Hymenophyllum multialatum</i> C.V. Morton	A	1800-2600	II-III	++	A-n	-	ML 1447	e
<i>Hymenophyllum myriocarpum</i> Hooker	A	2470-2600	III	+++	Am-C, S	-	ML 1406	e
<i>Hymenophyllum pedicellatum</i> Klotzsch	A	1800-2000	II	++	A	-	FW 1255	e
<i>Hymenophyllum plumieri</i> Hook. & Grev.	A	2500-2600	III	++	A	-	ML 1449	e
<i>Hymenophyllum polyanthos</i> (Sw.) Sw.	A	2500-2650	III	++	Pantrop	-	ML 1445	e
<i>Hymenophyllum ruizianum</i> (Klotzsch) Kunze	A	2490-2600	III	+++	A	-	ML 1448	e
<i>Hymenophyllum tomentosum</i> Kunze	A	2480	III	++	A	-	ML 884	e
<i>Hymenophyllum trichomanoides</i> Bosch	A	2470-2600	III	+++	Am-S	-	ML 1446	e
<i>Hymenophyllum trichophyllum</i> Kunth	A	2460-2660	III	++	Am-C, S	-	ML 1404	e
<i>Hymenophyllum undulatum</i> (Sw.) Sw.	A	2460-2660	III	+++	Am-C, S	-	ML 864	e
<i>Trichomanes angustatum</i> Carm.	A	1800-2000	II	+	Am-C, S	-	FW1303	e
<i>Trichomanes cellulosum</i> Klotzsch	A	2400	III	+	Am-S	-	ML 1481	e
<i>Trichomanes diaphanum</i> Kunth	A	1800-2000	II	+	Am-C, S	-	FW 745	e
<i>Trichomanes reptans</i> Sw.	A	1800-2000	III	+	Am-C, S	-	FW 746	e
<i>Trichomanes</i> sp. 1	A	1900	III	+	End	-	ML 1436	e
<i>Trichomanes</i> sp. 2	A	2400	III	+	End	-	ML 1482	e
<i>Trichomanes</i> sp. 3	A	2400	III	+	End	-	ML 1483	e
<i>Hymenophyllum microcarpum</i> Desv.	A	2400-2530	III	++	Am-C, S	-	ML 944	e, t
<i>Trichomanes lucens</i> Sw.	A	2460-2660	III	++	Am-C, S	-	ML 894	e, t
<b>Lomariopsidaceae</b>								
<i>Nephrolepis cordifolia</i> (L.) C. Presl	A	1800-1900	II	++	Am-Afr	-	Salazar L. I. s.n. (QCA)	t
<i>Nephrolepis pectinata</i> (Willd.) Schott	A	1800-2000	II	++	Am-C, S	-	FW 525	e, t
<b>Loxomataceae</b>								
<i>Loxosomopsis pearcei</i> (Baker) Maxon	A	2900	III	+	A	-	ML 798	t

	Locality	Elevation (range in m)	Vegetation type	Frequency	Range	Degree of novelty	Voucher	Chorotype
<b>Lycopodiaceae</b>								
<i>Lycopodiella andicola</i> B. Øllg., comb. ined.	A	1800-1900	II	+	End	-	ML 1095	t
<i>Lycopodiella</i> cf. <i>glaucescens</i> (C. Presl) B. Øllg.	A	2460-2470	III	++	A	-	ML 891	t
<i>Lycopodium clavatum</i> L.	A	1800-2700	II-III	+++	Subcos	-	Photo ML	t
<i>Lycopodium vestitum</i> Poir.	C	2950	IV	++	A-n	-	ML 830	t
<i>Huperzia campiana</i> B. Øllg.	A	2500-2600	III	+	A-n	-	ML 1431	e
<i>Huperzia ericifolia</i> (C. Presl) Holub	A	2000	II	++	A	-	ML 1083	e
<i>Huperzia eversa</i> (Poir.) B. Øllg.	A	2840	III	+	A	-	ML 822	e
<i>Huperzia tenuis</i> (Humb. & Bonpl. ex Willd.) Rothm.	A	2500-2600	III	+	A	-	ML 1442	e
<i>Huperzia wilsonii</i> (Underw. & Lloyd) B. Øllg.	T	2660	III	+	Am-C, S	-	ML 1015	e
<b>Marattiaceae</b>								
<i>Danaea</i> cf. <i>moritziana</i> C. Presl	A	2050	II	+	A-n	-	ML 842	t
<b>Ophioglossaceae</b>								
<i>Botrychium virginianum</i> (L.) Sw.	A	2500-3000	III	+	Subcos	-	Photo ML	t
<i>Cheiroglossa palmata</i> (L.) C. Presl	A	2000	II	++	Pantrop	-	Øllgaard B. 74929 (AAU)	t
<b>Polypodiaceae</b>								
<i>Campyloneurum angustifolium</i> (Sw.) Fée	A	1800-2000	II	++	Am-C, S	-	FW 874	e
<i>Campyloneurum angustipaleatum</i> (Alston) M. Meyer ex D.B. Lellinger	A	1800-2000	II	++	Am-C, S	-	FW 598	e
<i>Campyloneurum cochense</i> (Hieron.) Ching	T	2660	III	++	Am-C, S	-	ML 1012	e, t
<i>Campyloneurum phyllitidis</i> C. Presl	A	2500-2550	III	++	Am-C, S	-	ML 1401	e
<i>Campyloneurum vulpinum</i> (Lindm.) Ching	A	1800-2000	II	++	Am-C, S	-	FW 1025	e
<i>Microgramma percussa</i> (Cav.) de la Sota	A	1800-1900	II	++	Am-C, S	-	ML 1094	e
<i>Niphidium albopunctatissimum</i> D.B. Lellinger	A	1800-2500	II-III	++	Am-C, S	-	FW 1354	e, t
<i>Niphidium crassifolium</i> (L.) D.B. Lellinger	A	2500-2645	III	+++	Am-C, S	-	ML 1399	e, t

	Locality	Elevation (range in m)	Vegetation type	Frequency	Range	Degree of novelty	Voucher	Chorotype
<i>Pecluma divaricata</i> (E. Fourn.) Mickel & Beitel	A	1800-2000	II	++	A	-	ML 1397	e
<i>Pecluma eurybasis</i> (C.Chr.) M.G. Price, vel aff.	A	2500-2550	III	++	A	-	FW 646	e
<i>Pleopeltis fraseri</i> (Mett. ex Kuhn) A.R. Sm.	A	1800-2000	II	++	A-s	-	FW 527	e
<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.	A	2420	III	++	Am-Afr	-	ML 846	e
<i>Serpocaulon fraxinifolium</i> (Jacq.) A.R. Sm.	A	1800-2000	II	++	Am-C, S	-	FW 667	e
<i>Serpocaulon intricatum</i> (M. Kessler & A.R. Sm.) A.R. Sm.	A	1800-2000	II	++	A-s	-	FW 642	e
<i>Serpocaulon lasiopus</i> (Klotzsch) A.R. Sm.	A	1800-2000	II	++	S-AM	-	FW 1067	e
<i>Serpocaulon levigatum</i> (Cav.) A.R. Sm.	A	2420-2600	III	++	Am-C, S	-	ML 847	e
<i>Serpocaulon maritimum</i> (Hieron.) A.R. Sm.	A	1800-2000	II	++	Am-C, S	-	ML 725	e
<i>Serpocaulon ptilorhizon</i> (H. Christ) A.R. Sm.	A	2460-2640	III	+++	Am-C, S	-	ML 897	e
<i>Serpocaulon sessilifolium</i> (Desv.) A.R. Sm.	A	1800-2470	II-III	++	Am-C, S	-	ML 901	e
<i>Serpocaulon</i> sp. 1	A	2490	III	++	End	-	ML 861	e
<i>Serpocaulon</i> sp. 2	A	2550	III	++	End	-	ML 931	e
<b>Polypodiaceae (grammitids)</b>								
<i>Ceradenia cf. curvata</i> (Sw.) L.E. Bishop	A	2240	III	++	A-s	-	ML 1086	e
<i>Ceradenia glabra</i> A.R. Sm. & M. Kessler	A	2400-2600	III	++	A-s	-	ML 1495	e
<i>Ceradenia kookenamae</i> (Jenm.) L. E. Bishop, vel aff.	A	2470-2660	III	++	Am-S	-	ML 1072	e
<i>Ceradenia pilipes</i> (Hook.) L. E. Bishop	A	2480- 2660	III	++	A	-	ML 915	e
<i>Cochlidium moritzianum</i> Stolze	A	2660	III	+	Am-S	-	ML 917	e
<i>Cochlidium pumilum</i> C. Christ.	A	2480	III	+	Am-S	-	ML 881	e
<i>Cochlidium serrulatum</i> (Sw.) L.E. Bishop	A	2470-2860	III	++	Am-Afr	-	ML 870	e
<i>Enterosora parietina</i> (Klotzsch) L.E. Bishop	A	2400-2600	III	++	Am-C, S	-	ML 1379	e
<i>Grammitis bryophila</i> (Maxon) F. Seym.	A	2470-2600	III	++	A	-	ML 1382	e
<i>Lellingeria humilis</i> (Mett.) A.R. Sm. & R.C. Moran	A	2500-2660	III	++	A	-	ML 1408	e

	Locality	Elevation (range in m)	Vegetation type	Frequency	Range	Degree of novelty	Voucher	Chorotype
<i>Lellingeria major</i> (Copel.) A.R. Sm. & R.C. Moran	A	2400-2660	III	+++	A	-	ML 909	e
<i>Lellingeria myosuroides</i> (Sw.) A.R. Sm. & R.C. Moran	A	2400-2600	III	++	Am-C, A	-	ML 807	e
<i>Lellingeria phlegmaria</i> (J. Sm.) A.R. Sm. & R.C. Moran	A	1800-2000	II	++	A	-	FW 486	e
<i>Lellingeria subsessilis</i> (Baker) A.R. Sm. & R.C. Moran	A	2400-2645	III	++	A	-	ML 1499	e
<i>Melpomene firma</i> (J. Sm.) A.R. Sm. & R.C. Moran	A	2470-2650	III	+++	Am-C, S	-	ML 871	e, t
<i>Melpomene moniliformis</i> (Lagasca ex Sw.) A.R. Sm. & R. C. Moran	A	2650	III	++	Am-C, S	-	ML 1330	e, t
<i>Melpomene occidentalis</i> M. Lehnert, spec. nov. ined.	A	2320	III	++	End	-	ML 803	e
<i>Melpomene pilosissima</i> (M. Martens & Galeotti) A.R. Sm. & R.C. Moran	A	2600	III	++	Am-C, S	-	ML 984	e
<i>Melpomene pseudonutans</i> (Rosenst. & Christ) A.R. Sm. & R.C. Moran	A	2860	III	++	A-n	-	ML 808	e
<i>Melpomene sodiroi</i> (Rosenst. & H. Christ) A.R. Sm. & R.C. Moran	C, T	2975	III	++	A-n	-	ML 791	e
<i>Melpomene vernicosa</i> (Copel.) A.R. Sm. & R.C. Moran	A	2650	III	++	A-n	-	ML 1331	e, t
<i>Melpomene wolfii</i> (Hieron.) A.R. Sm. & R.C. Moran	A	1900-2980	III	+++	A-n	-	ML 958	e
<i>Melpomene xiphopteroides</i> (Liebm.) A.R. Sm. & R.C. Moran	A	2200-2490	III	++	Am-C, S	-	ML 856	e
<i>Micropolypodium blepharolepis</i> (C. Chr.) A.R. Sm.	A	2500-2600	III	++	A	-	ML 1426	e, t
<i>Micropolypodium</i> sp. 1	A	2550	III	+	End	-	ML 1419	e
<i>Micropolypodium truncicola</i> (Klotzsch) L.E. Bishop	A	2500-2600	III	++	A	-	ML 929	e
<i>Terpsichore anfractuosa</i> (Kunze ex Klotzsch) B. León & A.R. Sm.	A	2645	III	++	Am-C, S	-	ML 1035	e
<i>Terpsichore cf. subtilis</i> (Kunze ex Klotzsch) A.R. Sm.	A	2500-2660	III	++	Am-C, S	-	ML 1396	e

	Locality	Elevation (range in m)	Vegetation type	Frequency	Range	Degree of novelty	Voucher	Chorotype
<i>Terpsichore rufescens</i> M. Kessler & A. Moguel, sp. nov. ined.	A	2400-2600	III	++	A-n	-	ML 1385	e
<i>Terpsichore semihirsuta</i> (Klotzsch) A.R. Sm.	A	2500-2860	III	+++	Am-C, S	-	ML 1402	e
<i>Zygophlebia mathewsii</i> (Kunze ex Mett.) L.E. Bishop	A	2550-2640	III	++	A	-	ML 1070	e
<b>Pteridaceae</b>								
<i>Eriosorus aureonitens</i> (Hook.) Copel.	A	2500-2950	III-IV	++	A	-	ML 1358	t
<i>Eriosorus elongatus</i> (Hook. & Grev.) Copel.	A	2860	IV	++	A-s	-	ML 809	t
<i>Eriosorus flexuosus</i> (Kunth) Copel.	A	2490-2660	III	++	Am-C, S	-	ML 863	t
<i>Eriosorus orbygnianus</i> (Mett. ex Kuhn) A.F. Tryon	A	2460-2550	III	++	A	-	ML 904	t
<i>Eriosorus villosulus</i> (Maxon) Scamman, vel aff.	A	2660	III	+	Am-C, A	-	ML 905	t
<i>Jamesonia blepharum</i> A.F. Tryon	C	2900	III	++	A	-	ML 831	t
<i>Pteris muricata</i> Hook.	T	2660	III	++	Am-C, S	-	ML 1009	t
<i>Pterozonium brevifrons</i> (A.C. Sm.) D.B. Lellinger	A	1900	II	+	Am-C, S	-	ML 1435	s
<i>Polytaenium brasilianum</i> (Desv.) Benedict	A	1800-2000	II	++	Am-S	-	FW 629	e
<i>Polytaenium lineatum</i> (S.) J. Sm.	A	1800-2000	II	++	Am-C, S	-	FW 731	e
<i>Radiovittaria remota</i> (Fée) E.H. Crane	A	1950	II	++	A	-	ML 835	e
<i>Radiovittaria stipitata</i> (Kunze) E.H. Crane	A	1800-2000	II	++	Am-C, S	-	ML 1084	e
<i>Vittaria graminifolia</i> Kaulf.	A	1800-2000	II	++	Am-C, S	-	FW 1025	e
<i>Vittaria</i> sp. 1	A	1800-2000	II	++	End	-	FW 577	e
<i>Radiovittaria gardneriana</i> (Baker) C.F. Reed	A	2500-2600	II-III	+++	Am-C, S	-	ML 1391	e, t
<b>Schizeaceae</b>								
<i>Schizea elegans</i> Kaulf.	A	1800-2000	II	r	Am-S		Photo FW	t
<b>Selaginellaceae</b>								
<i>Selaginella novae-hollandiae</i> (Sw.) Spring	A	1800-2550	II	++	Am-C, S	-	ML 1092	t
<i>Selaginella</i> sp. 1	A	2650	II	+	End	-	ML 1048	t



	Locality	Elevation (range in m)	Vegetation type	Frequency	Range	Degree of novelty	Voucher	Chorotype
<b>Thelypteridaceae</b>								
<i>Macrothelypteris torresiana</i> (Gaudich.) Ching	A	1800-1900	II	++	Am-Afr	-	ML 1093	t
<i>Thelypteris brausei</i> (Hieron.) Alston	A	2500-2600	III	++	A	-	ML 1429	t
<i>Thelypteris</i> cf. <i>gardneriana</i> (Baker) C.F. Reed	A	2520	III	++	Am-S	-	ML 1058	t
<i>Thelypteris corazonensis</i> (Baker) A.R. Sm.	A	2650	III	++	A-n	-	ML 1052	t
<i>Thelypteris euchlora</i> (Sodirol) C.F. Reed	A	2645	III	++	A	-	ML 1046	t
<i>Thelypteris funckii</i> (Mett.) Alston	A	2650	III	++	Am-C, S	-	ML 1336	t
<i>Thelypteris minutula</i> C.V. Morton	A	2530-2650	III	++	End	-	ML 945	t
<i>Thelypteris pteroides</i> (Klotzsch) R.M. Tryon	A	2480	III	++	Am-C, S	-	ML 1005	t
<i>Thelypteris pusilla</i> (Mett.) Ching	A	2650	III	++	A	-	ML 1049	t
<i>Thelypteris</i> sp. 1	A	2500-2600	III	++	End	-	ML 1432	t

### II.3. Are ridge habitats special sites for endemic plants in tropical montane rain forests?

#### A case study of pteridophytes in Ecuador

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#### Abstract

**Question:** Do ridges, which are ecologically distinct from slopes, harbour specialized plant assemblages with a high representation of endemic species?

**Location:** Southeastern Ecuador.

**Methods:** We surveyed pteridophytes in 28 plots of 400 m<sup>2</sup> each in ridge and slope forests at 2430-2660 m at three different localities. Data analysis was based on those 147 species with reliable determinations and excluded 14 undetermined species. Range sizes were expressed as the latitudinal distance between the northern- and southernmost collections, and species were then assigned to range-size quartiles, with the 1<sup>st</sup> quartile including the 25% most widespread species, etc.. Differences in species richness per range size quartile were determined through G-tests and differences in the abundances through ANOVAs.

**Results:** We recorded 147 fern species represented by 92.000 individuals, including 106 terrestrial (20.000 individuals) and 98 epiphytic species (72.000). Ridges had fewer species than slopes, and there was no higher representation of localized species on ridges. Overall, widespread species were weakly ( $r^2 = 0.04$ ) but significantly more abundant than localized species. Ridges had significantly higher abundances of terrestrial – but not of epiphytic – species compared to slopes, especially among the widespread species of the 1<sup>st</sup> range size quartile.

**Conclusions:** The contribution of ridge habitats to overall pteridophyte diversity and as habitats for endemics in our study region is low. Methodologically, the application of range

quartiles to an ecological study is novel and effective, as statistically significant patterns were found only for species belonging to the 1<sup>st</sup> or 4<sup>th</sup> quartiles.

**Keywords:** Andes; Endemism; Ferns; Range size; Slopes.

## **Introduction**

Mountain forest ecosystems are characterized by a high diversity of environmental conditions and habitats. In addition to typical (zonal) vegetation on slopes of medium inclination, azonal vegetation types develop on very steep slopes, flat valley bottoms, and on ridges. The latter are usually characterized by special abiotic conditions, including higher exposure to winds, stronger fluctuations in air humidity, and often leached, acidic, and nutrient-poor soils (Hetsch & Hoheisel 1976; Grubb 1977; Tanner et al. 1998; Proctor et al. 1999; Kluge & Kessler in press). Accordingly, the vegetation on ridges is typically low-statured and open compared to adjacent slopes (Proctor et al. 1999). This difference in vegetation structure in turn influences the environmental conditions within the ridge forests, which typically have higher light availability near ground level and lower, more variable air humidity (Kluge & Kessler in press). In combination, these environmental differences determine floristic changes in the vegetation and ridge forests typically are composed of fewer species than zonal forests (Tanner 1977).

Despite these special features of tropical ridge forests, little research has so far focused on their contribution to plant diversity and even less on the representation of endemic plants in these habitats. Ridge forests are localized habitats of restricted distribution. Accordingly, species specialized to occur on ridges will have scattered populations of limited size, which can lead to population differentiation and the development of endemic taxa (Cowling et al. 1994; Brown et al. 1996; Gaston 1996; Kessler 2002 a, b). On the other hand, ridges are environmentally extreme habitats. Endemic plant species have often been considered to be competitively inferior to widespread species (Griggs 1940; Kruckeberg & Rabinovitz 1985; Major 1988; Kunin & Gaston 1993; Walck et al. 1999; Lavergne et al. 2005) and this may limit their occurrence in stressful situations. Accordingly, one may expect endemic plant species to be either especially abundant or rare on ridges.

Among pteridophytes (lycophytes and ferns), which are one of the most abundant and species-rich terrestrial and epiphytic herbaceous plant groups in tropical montane rain forests, Kessler (2001) found 10-20% lower species richness on ridges in a very wet montane region of central Bolivia, and very few species restricted to ridge forests. However, epiphytic ferns on ridges on average had smaller range sizes, i.e., higher levels of endemism, than in adjacent slope forests. Among terrestrials, the opposite pattern was found. This suggests that at least for epiphytic pteridophytes, ridge forests are an important habitat for endemic species. A more

recent study by Kluge & Kessler (in press) on the Caribbean slope of Costa Rica found a similar decrease of species richness on ridges and few species restricted to them, but the proportion of endemics remained constant relative to slope forests. These inconsistent results, with high endemism of epiphytes at one site and average endemism at the other, call for additional studies on this topic. In the present study, we analyzed patterns of fern richness and endemism at three montane forest sites in southeastern Ecuador. This area is particularly suitable for this kind of studies because the region is well-known for its high levels of biological endemism (Lozano et al. 2003) and the presence of extensive areas of stunted ridge forests (Gradstein et al. submitted manuscript).

## **Material and methods**

### **Study sites**

We studied upper montane ridge and slope forests in three different localities: Reserva Biológica San Francisco (RBSF), below the mountain pass El Tiro, and Cerro Tapichalaca Reserve (Fig. 1). Ranging between 1800 m and 3140 m, RBSF preserves some one thousand hectare of humid evergreen mountain rainforests and páramo vegetation (Beck & Müller-Hohenstein 2001). The high relief energy with steep and instable slopes, causing frequent occurrence of landslides, is a characteristic feature of the reserve. Geologically the area is made up of Paleozoic, weakly metamorphic rocks consisting of meta-siltstones, sandstones, and phyllites with some quartz veins, dated of Devonian-Permian age (Litherland et al. 1994). Consequently, soils are poor in nutrients (Wilcke et al. 2001). Towards higher elevations soils become less well developed, accumulation of organic material increases, and hygrophytic soil properties become prominent (Schumpf et al. 2001).

Mountain pass El Tiro (79°08'W, 03°59'S) is situated at ca. 2800 m along the Loja-Zamora road, 15 km W of the RBSF and on the border of Loja and Zamora-Chinipe provinces, on the crest of the cordillera. The pass separates the dry interandean Rio Zamora valley from the humid Rio San Francisco Valley leading towards the Amazonian lowland. Our study site was located some 200-450 m below the actual pass towards the east, in an area of very rugged topography with many small ravines and ridges overgrown by low-statured, shrubby cloud forest. Rocks at El Tiro belong to the same geological formation as in RBSF.

Cerro Tapichalaca Reserve (79°07'W, 04°29'S) is situated at ca. 2000-3400 m along the Loja-Zumba road in the Cordillera Real, ca. 90 km S of the town of Loja and just S of

Podocarpus National Park (Fig. 1). The area separates the dry interandean Río Solano valley from the wet Río Mayo valley oriented towards the Amazonian lowland and is made up of very wet montane cloud forest and páramo (Simpson 2004). Geologically, the Tapichalaca Reserve is made up of Mesozoic ortho-gneisses of late Triassic age (Litherland et al. 1994).

### **Field methods**

We established 28 plots of 20 m x 20 m in size or an equivalent of 400 m<sup>2</sup> if the terrain did not allow square plots to maintain a homogeneous forest structure, especially on narrow ridges. Pteridophytes were recorded as distinguishable morphospecies in the field. Abundance and life form (epiphyte, terrestrial and saxicolous) were noted for all species in each plot. Each fertile or fully grown plant was counted as one individual; in species with long creeping, branched rhizomes, each terminal bud that fronds had as nearly equal in size to those of the largest bud was counted as separate plant (*Sticherus*, *Elaphoglossum*); in *Hymenophyllum*, each leaf was counted as one plant, even though many presumably belonged to single, extensive clones. At least one voucher per morphospecies was collected and dried for later identification. Duplicates are deposited in herbaria in the following priority: QCA, UC, LOJA, GOET, AAU, and the herbarium at the Estación Científica San Francisco (ECSF); one set of *Elaphoglossum* specimens was sent to NY, one set of *Polystichum* is at VT. Determinations were done largely by ML at the Herbarium AAU (Apr 2004, Feb 2005); complicated groups were dealt with by specialists.

### **Data analysis**

For the data analysis we only considered those 147 species with reliable determinations and excluded those 14 species for which no names and hence no range sizes could be obtained. Range sizes for each species were expressed as the latitudinal distance between the northern- and southernmost collections, based on the holdings of the herbaria LPB, MO, NY, QCA, UC, and US as well as relevant literature, especially Tryon & Stolze (1989-1994), Moran & Riba (1995), Mickel & Smith (2004), and Kessler & Smith (in prep.). Because all our study species are montane, and because the Andes and Mesoamerican mountain ranges extend from north to south, latitudinal range is a good measure of overall range size (Kessler 2002a). Species were then assigned to range-size quartiles, with the 1<sup>st</sup> quartile including the 25% most widespread

species (latitudinal ranges 35-53 degrees), the 2<sup>nd</sup> with species with ranges of 26-33 degrees, the 3<sup>rd</sup> with species with ranges of 14-25 degrees, and the 4<sup>th</sup> with species with ranges of 1-13 degrees.

Abundance of each species was calculated as the mean number of individuals per plot for each species. Because the abundance distribution was extremely uneven, with 6.8% of the species accounting for 77% of all individuals, the abundance distributions were expressed as the abundance rank order. In this way, the abundance data approached normality and was tractable by parametric statistics. Differences in species richness per range size quartile were determined through G-tests, and differences in the abundances of the species numbers in the range size quartiles through ANOVAs. All statistical analyses were carried out with Systat 11.

## Results

In total, we recorded 147 fern species represented by ca. 92.000 individuals. Among these, 106 species with ca. 20.000 individuals grew terrestrially and 98 species with ca. 72.000 individuals epiphytically. Accordingly, 57 species were found to be both terrestrials and epiphytes. At the different study sites, we found 96 species at the RBSF (46 on ridges, 75 on slopes), 89 at El Tiro (42 on ridges, 85 on slopes), and 97 species at Tapichalaca (54 on ridges, 85 on slopes). The numbers of individuals per species were highly unevenly distributed (Fig. 2a). The filmy fern *Hymenophyllum fucoides* had the highest number, with ca. 14,400 individuals, followed by nine other *Hymenophyllum* species with ca. 11,800-1327 individuals. The most abundant non-filmy fern was *Melpomene wolfii* (Polypodiaceae) with 1285 individuals. At the opposite end of the scale, eight species were only represented by a single individual, four species by two individuals, and eight species by three individuals.

Latitudinal range sizes showed a more gradual distribution (Fig. 2b). Two species of *Asplenium*, *A. serra* and *A. auriculatum*, had the widest ranges, covering 53 and 52 degrees, respectively, followed by *Hymenophyllum polyanthos* with 50 degrees. In contrast, 14 species were localized endemics with ranges of only 1 degree, and a further 9 species had ranges spanning 2-7 degrees.

Looking at species richness per range-size-quartile at the three study sites, the 4<sup>th</sup> quartile had somewhat fewer species per site than the other three quartiles, but this difference was not significant at any site (G-tests; RBSF:  $G = 1.69$ ,  $P = 0.65$ ; El Tiro:  $G = 3.55$ ,  $P = 0.35$ ; Tapichalaca:  $G = 1.58$ ,  $P = 0.67$ ) (Fig. 3). However, Tapichalaca had significantly more species in the 1<sup>st</sup> quartile than in the other quartiles (G-test,  $G = 7.93$ ,  $P = 0.046$ ). It also had

more species in the 1<sup>st</sup> quartile than that quartile had at either the RBSF (G-test,  $G = 9.63$ ,  $P = 0.03$ ) or El Tiro (G-test,  $G = 7.32$ ,  $P = 0.052$ ), whereas there was no significant difference between the RBSF and El Tiro (G-test,  $G = 0.86$ ,  $P = 0.71$ ). This difference was not so evident when terrestrial and epiphytic species were analyzed separately, with the P-values of comparisons between Tapichalaca on the one hand and the RBSF and El Tiro on the other ranging between 0.17 and 0.27 (G-tests).

Comparing the species richness of the four range size classes on ridges versus slopes showed that ridges had fewer species than slopes. However, these differences were not significant neither for all sites combined (G-tests; all species:  $G = 4.08$ ,  $P = 0.29$ ; epiphytes:  $G = 2.74$ ,  $P = 0.42$ ; terrestrials:  $G = 3.95$ ,  $P = 0.31$ ) nor when sites were analyzed separately, except at El Tiro, where ridges had significantly fewer species than slopes in both the 1<sup>st</sup> and 4<sup>th</sup> quartiles (G-test,  $G = 12.52$ ,  $P = 0.008$ ) (Fig. 3).

Comparing the species richness of the range size classes between terrestrial and epiphytic species revealed no significant differences neither across all sites and habitats (G-Test;  $G = 0.86$ ,  $P = 0.71$ ) nor separately for sites and/or habitats (individual results not shown).

Turning towards the abundance of the species, latitudinal range size only explained 4.1% of the variance of ranked species abundance (linear regression,  $R^2 = 0.041$ ,  $P = 0.014$ ). However, the narrow-ranged species of the 1<sup>st</sup> quartile had significantly lower abundances than the other three quartiles (two-way two-tailed ANOVA,  $F_{3,147} = 4.159$ ,  $P = 0.007$ ), although the trend was rather weak (Fig. 4). This trend was based mainly on the epiphytic taxa (two-way two-tailed ANOVA,  $F_{3,98} = 6.373$ ,  $P = 0.001$ ) and less so on the terrestrial ones (two-way two-tailed ANOVA,  $F_{3,106} = 2.655$ ,  $P = 0.056$ ).

The distribution of ranked abundance among the four range size classes did not differ between epiphytic and terrestrial species (two-way two-tailed ANOVA,  $F_{1,198} = 0.920$ ,  $P = 0.34$ ). Comparing the three study sites, there were no significant differences in the abundances of species per quartile neither for all species (two-way two-tailed ANOVA,  $F_{2,296} = 0.729$ ,  $P = 0.62$ ) nor terrestrial (two-way two-tailed ANOVA,  $F_{2,177} = 1.458$ ,  $P = 0.24$ ) or epiphytic species (two-way two-tailed ANOVA,  $F_{2,166} = 0.146$ ,  $P = 0.86$ ).

Comparing ridges and slopes, ridges generally had much higher species abundances than slopes among terrestrial species (two-way two-tailed ANOVA,  $F_{1,170} = 10.038$ ,  $P = 0.002$ ) but not among epiphytic species (two-way two-tailed ANOVA,  $F_{1,182} = 0.636$ ,  $P = 0.43$ ). All species combined hinted on the pattern of the terrestrial species, but not



significantly so (two-way two-tailed ANOVA,  $F_{1,147} = 1.403$ ,  $P = 0.24$ ), certainly due to the leveling effect of the epiphytic species. However, there were no significant differences between the range size quartiles within any given habitat, neither for all species combined (two-way two-tailed ANOVA,  $F_{1,147} = 1.161$ ,  $P = 0.33$ ), nor for terrestrials (two-way two-tailed ANOVA,  $F_{1,70} = 2.200$ ,  $P = 0.09$ ) or epiphytes (two-way two-tailed ANOVA,  $F_{1,82} = 0.245$ ,  $P = 0.87$ ) analyzed separately. Interactions between quartiles and habitat were not significant either (data not shown). However, when the sites were analyzed separately, terrestrial species of the 1<sup>st</sup> quartile were significantly less abundant on slopes compared to ridges at all three sites (two-way two-tailed ANOVAs; RBSF:  $F_{3,50} = 2.783$ ,  $P = 0.044$ ; El Tiro:  $F_{3,61} = 2.830$ ,  $P = 0.045$ ; Tapichalaca:  $F_{3,66} = 2.953$ ,  $P = 0.038$ ) (Fig. 5). We could not detect any taxonomic or ecological difference between the narrow-ranged terrestrial species on ridges compared to those on slopes, with tree ferns and various Polypodiaceae being the dominant taxa in all cases.

## Discussion

The starting point of our study was the question whether ridge habitats, with their strikingly different environmental conditions, harbored specialized pteridophyte assemblages with an overrepresentation of species with restricted ranges. We found that ridges in the area of the Podocarpus National Park had fewer species than slopes (Fig. 3) and that this reduction of species richness affected species belonging to all four range size quartiles in a similar way. Our study therefore confirms the pattern found by Kluge & Kessler (in press) in Costa Rica, and contrasts with the observations of Kessler (2001) who found a relatively higher representation of endemic pteridophytes on ridges compared to adjacent slopes in Bolivia. The latter pattern was also documented on Cordillera Mosestenes in Bolivia, where range sizes of pteridophytes on ridges at 1500-1600 m averaged ca. 25% smaller than in adjacent slope forests at 1400-1500 m (M. Kessler, I. Jimenez & T. Krömer, unpubl. data). Apparently, ridge habitats are more suitable for range-restricted pteridophyte species in some situations, whereas in others this is not the case. Whether this discrepancy is a regional phenomenon or whether it varies on a more local basis cannot yet be answered with the geographically limited data at hand. Importantly, however, none of the four studies found a lower representation of endemics on ridges, showing that the stressful abiotic conditions on ridges do not affect range-restricted species more strongly than widespread taxa.

Turning towards the abundances of species, ridges had significantly higher abundances of terrestrial species compared to slopes, certainly as a result of the low, open canopy structure that allows high light levels to reach the ground level, leading to the development of a dense herbaceous layer in which pteridophytes feature prominently. In contrast, the tall, dark slope forests have a sparse herb layer with scattered pteridophyte individuals. Interestingly, this effect appeared to be most pronounced among the widespread species of the 1<sup>st</sup> quartile, indicating that they were most sensitive to the ecological differences between slopes and ridges. Alternatively, one may argue that terrestrial species with restricted ranges (4<sup>th</sup> quartile) were less abundant on slopes than more widespread species. The positive relationship of range size and local abundance is a common pattern in macroecology (Gaston et al. 1997, 1998), although it is often rather weak (Gaston 1996), as also found by us. In our case this pattern was mainly due to the low abundances of narrow-ranged species on slope habitats. Endemic plant species have often been considered to be competitively inferior to widespread taxa (Griggs 1940; Kruckeberg & Rabinovitz 1985; Major 1988; Kunin & Gaston 1993; Walck et al. 1999; Lavergne et al. 2005) and it has been argued that this low competitive ability might be one of the reasons limiting their capability of establishing new populations beyond their existing ranges, thereby limiting their range sizes (Kessler 2002 a, b). If this reasoning is followed, then a paradoxical situation emerges for the evaluation of the stressfulness of ridge habitats: on the one hand they harbor fewer species suggesting that they are abiotically stressful habitats, on the other hand they have a higher abundance of terrestrial species, especially presumably competitively inferior species with restricted ranges, suggesting that they are biotically less stressful habitats. Apparently, abiotic stress influences the species richness and the abundance of species in different ways.

Contrary to terrestrial species, epiphytes did not show differences in abundances between slopes and ridges, probably due to the greater ecological similarity of the canopy habitat between ridges and slopes relative to the terrestrial environment.

In conclusion, pteridophyte assemblages on ridges in our study area had a higher abundance of terrestrial species, especially those with restricted ranges, and with no conspicuous differences at the level of epiphytes. Accordingly, the contribution of ridge habitats to overall pteridophyte diversity in a given region such as the Podocarpus National Park is low. The major contribution, if any, might be that some range-restricted species have their main populations on ridges, even if they also occur on slopes. Conceivably, the latter populations might not be self-sustaining, but represent sink populations dependent on ridge

populations for continued survival. The documentation of such source-sink relationships requires detailed, long-term data on population dynamics greatly exceeding the possibilities of a study like ours (Eriksson 1996).

A final, striking pattern was that at Tapichalaca the 1<sup>st</sup> quartile was significantly more species rich than the other quartiles as well as the 1<sup>st</sup> quartile at the other two study sites. A possible interpretation of this pattern involves the degree of human influence at the three study localities. Tapichalaca appears to have been subject to stronger human disturbance than the other two sites (pers. obs.). It is a young reserve established in 2001 and was acquired from local farmers who selectively logged the forest in the past. It borders directly to long-used farmland and meadows so there is still some impact of straying cattle in the reserve itself and some of our study plots that were placed close to the forest margin showed influence of cattle and logging. Widespread plant species are known to often fare better in strongly disturbed ecosystems than endemics (Brown 1984) and this may have caused the observed increase in species number and abundance compared to undisturbed forests and ridges, where human impact is generally lower.

Concluding with a methodological comment, this is only the second ecological study using range quartiles at the local scale to apply the subdivision of range-sizes of species within assemblages, compared to the regional to global scale at which this approach has previously been used (e.g., Jetz & Rahbek 2002, Kreft et al. 2006). Our results show that this approach can be successfully applied to the local scale and that relative to previous methods, where range-size measures were applied across all species, e.g., by averaging their range sizes (Usher 1996, Kessler 2002a, b), the distinction between the quartiles provides more detailed information. In our study, statistically significant patterns were found only for species belonging to the 1<sup>st</sup> or 4<sup>th</sup> quartiles, suggesting that the half of all species with intermediate range sizes are not strongly affected by the studied habitat conditions, and that only the species with the most extreme ranges, be it large or small, show detectable patterns.

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### Figure captions

Fig. 1: Map of the study region showing the location of the study sites.

Fig. 2. Rank-abundance (a) and rank-range size (b) plots for all 147 species included in this study. The stippled lines denote the range size quartiles.

Fig. 3. Species richness per range size quartile and habitat (a = all; r = ridges; s = slopes) for three study sites.

Fig. 4. Ranked species abundance per range size quartile among all 147 species included in this study.

Fig. 5. Relative species abundances per quartile comparing ridge habitats (left box for each quartile) and slope habitats (right boxes). In order to exclude the overall differences in abundances between ridge and slope habitats, for this graph the abundances among each habitat type were relativized, with 100% corresponding to the mean value within each habitat.

Fig. 1.

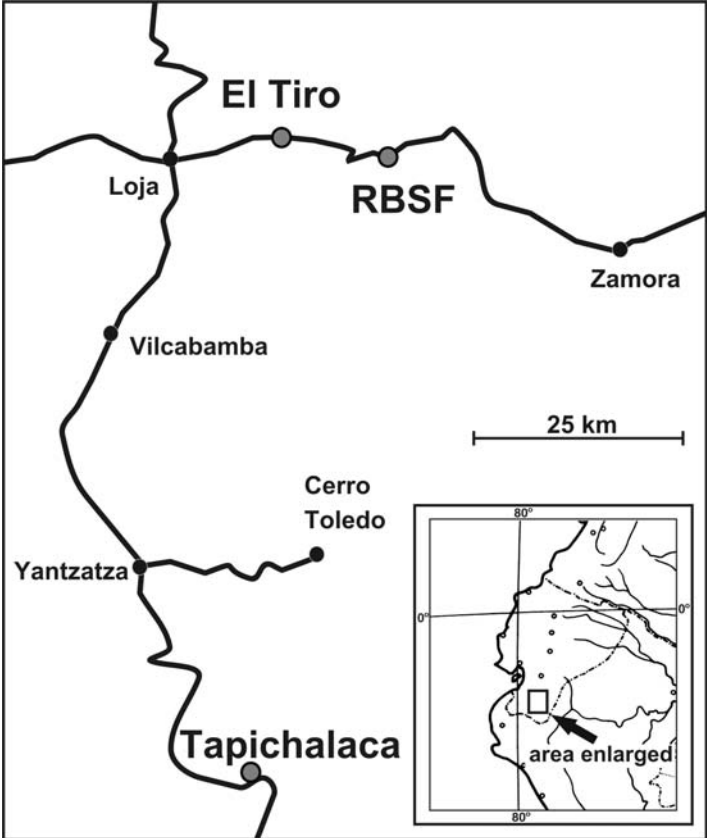




Fig. 2.

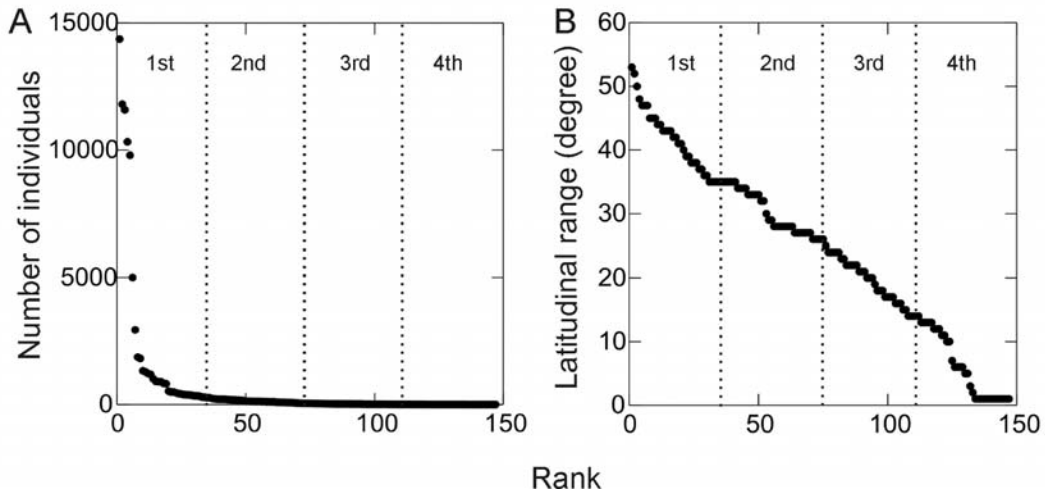


Fig. 3.

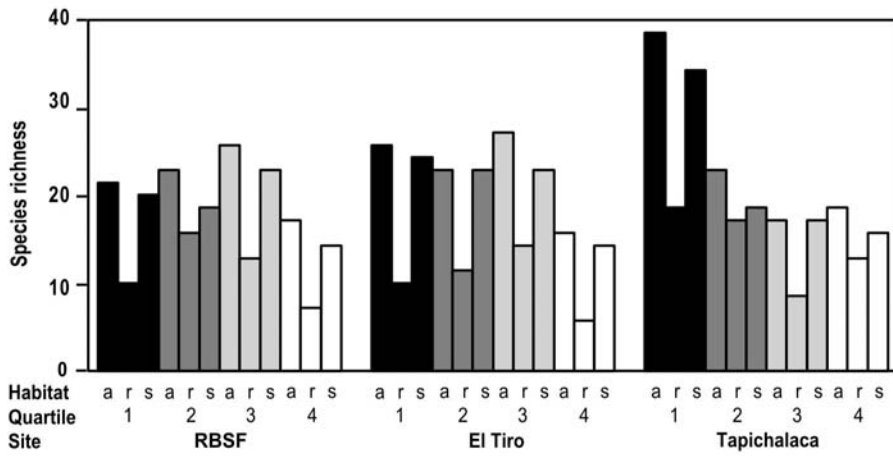
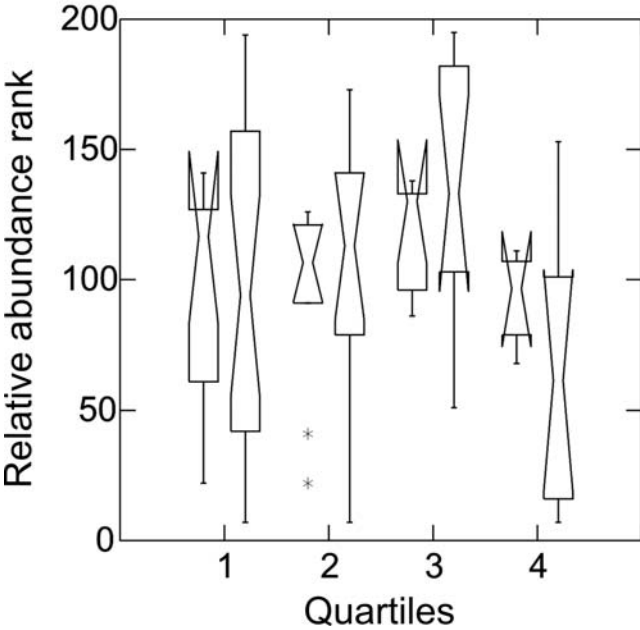


Fig. 4.



Fig. 5.



#### **II.4. Comparative analysis of vegetation zonation in four neotropical fern communities**

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Abstract. - The many existing schemes of altitudinal vegetation zonation are heterogenic and only partly comparable because of local peculiarities of the individual study sites. Most impact has the size of the mountain or mountain range because different height and mass lead to different heat capacities, wind speeds, and condensation levels. These factors result in the well-known “Massenerhebungseffekt,” which describes the upward shift of isotherms on higher mountains compared to lower mountains. Consequently, plants with certain demands to the temperature should follow these isotherms in their elevational distribution. The Huancabamba depression in southern Ecuador and northern Peru is a small stretch of relatively low elevation between the northern and central Andes with apparent floristic peculiarities (low treeline, lack of true páramo vegetation, absence of the genus *Polylepis*). We wanted to test if the vegetation zones in the Huancabamba depression have experienced a downshift compared to the adjacent parts of the Andes, or if the present plant composition is the same found elsewhere in the Andes at that elevation but distorted in its general aspect. Thus we conducted a comparative analysis of the upper elevational distribution limits of pteridophytes along transects in the Huancabamba depression (Reserva Biológica San

Francisco, Ecuador, Prov. Zamora-Chinchiipe) and other parts of the Neotropics (Costa Rica, Peru, and Bolivia). The 114 species of ferns and lycophytes included in our analysis showed a significant downshift of their upper elevational limit at the RBSF compared to the other Andean study sites, but had the same limits as in the transect in Costa Rica, which had the same maximum elevational extension.

Key words: altitudinal zonation, Amotape-Hancabamba zone, Andes, Ecuador, elevation, isotherm, pteridophytes.

### Introduction

The first scheme of vegetation zones dates back to von Humboldt (1807). His famous illustration of the Ecuadorian Andes has been an inspiration to many scientist to find a universal formula that describes the recurrent patterns of vegetation change with elevation in the tropics and worldwide. Until today, however, consent has not been found because nearly every study came to different results (Frahm & Gradstein, 1987), caused by regional peculiarities in topography and species composition.

A phenomenon already observed by von Humboldt is the “Massenerhebungseffekt,” which describes the upward shift of vegetation zones on larger mountain compared to smaller mountains at the same latitude. The vertical limits of the plants follow in this case the isothermes on the mountains (Troll, 1948; Hooghiemstra & van der Hammen, 2004); the temperature in turn is conditioned by the mass of the mountain, cooling wind effects, and adiabatic phenomena (Barry, 1981; Körner, 1999; Jiang, 2003). The latter accounts for fog belts that may moderate sun exposure and albedo (Killeen et al., 2007). The “Massenerhebungseffekt” has always been applied to isolated mountains or to whole ranges in a uniform way (Grubb, 1971). Little has been looked at the rugged orography of a mountain chain. It seems plausible that we should observe a “Massenerhebungseffekt” at higher, exposed peaks and at depressions in otherwise evenly high ranges. Again the Andes are a perfect model for testing such a hypothesis.

The Andean range is roughly divided into a northern, central, and southern aprt. While the transition between southern and central Andes is marked by the Andean deflection in an area of relatively even topography (Killeen et al., 2007), the northern Andes are separated from the central Andes by the Amotape-Huancabamba-depression (Molau, 1988; Lunde & Pacheco, 2003) in northern Peru and southern Ecuador. This area stands out as the lowest and narrowest stretch of the Andes and shows peculiarities in climate, soil, and wildlife.

The tree line itself is lowered compared to the average in the Andes (pers. obs.; Troll, 1948), and according to the abovementioned effects, the ridges already support a treeless, páramo-like vegetation at 2800-3000 but with some important elements lacking. Most strikingly, this region is devoid of *Polylepis* (Rosaceae; Kessler, 1995), a genus of small trees that usually form the forests bordering the tree line in the Andes. In most classifications, the treeless vegetation on the mountaintops in the Amotape-Huancabamba-zone is not considered as real páramos (Luteyn, 1999). The question arises if it is really assignable to a vegetation zone that has been downshifted in the depression (i.e., the páramo zone), or if it is more comparable to the plant communities elsewhere in the Andes at the same elevation (i.e.,

mountain rain forest), except for some distortion in the general aspect by local climate and/or soils. The easiest way of answering this question is by comparing the elevational distribution limits of the different populations of species occurring in the depression and on the adjacent mountain ranges.

It has to be pointed out here that the Amotape-Huancabamba-zone has a high percentage of endemism in plants and animals alike (Weigend, 2002; Lunde & Pacheco, 2003). Therefore, we have chosen the pteridophytes (i.e., lycophytes and ferns, sensu Smith et al., 2006) as example plant group because they show a lower rate of endemism due to their easy dispersal by small spores (Smith, 1971; Barrington, 1993; Wolf et al., 2002). A plethora of fern species, with little morphological variation throughout their range and thus confidently identifiable, can be found from Costa Rica to Bolivia. Furthermore, ferns do not rely on animals for fertilization and dispersal as many angiosperms do. Their occurrence in a given area may thus give direct evidence about the prevalent abiotic factors (temperature, humidity, fog frequency).

### **Study areas**

Our primary focus lays on the Reserva Biológica San Francisco (RBSF) between the towns of Loja (Prov. Loja) and Zamora (Prov. Zamora-Chinchipe) in southern Ecuador, Prov. Zamora-Chinchipe, which is situated in the northern half of the Amotape-Huancabamba zone (3°58'S, 79°04'W). A checklist to the pteridophytes of the reserve was compiled in the course of our studies (Lehnert et al., submitted manuscript). The RBSF is a private reserve encompassing 1000 ha of largely undisturbed montane rainforest at 1800-3150 m situated on the southern slopes of the Río San Francisco valley. For comparison, we chose three neotropical areas for which floristic studies are available: the Braulio Carrillo National Park in Costa Rica (in the following abbreviated as CR; Kluge & Kessler, 2006; Kluge et al., 2006); the Río Abiseo National Park in Peru (PE; Young & León, 1990, 1991); and the transects in the Carrasco National Park, Dept. Cochabamba (Kessler et al., 1999) and the Cotapata National Park, Dept. La Paz in central Bolivia (Bach, 2004). The Bolivian study sites (BO) were combined because of their spatial proximity.

The climate at all study sites can be characterized as tropical and perhumid. The exposure of the studied areas is more or less east-facing, so that they receive the full impact of the westbound trade winds (Killeen et al., 2007). The mean annual precipitation in the Braulio Carrillo National Park is constantly above 3000 mm/a at 30-2600 m with a maximum of 5000 mm/a at 1000 m (Watkins et al., 2006). The RBSF receives even more rain

(Rollenbeck, 2006; Gradstein et al., submitted manuscript). The large distance to the equator of the Bolivian study sites leads to a stronger seasonality of the climate than at the other three study sites (Troll, 1948), but resulting only in a relative dry season from April to September (Schawe, 2005). The mean annual precipitation is still high, ranging from 2310 mm/a at 1850 m to 5150 mm/a at 3050 m at the Cotapata National Park (Schawe, 2005). We lack reliable climate data for the Río Abiseo National Park, Peru.

### **Material and Methods**

We compared the elevational distribution of the shared pteridophyte species of the four study areas. The upper elevational distribution limits of all involved species (114) (Tab. 1) were compared between the study areas as follows (shared species in brackets): EC/PE/BO (27); EC/CR (66), EC/PE (44), EC/BO (90). A comparison of all four study areas together was omitted because the number of commonly shared species was too low. The differences were ranked and tested using the Wilcoxon's test in SYSTAT 7.0.

Climate data including mean annual air temperature and precipitation were obtained for Bolivia from Bach (2004) and Schawe (2005), for Ecuador from Rollenbeck (2006) and Gradstein et al. (in prep.), and for Costa Rica from Kluge (2006). Corresponding data were not available for the Río Abiseo National Park, Peru; mean annual temperature was estimated here from available soil temperature measurements (Ken Young, unpubl. data). Additional information about the temperatures along our latitudinal gradient was taken from literature (Hooghiemstra & van der Hammen, 2004). The altitudinal temperature gradient was interpolated with an averaged increment of 0.6°C/100 m (Bruenig, 1989; Schawe, 2005).

Information about the altitudinal maxima of the Andes and the forest limits bases on Kessler (1995, 2000; pers. obs.).

### **Results**

The comparison of the Andean study sites (EC, PE, BO) revealed that the upper elevational limit of the shared species is significantly lower in Ecuador (Tab. 2), where the species reach up to 2542 m in average compared to 3274 m in Peru and 2884 m in Bolivia. If compared pair wise, the pattern stays the same (Tab. 3); the mean upper elevational limits are comparable (Ecuador, 2495 m; Peru, 3281 m) or even identical (Bolivia, 2884 m). The significance in each case is high (Wilcoxon's test,  $p < 0.01$ ). The upper limit follows roughly the course of the treeline in the latitudinal gradient (Fig. 3); the already considerable distance of Bolivia from the equator, which leads to the onset of general latitudinal effects (Troll, 1948), may cause the

lower values. In the transect in Costa Rica, however, the ferns show an almost identical upper limit (2494 m) to the Ecuadorian site. Both areas have the same maximum in elevation. Information about the lower elevational limit of the investigated species was not available from the studies. At all upper elevational limits, the same mean annual temperature of 11.0-11.5° C was recorded (Tab. 2; Fig. 4).

### Discussion

The pteridophyte species seem to be restricted in their elevational distribution by temperature. At least the upper elevational limit follows roughly the 11°C isotherm. Since we lack confident data about the lower limits of the pteridophyte species, we cannot conclude that the whole vegetation zone is shifted downwards, or that the zones below and above act the same way. However, there are indications supporting these assumptions. In other Andean gradients, the transition from species-rich upper montane forest to species-poor forests dominated by *Polylepis* (Kessler, 2000), corresponding with the timberline ecotone sensu Körner & Paulsen (2004), was marked by high species turnover at 3400-3600 m. At the study site in the Río San Francisco valley, we observed a similar transition from montane forest to shrubby páramos at 2800-2900 m (annual mean temperature 9.8°C; Gradstein et al., submitted manuscript).

The Ecuadorian study site at the RBSF clearly shows a lowering of the 11°C isotherm and the upper elevational limit of pteridophytes compared to elsewhere in the Andes, which may be response to the “Massenerhebungseffekt”. The question remains why this part of the Andes acts like a single mountain range of the comparable elevation (like in Costa Rica) and not like a foothill range elsewhere in the Andes.

Topographically, the Andes have the smallest volume at our Ecuadorian study site. Here, the narrowest and lowest spot in the Cordillera functions as an outlet for the trade winds coming from the east. The frequent winds have a cooling effect; the moisture they carry with them condenses as long persisting fogs (Killeen et al., 2007).

Searching for an explanation for the Massenerhebungseffekt in tropical mountains, Grubb (1971) excluded a response to temperature because there is no greater lapse in smaller mountains. This may be true, but more important is the starting point of the temperature gradient at the mountain base, which can be a different temperature. The comparison of a temperature gradient in Costa Rica (Kluge et al., 2006) with the data presented by Hooghiemstra and van der Hammen (2004) for southern Colombia shows that the lapse rate is the same in both regions (0.6°C/100 m), but the mean temperature at sea level in Costa Rica is 5°C lower than that in Colombia (25°C vs. 30°C). By this way, the same mean annual



temperature that marks the change from Andean forest to treeless páramo is reached at 500 m higher in Colombia than in southern Ecuador. Temperature is a determining factor, as has often been assumed (Körner, 1999; Körner & Paulsen, 2004).

Factors like the frequency and intensity of clouds and fog at the observed upper limits apparently do not influence the observed “Massenerhebungseffekt” significantly. A discrete and spatially limited belt of constant fog and clouds may shelter from the sun and prevent the regular heating occurring above and below the belt (Körner, 1999). The cooling effect should lead to a dent or curve in the otherwise linear temperature gradient, but this is not the case (Bruenig, 1989; Kluge et al., 2006). If cooling occurs, then other effects caused by the cloud belt, e.g., protection against heat loss (albedo), equalize it (Körner, 1999).

The available data on fog and cloud frequency at our study sites is incomplete, but shows a weak correlation with the distribution of the investigated ferns. In the RBSF (EC), highest cloud frequency is observed between 2500 m and 3400 m, coinciding with the upper distributional limit of pteridophytes (2495 m). However, the highest observed fog frequency of about 80 % is found at a much higher elevation of 3200 m (Rollenbeck, 2006). Young & León (1991) report the highest fog frequency from the Río Abiseo National Park starting from 3100 m, which roughly correlates with the observed upper limit at 3285 m. Apparently cloud and fog belts underlie the same temperature regulations (Körner, 1999) as the elevational distribution of ferns and lycophytes, but have no impact on the “Massenerhebungseffekt.”

### Conclusions

The upper elevational limit of pteridophytes is lowered in southern Ecuador. The area, which is part of a continuous mountain range, acts like an isolated mountain of the same elevation („Massenerhebungseffekt“). Since we lack sufficient data on the lower elevational distribution limit of the studied species, we are currently not in the position to postulate that the whole vegetation zones have experienced a downshift in the Amotape-Huancabamba zone. We aim to fill this gap in the future, and to broaden our database regarding transect number, climate data, and ecological information. Nonetheless, our preliminary results indicate that a universal altitudinal zonation scheme is preferably designed on a relative scale and not related to fixed elevations.

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### Figure captions

Tab. 1. List of all species shared between the RBSF (EC) and at least one comparative study site (EC, PE, BO); the known upper elevational limit (m) at each site is given.

Tab. 2. Comparison of the upper elevational limits commonly shared between three Andean study sites (EC, PE, BO).

Tab. 3. Pairwise comparison of the upper elevational limits of the shared pteridophyte species between the four study sites (CR, EC, PE, BO).

Fig. 1. Map of northwestern South America showing the four study sites in Costa Rica (CR), Ecuador (EC), Peru (PE), and Bolivia (BO).

Fig. 3. Diagram showing highest peaks and forest limit from Costa Rica (ca. 8°N, right) to northern Argentina (22°S, left). Upper elevational limits of pteridophytes marked with “x” with mean deviation for study sites in Bolivia (BO), Peru (PE), Ecuador (EC), and Costa Rica (CR).

Fig. 4. Diagram showing highest peaks, forest limit, and 11°C isotherm from Costa Rica (ca. 8°N, right) to northern Argentina (22°S, left). “x” marks upper elevational limits of pteridophytes for study sites in Bolivia (BO), Peru (PE), Ecuador (EC), and Costa Rica (CR), and additional information of mean annual temperature for Colombia (CO) taken from Hooghiemstra and van der Hammen (2004).

Fig. 5. Map showing detail of the Huancabamba-Amotape region (altered from Lunde & Pacheco, 2003). Predominant winds indicated with arrows, showing easy passage across the Andes near study area (square).

Tab. 1. List of all species shared between the RBSF (EC) and at least one comparative study site with upper elevational limits (m).

Species	substrate	upper elevational limit (m)			
		EC	CR	PE	BO
<i>Alsophila erinacea</i> (Karst.) Conant	terrestrial	2050	1800		2300
<i>Arachniodes denticulata</i> (Sw.) Ching	terrestrial	2600	3200		2950
<i>Asplenium alatum</i> Willd.	terrestrial	2050	3000		1800
<i>Asplenium auritum</i> Sw.	terrestrial	2660	1700		2750
<i>Asplenium cristatum</i> Lam.	terrestrial	2000		3200	
<i>Asplenium cuspidatum</i> Lam.	terrestrial	2660	2700	3450	2000
<i>Asplenium harpeodes</i> Kunze	terrestrial	2000	3000	3200	
<i>Asplenium hastatum</i> Klotzsch ex Kunze	terrestrial	2550	2800	3100	
<i>Asplenium serra</i> Langsd. & Fisch.	epiphytic	2550	3200	3300	3075
<i>Asplenium tricholepis</i> Rosenst.	terrestrial	2000			1975
<i>Blechnum acutum</i> (Desv.) Mett.	terrestrial	2000			1920
<i>Blechnum cordatum</i> (Desv.) Hieron.	terrestrial	2600		3500	2620
<i>Blechnum divergens</i> (Kze.) Mett.	terrestrial	2640	2700		3250
<i>Blechnum ensiforme</i> (Liebm.) C. Chr.	epiphytic	2530	2400		2550
<i>Blechnum fragile</i> (Liebm.) Morton & Lellinger	epiphytic	2640	2000		3400
<i>Blechnum schomburgkii</i> (Klotzsch) C. Chr.	terrestrial	2600		2750	
<i>Blotiella lindeniana</i> (Hook.) R.M. Tryon	terrestrial	2200	1700		2200
<i>Botrychium virginianum</i> (L.) Sw.	terrestrial	3000	3000	3450	
<i>Campyloneurum angustifolium</i> (Sw.) Fée	epiphytic	2000	3200	2700	1300
<i>Campyloneurum vulpinum</i> (Lindm.) Ching	epiphytic	2000			1800
<i>C. angustipaleatum</i> (Alston) M. Meyer ex D. B. Lellinger	epiphytic	2000			2000
<i>Ceradenia curvata</i> (Sw.) L.E. Bishop	epiphytic	2240			2600
<i>Ceradenia pilipes</i> (Hook.) L.E. Bishop	epiphytic	2660	2800		
<i>Cheiroglossa palmata</i> (L.) C. Presl	epiphytic	2000			2500
<i>Cochlidium serrulatum</i> (Sw.) L.E. Bishop	epiphytic	2860	2700		2100
<i>Culcita coniifolia</i> (Hook.) Maxon	terrestrial	2900	3200	3300	3075
<i>Cyathea atahuallpa</i> (R.M. Tryon) Lellinger	terrestrial	2730		3450	
<i>Cyathea bipinnatifida</i> (Baker) Domin	terrestrial	2550			2550
<i>Cyathea parvifolia</i> Sodiro	terrestrial	3050			3000
<i>Cyathea frigida</i> (H. Karst.) Domin	terrestrial	3000		3300	
<i>Cyathea squamipes</i> H.Karst	terrestrial	2550			2600
<i>Cyathea xenoxyla</i> M. Lehnert	terrestrial	2450		2700	2350
<i>Danaea moritziana</i> C. Presl	terrestrial	2050			2650
<i>Dennstaedtia globulifera</i> (Poiret) Hieron.	terrestrial	2400	2600	3100	
<i>Dicksonia sellowiana</i> Hook.	terrestrial	2700	2700		2300
<i>Diplopterygium bancroftii</i> (Hook.) A. R. Sm.	terrestrial	2520	2000		2350
<i>Elaphoglossum andicola</i> (Fée) T. Moore	epiphytic	2600			3050
<i>Elaphoglossum erinaceum</i> (Fée) T. Moore	epiphytic	2550	2900		3000
<i>Elaphoglossum eximium</i> (Mett.) H.Christ	terrestrial	2550	2500		1600
<i>Elaphoglossum glossophyllum</i> Hieron.	epiphytic	2550			3700
<i>Elaphoglossum latifolium</i> (Sw.) J. Sm.	epiphytic	2400			3250
<i>Elaphoglossum lingua</i> (Raddi) Brack.	epiphytic	2640	2100		3500
<i>Elaphoglossum lloense</i> (Hooker) Moore	epiphytic	2860			3025
<i>Elaphoglossum notatum</i> (Fée) T. Moore	epiphytic	2860			2800
<i>Elaphoglossum pachyphyllum</i> (Kunze) C. Chr.	epiphytic	2660			1850
<i>Elaphoglossum papillosum</i> (Baker) H. Christ	terrestrial	2630	2800		3200
<i>Elaphoglossum petiolosum</i> (Desv.) Moore	epiphytic	2600			3700
<i>Elaphoglossum tenuiculum</i> (Fée) Baker	terrestrial	1900			2200
<i>Elaphoglossum vulcanicum</i> H. Christ	epiphytic	2660			3600
<i>Eriosorus flexuosus</i> (Kunth) Copel.	terrestrial	2660	3400		3250
<i>Eriosorus orbygnianus</i> (Mett. ex Kuhn) A.F. Tryon	terrestrial	2550			2550
<i>Grammitis bryophila</i> (Maxon) F. Seym.	terrestrial	2600	2600		2600
<i>Histiopteris incisa</i> (Thunb.) J. Sm.	terrestrial	2660	2900		3400
<i>Huperzia tenuis</i> (Humb. & Bonpl. ex Willd.) Rothm.	epiphytic	2600		3500	

Species	substrate	upper elevational limit (m)			
		EC	CR	PE	BO
<i>Huperzia wilsonii</i> (Underw. & Lloyd) B. Øllg.	epiphytic	2660	2000	2750	2410
<i>Hymenophyllum fragile</i> (Hedw.) C.V. Morton	epiphytic	2660	1700	3300	2350
<i>Hymenophyllum fucoides</i> (Sw.) Sw.	terrestrial	2600	3200	3500	3300
<i>Hymenophyllum microcarpum</i> Desv.	terrestrial	2530	2400		2700
<i>Hymenophyllum multialatum</i> C.V. Morton	epiphytic	2600		3350	
<i>Hymenophyllum myriocarpum</i> Hooker	epiphytic	2600	3200	3600	
<i>Hymenophyllum plumieri</i> Hook. & Grev.	epiphytic	2600		3400	3125
<i>Hymenophyllum polyanthos</i> (Sw.) Sw.	epiphytic	2650	3200	3100	3150
<i>Hymenophyllum ruizianum</i> (Klotzsch) Kze.	epiphytic	2600			3200
<i>Hymenophyllum trichomanoides</i> Bosch	epiphytic	2600			3350
<i>Hymenophyllum trichophyllum</i> Kunth	epiphytic	2660		3350	3400
<i>Hymenophyllum undulatum</i> (Sw.) Sw.	epiphytic	2660	3400		3015
<i>Lellingeria subsessilis</i> (Baker) A. R. Sm. & R.C. Moran	epiphytic	2645	2500		3500
<i>Lophosoria quadripinnata</i> (Gmel.) C.Chr.	terrestrial	2600	2700	3500	3250
<i>Loxsomopsis pearcei</i> (Baker) Maxon	terrestrial	2900			3000
<i>Lycopodiella glaucescens</i> (C. Presl) Øllgaard	terrestrial	2470		2750	
<i>Lycopodium clavatum</i> L.	terrestrial	2700	3400	3550	3600
<i>Lycopodium vestitum</i> Poir.	terrestrial	2950		3500	
<i>Melpomene firma</i> (J. Sm.) A. R. Sm. & R. C. Moran	epiphytic	2650	2700	3600	3400
<i>M. moniliformis</i> (Lagasca ex Sw.) A. R. Sm. & R. C. Moran	epiphytic	2650	3400	3650	3800
<i>Melpomene pseudonutans</i> (Rosenst. & Christ) A. R. Sm. & R.C. Moran	epiphytic	2860		3600	
<i>M. xiphopteroides</i> (Liebm.) A. R. Sm. & R. C. Moran	epiphytic	2490	2100		2250
<i>Microgramma percussa</i> (Cav.) de la Sota	epiphytic	1900	500		1920
<i>Micropolypodium truncicola</i> (Klotzsch) L.E Bishop	epiphytic	2600	1900		2200
<i>Nephrolepis pectinata</i> (Willd.) Schott	terrestrial	2000	1700		
<i>Niphidium albopunctatissimum</i> D. B. Lellinger	epiphytic	2500			3500
<i>Niphidium crassifolium</i> (L.) D. B. Lellinger	epiphytic	2645		3400	2725
<i>Olfersia cervina</i> (L.) Kunze	terrestrial	1950	1400		2000
<i>Paesia glandulosa</i> (Sw.) Kuhn	terrestrial	2600			3250
<i>Pecluma divaricata</i> (E. Fourn.) Mickel & Beitel	epiphytic	2550	2900		2200
<i>Pecluma eurybasis</i> (C.Chr.) M. G.Price, vel aff.	epiphytic	2000	3000	3600	2600
<i>Pleopeltis fraseri</i> (Mett. ex Kuhn) A. R. Sm.	epiphytic	2000	3200		
<i>Polybotrya osmundacea</i> Humb. & Bonpl. ex Willd.	epiphytic	2000	1000		1900
<i>Polystichum platyphyllum</i> (Willd.) C. Presl	terrestrial	2600			1870
<i>Polytaenium lineatum</i> (Sw.) J. Sm.	epiphytic	2000	1000	3200	2200
<i>Pteris muricata</i> Hook.	terrestrial	2660		3100	2100
<i>Radiovittaria gardneriana</i> (Baker) C. F. Reed	terrestrial	2600	1900	2700	3450
<i>Radiovittaria remota</i> (Fée) E. H. Crane	epiphytic	1950	1400		2600
<i>Radiovittaria stipitata</i> (Kunze) E. H. Crane	epiphytic	2000	1100		2050
<i>Serpocaulon fraxinifolium</i> (Jacq.) A. R. Sm.	epiphytic	2000	1400	2750	2750
<i>Serpocaulon levigatum</i> (Cav.) A. R.Sm.	epiphytic	2600			2400
<i>Serpocaulon ptilorhizon</i> (H. Christ) A. R. Sm.	epiphytic	2640	2600		2250
<i>Serpocaulon sessilifolium</i> (Desv.) A. R.Sm.	epiphytic	2470	3200		2200
<i>Sticherus revolutus</i> (Kunth) Ching	terrestrial	2860		3500	3950
<i>Sticherus rubignosus</i> (Mett.) Nakai	terrestrial	2600	1700	3350	
<i>Terpsichore anfractuosa</i> (Kunze ex Klotzsch) B. León & A. R. Sm.	epiphytic	2645	3000		2725
<i>Terpsichore semihirsuta</i> (Klotzsch) A. R. Sm.	epiphytic	2860	3000	3400	3050
<i>Terpsichore subtilis</i> (Kunze ex Klotzsch) A. R. Sm.	epiphytic	2660	2700		
<i>Thelypteris pusilla</i> (Mett.) Ching	terrestrial	2650	2700		2650

Species	substrate	upper elevational limit (m)			
		EC	CR	PE	BO
<i>Thelypteris brausei</i> (Hieron.) Alston	terrestrial	2600		3600	3200
<i>Thelypteris euchlora</i> (Sodirol) C. F. Reed	terrestrial	2645			3400
<i>Thelypteris funckii</i> (Mett.) Alston	terrestrial	2650	2900	3450	
<i>Thelypteris pusilla</i> (Mett.) Ching	terrestrial	2650	2700		2650
<i>Trichomanes lucens</i> Sw.	terrestrial	2660	2100	3300	
<i>Trichomanes rigidum</i> Sw.	terrestrial	2650	2200		
<i>Trichomanes reptans</i> Sw.	epiphytic	2000	2900		
<i>Vittaria graminifolia</i> Kaulf.	epiphytic	2000	3200		2400
<i>Zygophlebia mathewsii</i> (Kunze ex Mett.) L.E. Bishop	epiphytic	2640			2900
<i>Thelypteris pusilla</i> (Mett.) Ching	terrestrial	2650	2700		2650
<i>Trichomanes lucens</i> Sw.	terrestrial	2660	2100	3300	
<i>Trichomanes rigidum</i> Sw.	terrestrial	2650	2200		
<i>Terpsichore anfractuosa</i> (Kunze ex Klotzsch) B. León & A. R. Sm.	epiphytic	2645	3000		2725

Tab. 2. Comparison of the upper elevational limits commonly shared between three Andean study sites (EC, PE, BO).

<b>Site</b>	<b>EC</b>	<b>CR</b>	<b>PE</b>	<b>BO</b>
Species number		27		
Upper limit (m)	2542	-	3274	2884
compared with EC	-	-	higher	higher
Wilcoxon's test	-	-	$p < 0.002$	$p < 0.02$

Tab. 3. Pairwise comparison of the upper elevational limit of the shared pteridophyte species between the four study sites (CR, EC, PE, BO).

<b>Site</b>	<b>EC</b>	<b>CR</b>	<b>PE</b>	<b>BO</b>
	total		shared with EC	
Species number	114	66	44	90
Upper limit (m)	2496	2495	3281	2884
Compared with EC	-	equal	higher	higher
Wilcoxon's test	-	n. s.	$p < 0.002$	$p < 0.002$



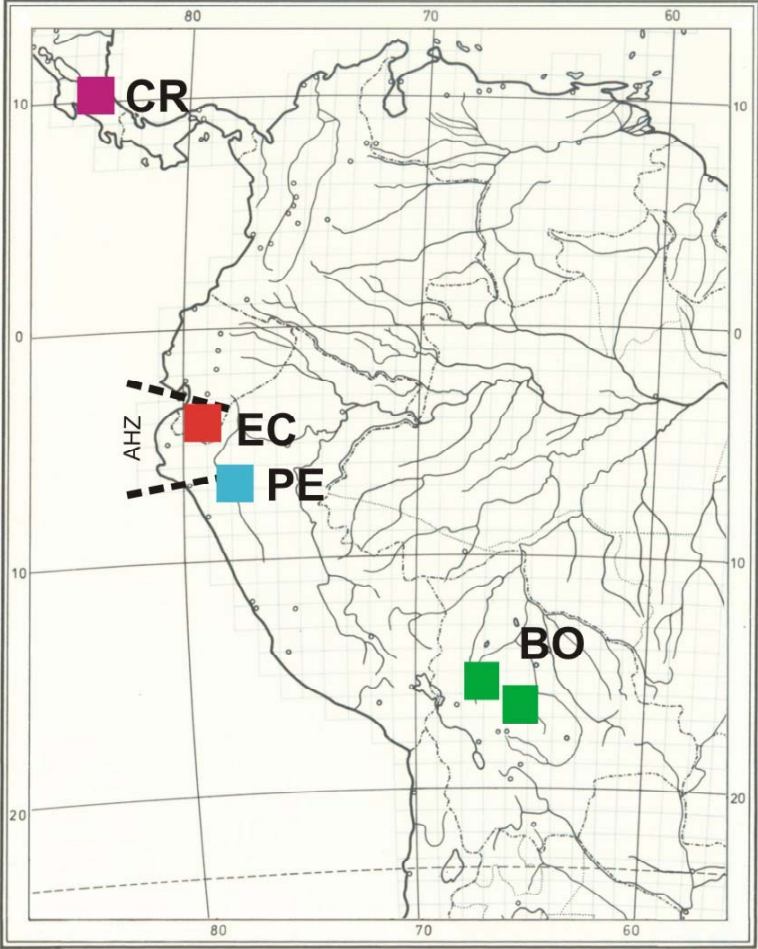


Fig. 1. Map of northwestern South America showing the Amotape-Huancabamba zone (AHZ) and the four study sites in Costa Rica (CR), Ecuador (EC), Peru (PE), and Bolivia (BO).

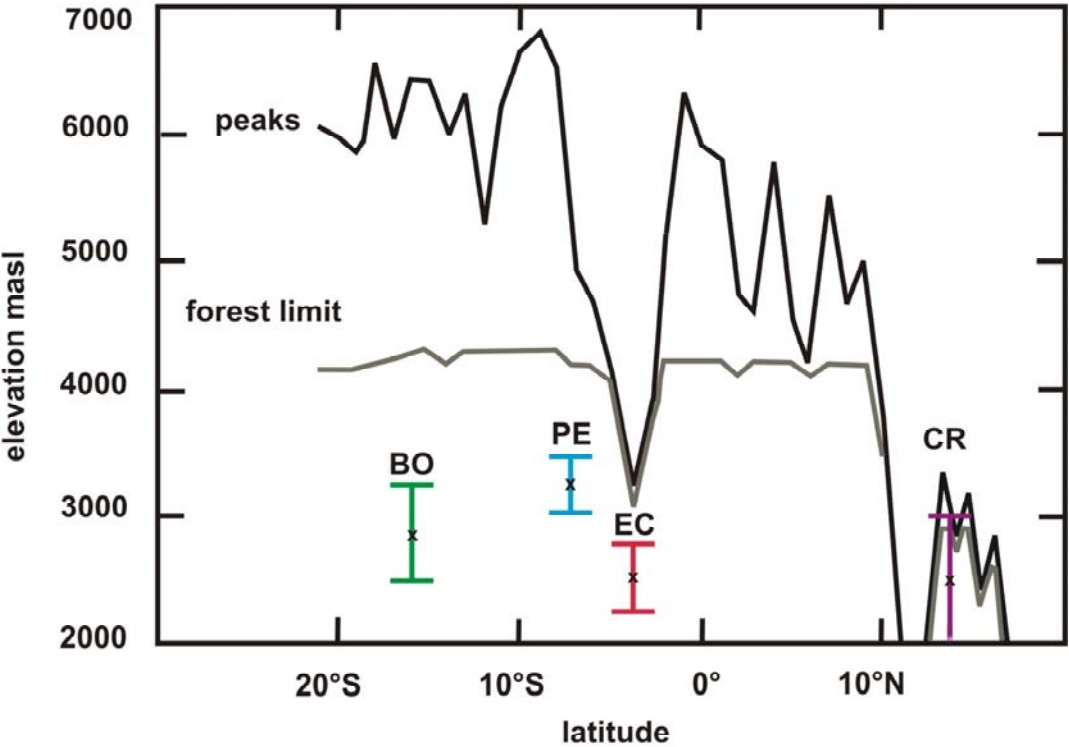


Fig. 3. Diagram showing highest peaks and forest limit from Costa Rica (ca. 8°N, right) to northern Argentina (22°S, left). Upper elevational limits of pteridophytes marked with “x” with mean deviation for the study sites in Bolivia (BO), Peru (PE), Ecuador (EC), and Costa Rica (CR).

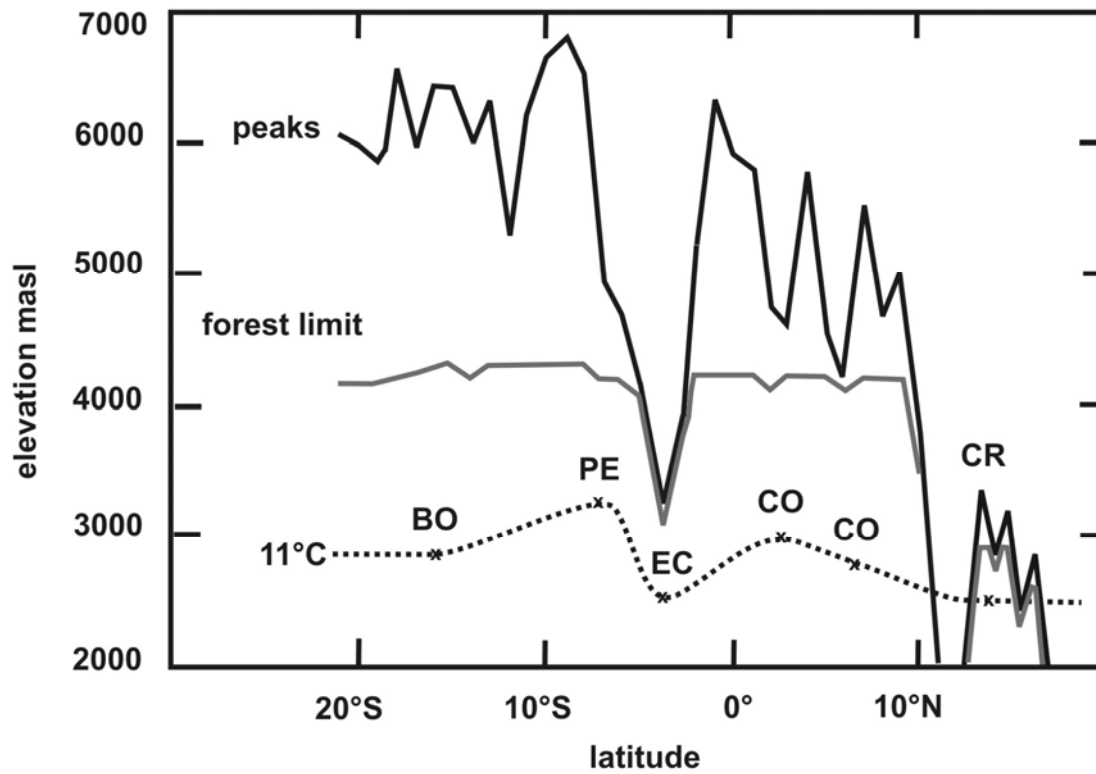


Fig. 4. Diagram showing highest peaks, forest limit, and 11°C isotherm from Costa Rica (ca. 8°N, right) to northern Argentina (22°S, left). “x” marks upper elevational limits of pteridophytes for study sites in Bolivia (BO), Peru (PE), Ecuador (EC), and Costa Rica (CR), and additional information of mean annual temperature for Colombia (CO) taken from Hooghiemstra and van der Hammen (2004).

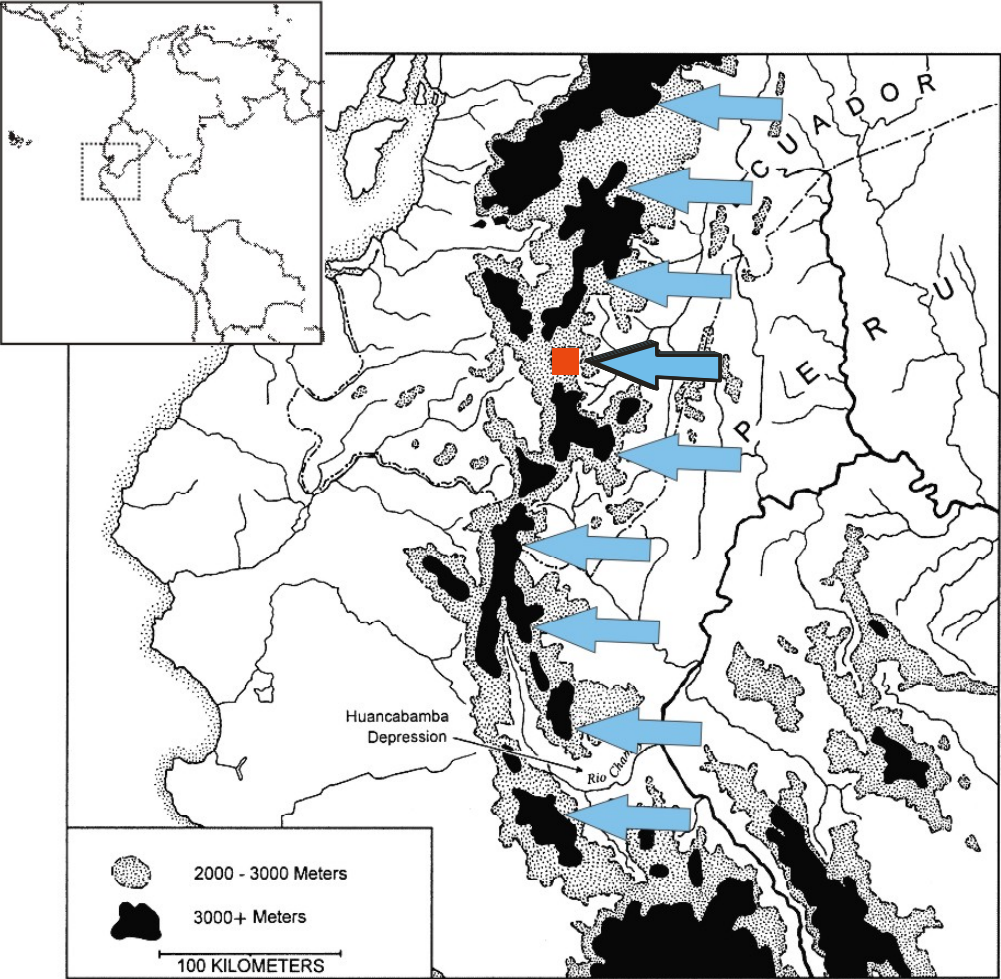


Fig. 5. Map showing detail of the Huancabamba-Amotape region (altered from Lunde & Pacheco, 2003). Predominant winds indicated with arrows, showing easy passage across the Andes near study area (square).

## Chapter III

### **Ferns in communities: ecology**

“Science is organized common sense where many a beautiful theory was killed by an ugly fact.”

*Thomas Huxley*

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**D**espite their evolutionary age, ferns and lycophytes are still frequent components of most terrestrial biotopes on earth (Kramer et al., 1995). They are missing only in the driest habitats; otherwise they are at least present with a small number of especially adapted species. They can be found in semi-deserts, savannas, in sand dunes, on rocky shores, and in permafrost soil.

The pteridophytes – understood in the broad sense as the paraphylum containing lycophytes and ferns (Kramer et al., 1995; Pryer et al., 2001; Smith et al., 2006) – have dominated the terrestrial ecosystems during the Paleozoic and for most of the Mesozoic (Willis & McElwain, 2002); lycophytes are the closest living relatives to the first tracheophytes that conquered the dry land (Retallack, 1985; Doyle, 1998). Looking at the ecology of recent pteridophytes may thus give some hints how they functioned in early ecosystems. One peculiarity of the tracheophyte blueprint is the ability to produce trees; trees may form closed stands (woods or forest) that have a major impact on local climate and soil chemistry. The ecosystems we find today are the product of ever more complicated species/biotope interactions during earth history (Retallack, 1984). Reconstructing paleoecosystems is always more complicated than tracing the phylogenetic history of taxa (Feild & Arens, 2005). The assumptions we make are based on scanty fossil material (Retallack, 1981) and largely on the demands of extant species to their biotope (Wing & Sues, 1984; Kidwell & Flessa, 1995). The preamble is that environmental changes caused the extinction of old taxa and triggered the evolution of new taxa. Extant ancient lineages are likely to have survived in relicts of their original habitat; they have remained unchanged because their ecological requirements have not changed, due to an unaltered environment. Alternatively, there is also the possibility that only the functionality but not the morphology of a character may have changed over time (“exaptation” sensu Gould & Vrba, 1982), enabling basal lineages to adapt to a new habitat in the same way as derived ones. As it appears, there is a parsimonious way to estimate paleoecological conditions, but always with great uncertainty.

In this chapter, I try to evaluate the correlation of the evolution of ferns with the development of soils over geological time. After a first enumeration of the soil preferences of extant fern lineages (chapter III.1), I will examine mycorrhizae among ferns. This classical symbiosis between plant root and soil fungi often enables green plants to survive in harsh environments (Allen et al., 2003); it is even hypothesized that it was due to mycorrhizae that tracheophytes were able to first colonize the barren continents of the Paleozoic (Brundrett, 2002). Before this background it is interesting to know how much recent ferns depend on

mycotrophy. The mycorrhizal status of extant fern groups is summarized from studies all over the world (chapter III.2 & III.3), also considering the evolution of mycotrophy among the various pteridophyte groups (chapter III.2).

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### III.1. The influence of soil evolution on pteridophyte diversification

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**Abstract:** Our study aimed to resolve whether basal pteridophyte lineages are overrepresented on nutrient deficient soils compared to more derived lineages. Based on the latest phylogenies and classification, we grouped the extant pteridophyte families into nine groups and evaluated their soil preferences. First, we plotted the preferred substrate type of all estimated 11430 sp. worldwide against the phylogeny. Then we looked at the real distribution of the pteridophytes along a soil nutrient gradient in western Amazonia and the Andes. More derived pteridophyte lineages increase in present species number with higher cation content whereas most basal lineages are better represented on nutrient deficient soils. Exceptions include pteridoid and dennstaedtioid ferns, which are also well represented on poorer soils, and Marattiaceae, Selaginellaceae, and the tree fern lineage, which are generally found on more fertile soils. The results are discussed with the current knowledge about the evolution of soils and vegetation in the Mesozoic.

Key words: Angiosperms, gymnosperms, litter decomposition, pteridophytes, soil, substrate preference.

## Introduction

Extant vascular plants (Eutracheophyta) consist of three major lineages: lycophytes are the phylogenetic sister group to all other vascular plants, collectively called euphyllophytes (Doyle, 1998), among which, in turn, ferns (incl. Equisetaceae) are the sister group to seed plants (Pryer et al., 2001, 2004). Lycophytes and ferns are traditionally combined as the “Pteridophyta”, which is now known to be paraphyletic (Pryer et al., 2001; Smith et al., 2006). However, because lycophytes and ferns share fundamental morphological and ecological traits, they are often combined in floristic and ecological studies and are still commonly referred to as pteridophytes (e.g., Mickel & Smith, 2004).

Most of the major pteridophyte lineages evolved prior to the diversification of the angiosperms, but about 80% of the contemporary fern diversity evolved after the diversification of angiosperms (Schneider et al., 2004). This contrast of old lineages and recent radiations offers a superb opportunity to study the effects of phylogenetic conservatism and changing environmental conditions on the evolution of plants (Willis & McElwain, 2002). DiMichele & Phillips (2002) characterize the Paleozoic origin of the ferns as a response to an unstable environment with disturbed substrates and frequent fire; ferns and fern allies were able to develop a wide range of ecological adaptations (e.g., herbs, trees, lianas) and life history traits, which were lost and regained several times in different lineages during the following eras. Thus, ferns display a great evolutionary flexibility and a great responsiveness to ecological challenges (DiMichele & Phillips, 2002). One of the major ecological changes during the evolution to which the “bauplan” of ferns had to respond to was the development of forests dominated by angiosperms about 70-50 Mya in the late Cretaceous to early Tertiary (Willis & McElwain, 2002; Schneider et al., 2004). Ecologically, angiosperm-dominated forests differ in several important ways from forests dominated by gymnosperms and/or pteridophytes. Most obviously, the tree canopy layers are denser, allowing less light to reach the understory (Bond, 1989; Becker, 2000; Coomes et al., 2005). Schneider et al. (2004) proposed that the evolution of a highly light-sensitive photoreceptor among the crown lineage of ferns (Schneider-Pötsch et al., 1998; Kawai et al., 2003) allowed the occupation of the dark angiosperm forest undergrowth by ferns and hence their diversification as forest ground forbs. However, some basal fern groups lacking this photoreceptor also thrive on the ground of dark forests, suggesting that light availability and photosynthetic capabilities are only part of the story. As a further influence, variation in the architecture of angiosperm trees allowed the colonization of tree crowns and subsequent diversification in numerous epiphytic lineages (Schneider et al., 2004).

The effects of changing soils on pteridophyte evolution have received less attention. Recent studies have shown that many pteridophyte species have specific soil requirements, both in temperate (e.g., Barrington, 1993; Richard et al., 2000; Guo et al., 2003; Wild & Gagnon, 2005) and tropical ecosystems (e.g., van der Werff, 1990, 1992; Tuomisto & Poulsen, 1996; Tuomisto et al., 2003; Poulsen & Tuomisto, 2006). However, to date no study has addressed the question whether these soil preferences contain a phylogenetic signal. Under present-day conditions, soils based on the same geological substrate tend to have a higher nutrient availability under angiosperm-dominated vegetation than those under gymnosperm- and/or pteridophyte-dominated vegetation types, due to the higher nutrient content and easier mineralization of angiosperm-produced litter (Thomas, 1968; Xiong & Nilsson, 1999; Prescott et al., 2000; Ponge, 2003; Wardle et al., 2003; Allison & Vitousek, 2004). We assume that this was also the case in prehistoric times.

Because the basal pteridophytes lineages evolved prior to the angiosperm diversification (Schneider et al., 2004), we hypothesized that phylogenetically more basal lineages would at least originally have been adapted to poorer soil conditions, whereas the diversification of modern plant lineages, including the more derived lineages of pteridophytes, may have been at least partly related to development of altered soil conditions.

Based on this general scenario and using terrestrial pteridophytes as our focal group, we asked two inter-related questions:

1) Is there a relationship of soil quality requirements and phylogenetic position among pteridophytes?

2) Are contemporary soil types of limited nutrient availability inhabited by terrestrial pteridophyte communities including a higher proportion of so-called basal lineages – those that diverged before the radiation of the crown groups of polypods generating more than 80% of current fern diversity (Schneider et al., 2004) – than nutrient-rich soils?

## Methods

The study consisted of two parts. First, we conducted a survey of soil requirements across all extant pteridophyte lineages to test the hypothesis that a higher number of basal lineages have lower nutrient requirements. Second, we searched for a phylogenetic signal among pteridophyte assemblages growing on soils with different nutrient contents, hypothesizing that a higher proportion of species and individuals from basal lineages inhabits poorer soils. For both analyses, we divided the pteridophytes into ten major phylogenetic groups (Tab. 1, Fig.

1) based on the latest phylogenetic hypotheses (Pryer et al. 2004, Schneider et al. 2004; Smith et al., 2006); the water fern lineage (Salviniaceae, Marsileaceae) was omitted from further consideration because of their restriction to at least temporarily aquatic habitats.

For the first analysis, for each extant pteridophyte genus, we estimated the number of species regularly growing on seven broad substrate types (Tab. 1) based on our ecological field data, personal field experience, information from the literature, and correspondence with botanists having actual field experience with some little-known genera. The substrate types are: (i) *poor*, i.e., nutrient-poor, often acidic soils including sandy soils and leached soils such as tropical quartz sands and ultramafic soils, (ii) *rich*, referring to regular, brown soils influenced by angiosperm litter without strong nutrient limitation; (iii) *peat*, referring to acidic, water-logged bogs and moors; the self-explanatory terms (iv) *epiphytic*, (v) *saxicolous* (*lithophytic*), (vi) *aquatic*, and (vii) *rheophytic* were used here in the general sense and these categories are not further analyzed here. This classification is admittedly very rough, but more detailed ecological information simply is not available for the majority of pteridophyte species. Some species were assigned to more than one substrate, thus the numbers of each substrate type do not necessarily sum up to the estimated total species number of each family. The percentages of species per substrate type were calculated (Tab. 1) and added up across the nine major phylogenetic groups (Fig. 1).

For the second analysis, contemporary pteridophyte assemblages were sampled at sites with different nutrient availability the Andes of southern Ecuador (22 plots) and in Amazonian Peru (14 transects). In Ecuador, plot size was 400 m<sup>2</sup>, usually staked as 20 x 20 m parcels. In Peru, transects measured 5 x 500 m. On each plot, the species composition and abundance of terrestrial pteridophyte assemblages were recorded; for the Peruvian site, abundance is available only for 8 transects. All species recorded were assigned to the nine phylogenetic groups, and the percentages of species and individuals (Tab. 2) per plot were calculated. From the Ecuadorian sites, soil samples were taken from the organic layer, Ah- and B-horizons, air-dried, ground, and sieved for C/N analysis; the soils were characterized by physical and chemical parameters. Laboratory analyses were carried out at the Technische Universität Dresden, Abt. Bodenkunde in Tharandt, Germany. In the Peruvian study area, samples were taken from the top mineral layer in 14 plots and analysed at the University of Turku, Finland, using standard methods (van Reeuwijk, 1993).

In order to exclude biases caused by the different analytical methods, we chose the exchangeable cation content (sum of cations Na, K, Ca, and Mg) available in the upper mineral horizon to express the fertility of soils. This measure has previously been shown to

correlate well with the distribution of plants in Amazonia (Tuomisto & Poulsen 1996, Tuomisto et al., 2003). The change in frequency and abundance of each pteridophyte group along the soil nutrient gradient were analyzed by linear regression with SYSTAT 7.0 (Systat, 1987).

## Results

### Soil preferences among phylogenetic groups

Of the estimated total 11430 pteridophyte species worldwide, about 62 % (7166 sp.) were categorized to grow on soils without obvious nutrient deficiency (Tab. 1). The epiphytic habitat is utilized by 14 % (1589 sp.), and a comparable value of 13 % (1473 sp.) of all pteridophyte species occur on nutrient-poor soils. About 6 % (702 sp.) of the pteridophytes grow directly on rocks; peaty (3%, 353 sp.), aquatic (2%, 230 sp.), and rheophytic (2%, 205 sp.) habitats are inhabited by only 7 % of all species.

Among the basal groups (groups I-IV), species occurred predominantly on poor soils (e.g., group IV, 66 %), peat, or as epiphytes (e.g., group III, 65 %) (Fig. 1). Lycophytes (group I) and the basal ferns (group II) showed a surprisingly high percentage of species growing on nutrient rich soils. However, this pattern was driven only by two families, the Selaginellaceae and Marattiaceae, both of which occur almost exclusively on nutrient rich soils. The other families included in these groups were characteristic of poor soils (Lycopodiaceae, 44 %; Ophioglossaceae, 82 %), peat (Lycopodiaceae, 22 %; Osmundaceae, 63 %; Equisetaceae, 88 %), or for the epiphytic habitat (Lycopodiaceae, 40 %; Psilotaceae, 93 %). Within the remaining groups (V-X), the majority of species grows on nutrient-rich soils. However, relatively high percentages of species inhabiting poor soil are found among the dennstaedtioid and pteridoid ferns (30 % and 28 %, respectively).

### Phylogenetic trends among neotropical fern communities on different soils

Considering each study area separately, the tendencies of increase and decrease along the nutrient gradient were weak and insignificant. In Peruvian Amazonia, the number of species decreased with higher cation exchange capacity for groups I, II, V, VII, and VIII, whereas for groups III, IV, VI, and IX it increased, but among these only group IV (schizaeoid & gleichenoid ferns) showed a significant signal ( $r = 0.564$ ,  $p = 0.036$ ). Looking at the number of individuals per plot, groups I and III-VI decreased with higher cation exchange capacity whereas groups II and VII-X increased; among them only group II with significant values ( $r =$

0.940,  $p = 0.001$ ). In the Ecuadorean Andes, groups I and III-V showed a decline of species richness whereas the rest increased. Regarding individual numbers per plot, groups I-IV, VI, and VII increased whereas groups V and VIII through IX decreased. Significant values were not obtained in either approach. Comparing the tendencies between two study sites, not all groups were matching: between the Ecuadorean and Peruvian sites, tendencies in abundance agreed in groups II, and V-VIII, and in species numbers in groups I, V, VI, and VIII.

### Discussion

It appears that phylogenetically more basal pteridophyte groups preferentially occupy nutrient-poor soils and that more derived fern groups are most diverse on nutrient-rich soils. In our phylogenetic analysis there are some noteworthy exceptions, namely the preference of nutrient-rich soils by basal Selaginellaceae and Marattiaceae, and the preference of nutrient-poor sites by derived dennstaedtioid and pteridoid ferns.

In our comparison of extant neotropical pteridophyte assemblages, we found that at least at the Ecuadorean site, the phylogenetically basal lineages up to and including the tree fern lineage (group V) showed a decrease of species number with increasing soil cation content (Tab. 2). Except for group VI, this is congruent with our results from the phylogenetic overview. Again, the basal ferns (group II) are more frequent on fertile soils. The abundance unexpectedly increased with higher cation content in most groups, except for the more derived groups V, VI, and IX, in which the abundance decreased. This is largely discordant with our results from the phylogenetic analysis.

In Peru, the trends concerning the species number are less clear than in Ecuador (Tab. 2). Among the basal groups (I-VI), only I and V show the expected decrease in species number. The decrease in the diversity in the basal ferns (group II) is unanticipated, while the decrease of dennstaedtioid ferns (group VI) is matching with the results of the phylogenetic overview. We have no explanation for the decrease in group VIII (Polypods 1). Contrary to our general overview on the substrate preferences, groups I and II did not fall out of the scheme in this approach because the rich substrate preferring families Selaginellaceae and Marattiaceae were only represented by at most 1-2 species per plot and were often missing. These exceptions are discussed below. The abundances in Peru, however, showed a decrease in the basal lineages (groups I-VI), except for group II, and an increase in the derived lineages (groups VII-IX).

The data for abundance are less clear than those for species number, presumably because evolutionary events translate directly into species numbers, whereas abundances are further influenced by diverse ecological factors, diluting the phylogenetic signal. The question now is whether these patterns can be attributed to changes in the quality of soils induced by the diversification and ecological dominance of angiosperms in the Cretaceous. As is so often the case with paleoecological inferences, argumentations must be based on circumstantial evidence, in this case data on horticultural experience, soil evolution, fossil pteridophyte records, and phylogenetic hypotheses based on extant ferns.

Some of the most striking indications for a phylogenetically determined preference of nutrient-poor soils by basal pteridophyte lineages come from horticultural experience. Several pteridophyte groups that naturally thrive on raw, nutrient-poor soils, such as Lycopodiaceae, Gleicheniaceae, Matoniaceae, and Dipteridaceae are difficult or impossible to cultivate in botanical gardens (Page, 2002; M. Lehnert, M. Kessler, & H. Schneider, pers. obs.). The causes for this have not been studied in detail, but may involve either mycorrhizal associations (although many other ferns that are known to have mycorrhizae can be easily cultivated), or a susceptibility of the taxa to high soil nutrient conditions. The latter assumption is supported by the fact that the taxa in question take longest to die when grown in very poor soils such as pure sand (M. Lehnert, M. Kessler, & H. Schneider, pers. obs.).

Studies of paleosols indicate that there has been an evolution of soils during earth's history, resulting in ever more complex horizontal structures (Retallack, 1981). One of the strongest impacts is seen in the advent of vascular land plants whose roots added to the mechanical breakdown of the parent material (Retallack, 1985, 1986) increasing the amount of available nutrients and, at the same time, stabilizing the produced fine material. In contrast, the dominance of angiosperms has not left a major signature on the structure of palaeosols (Retallack, 1986). However, nutrient availability, which is the main difference between angiosperm- and gymnosperm-influenced soils (e.g., Liu et al, 2004), cannot be directly inferred from paleosols because their chemistry is highly altered by the fossilization process (Retallack, 1981, 1986). Rising oleanane contents, which are only found in angiosperms, in paleosols are taken as evidence by Wing and Boucher (1998) "that angiosperms may have been a smaller part of the biomass of terrestrial vegetation in the Cretaceous than in the Cenozoic." No matter in which way angiosperms alter the soils, it was a gradual process that followed the diversification of this group. In order to know the quality of this, we can only rely on what is known of the extant tracheophytes and their impact on soil chemistry. Basing on the latest phylogeny and the ecophysiology of extant members of the basal branches of the

angiosperm tree, one hypothesis envisions the origin of early angiosperm in the understory of tropical forests as mesophyllous shrubs (Feild et al., 2004; Feild & Arens, 2005). In comparison to modern ecosystems, we can here deduce further that the habitats preferred by early angiosperms had the soils with the best nutrient supply. In present-day tropical rain forests, gorges and riversides receive and temporarily retain the down-flow of leached nutrients from the adjacent ridges and slopes (Wilcke et al., 2001). Together with a balanced water regime, this renders these areas the most productive sites in tropical forests (Grubb, 1995; Saunders et al., 2006). It is imaginable that the nutrient availability enabled the development of short-lived, frequently disposed leaves, which are typical of most angiosperms. Mesophyllous leaves, as we know them today appear to be primordial in angiosperms, and most likely their properties and influences on ecosystems, too.

In comparison, investigations focused on conifers (i.e., *Agathis* and *Phyllocladus*, Enright & Ogden, 1987; *Pinus*, *Picea*, *Larix*, *Pseudotsuga*, *Chamaecyparis*, and *Cunninghamia*, Liu et al., 2004) show that their litter generally decomposes slowly and builds up nutrient-poor humus. These studies indicate that the derived Pinaceae, which evolved simultaneously with the angiosperms, do not differ from extant members of the ancient lineages of Podocarpaceae and Araucariaceae. Thus, present day conifer-dominated stands may be taken as proxies for Mesozoic gymnosperm dominated vegetation. Data for deciduous mesophyllous gymnosperms (e.g., *Ginkgo*, *Taxodium*, *Metasequoia*) is lacking.

Decomposition of leaves and the release of contained nutrients is related to leaf structure and longevity. In average, leaves live longer in basal tracheophytes (gymnosperms, pteridophytes) than in more advanced lineages (angiosperms) (Enright, 1999; Rogers & Clifford, 1993; Liu et al., 2004) and are energetically larger investments for gymnosperms than for angiosperms (Lusk et al., 2003). Indications for a tighter nutrient regime in conifers are the N contents in the leaves (Lusk et al., 2003), which are lower than in mesophyllous angiosperms if compared by specific leaf area. Studies in Hawaiian forests with a high percentage of pteridophytes also show a pronounced scarcity of micronutrients because of low nutrient content and generally slow decomposition of pteridophyte litter (Allison & Vitousek, 2004). Judging from extant data, it seems likely that basal tracheophytes like conifers and ferns generally build up organic layers of lower nutrient accessibility than those built up by angiosperms.

Fossils provide only indirect evidence of soil preferences of extinct taxa. In particular, the fossil record includes a number of problems. First, there are large gaps especially in the early stages of pteridophyte evolution and usually only a minimum age can be given for a



given taxon (Pryer et al., 2004). Second, the substrate preference of the terrestrial plants is not readily deduced from the mineral deposit in which they are found. Most plant fossils are gathered from sediments of former lakes, swamps, and lagoons, but that does not mean that they have been aquatics or swamp plants, as can be deduced from their morphology (Retallack, 1981). Distant from aquatic habitats, in situ-fossilisation is rare because dead plant material usually is decomposed (Retallack, 1986). However, root traces are often found in paleosol profiles (Retallack, 1981, 1986) and give indirect testimony of the plants that have grown on them. Only catastrophic events like sudden floods of higher grounds, sandstorms, or volcanic eruptions which bury larger areas under sediments and ashes may preserve communities of plants and animals in a way that chronological and ecological relationship is unequivocally inferred (e.g., Thorn, 2005; Wing et al., 1993), but these cases are rare. Accordingly, many paleoecological studies infer the ecological preferences of fossil plants from those of their extant relatives (e.g., Banks, 1970), but this easily leads to circular argumentation (Donaghue et al., 1989; Page, 2002).

Bearing these constraints in mind, the fossil record of many prehistoric pteridophyte (as well as gymnosperm) lineages show a sharp decline in frequency and diversity around 90-100 Mya (Collinson, 2001; Willis & McElwain, 2002). This coincides with the advent of angiosperms, suggesting causality. After this floral shift, many “old” fern taxa like the Marattiaceae, Schizaceae, Dipteridaceae, and Matoniaceae were still more widely distributed than today, but their fossil record is scarcer and ambiguous (Skog, 2001). Apparently less biomass of these families found its way to the fossilization sites, the reasons being either general loss of abundance and diversity, or an ecological or geographical shift to areas where plant remains are not easily fossilized. In contrast, the radiation of the more derived ferns in the Tertiary is fairly well proven (Schneider et al., 2004, and references therein).

Looking at the evolution of pteridophytes as inferred from phylogenetic studies of extant taxa, the crucial information comes from the timing of radiations. It is in this context that the “exceptions” outlined above are especially informative. The Selaginellaceae, in particular, are a historically old lineage, but fossil evidence is scarce and it is probable that the evolutionary radiation of contemporary Selaginellaceae post-dates the diversification of angiosperms (Korall & Kenrick, 2001; Schneider et al., 2004). Most Selaginellaceae species today grow on the forest floor in tropical regions and it is likely that this diversification took place relatively recently, i.e., after the development of the angiosperm-dominated forests (Wing & Boucher, 1998; Willis & McElwain, 2002). This scenario of a recent radiation would easily explain why such an old lineage has comparatively high species richness and a preference for

nutrient-rich soils. In the case of the Hymenophyllaceae, a recent radiation is observed in the predominantly epiphytic genus *Hymenophyllum* (broadly defined as in Kubitzki & Green, 1990; Pryer et al., 2001; Schuettpelz & Pryer, 2006). The extant Marattiaceae, another basal group most common on rich soils, are generally found in the darkest and dampest spots in tropical forests, especially along streams and in ravines (Murdock, 2005). They may represent taxa that have adapted to humid, shaded places prior to the origin of angiosperms (DiMichele & Thomas, 2005) because of their high water demand (Murdock, 2005) and not so much because of the nutrient availability at these spots. In contrast, the evolutions of the dennstaedtioid and pteridoid fern lineages, which have a preference for nutrient-poor soils, post-date the angiosperm diversification. Their preference for poor soils, mostly either raw soils on landslides or river banks, or poorly developed soils in arid regions (Kubitzki & Green, 1991; Tryon & Tryon, 1982)) cannot be interpreted through phylogenetic conservatism but must be regarded as an evolutionary novelty. Taken together, these exceptions therefore do not contradict the overall hypothesis of an ecological impact of soil improvement on pteridophyte evolution and diversification, but rather reveal specific cases of delayed diversification, early niche specificity, or late ecological reversal, respectively.

In conclusion, our survey suggests that the gain of ecological dominance by angiosperms in the late Cretaceous (Wills & McElwain, 2002) influenced the evolution and diversification of pteridophytes not only through the creation of a dark forest undergrowth and the availability of habitats for epiphytic species (Schneider et al. 2004), but also through the improvement of soil nutrient conditions. Many basal pteridophyte lineages that evolved on soils of poor nutrient availability prior to the angiosperm dominance, apparently remained phylogenetically constrained to these conditions and only some lineages such as Selaginellaceae or Hymenophyllaceae, which have managed to adapt to the changes induced by the angiosperms, have diversified after the Late Cretaceous. More derived fern lineages that first appeared after the Cretaceous adapted from the beginning to angiosperm-influenced soil conditions and diversified under these conditions.

The evidence supporting this scenario is still rather thin, as discussed by Boucot & Gray (2001) for hypotheses describing early evolutionary pathways in general. We hope that this paper raises awareness of this hypothesis and will inspire researchers to further explore the topic of soil evolution and pteridophyte evolution in the Cretaceous and Tertiary. Possible lines of research include observational and experimental ecological studies on the soil and nutrient requirements of different pteridophyte lineages, including the hard-to-cultivate ones such as Lycopodiaceae and Gleicheniaceae. Comparisons of pteridophyte assemblages and

their nutrient conditions in present-day pteridophyte- and/or gymnosperm-dominated forests and adjacent angiosperm-dominated forests under otherwise comparable climatic and geological conditions would be particularly informative. Phylogenetic studies should be aimed at more precisely dating the radiations of species-rich terrestrial pteridophyte taxa, and to attempt to link these to the timing of angiosperm radiations. Finally, mycorrhizal symbionts of pteridophytes may provide important insights, based on the assumption that these are ecologically important in pteridophyte assemblages on poor soils (Brundrett, 2002; Allen et al., 2003) and better-represented overall in phylogenetically basal lineages (Boullard, 1958, 1979). Recent comparative studies on bryophytes have shown a differentiation of one primeval and one advanced type of mycorrhiza, and suggest that once the primeval mycorrhiza is lost, it cannot be regained (Kottke & Nebel, 2005). New associations can only be made with the fungi of advanced mycorrhizoid types. We expect a similar pattern in ferns, suspecting modern lineages to be non-mycorrhizal or only facultatively mycorrhizal on nutrient-rich soils, or, if they adapted again to nutrient-poor substrates, to have a different kind of mycorrhiza than basal lineages.

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**Figure captions**

Fig. 1. Phylogenetic tree of vascular plants following Smith et al. (2006). Pteridophytes (ferns and lycophytes) resolved on family level and divided into ten phylogenetic groups. Columns behind each group represent the percentage of species occurring on the respective type of substrate.

Tab. 1. Absolute and relative species number of ferns and lycophytes on the different substrate types recognized in this study. The families are divided into ten phylogenetic groups according to Pryer et al. (2004). Groups I and II are shown in detail to show the overrepresentation of Selaginellaceae and Marattiaceae on rich soils (marked with double asterisks, \*\*). Subtotals do not sum up to the grand totals because some species have been assigned to more than one substrate type.

Tab. 2. Linear regression between species number (sp.)/abundance (abund.) of pteridophytes and increasing soil fertility measured as cation content ( $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{++}$ ,  $\text{Mg}^{++}$ ).

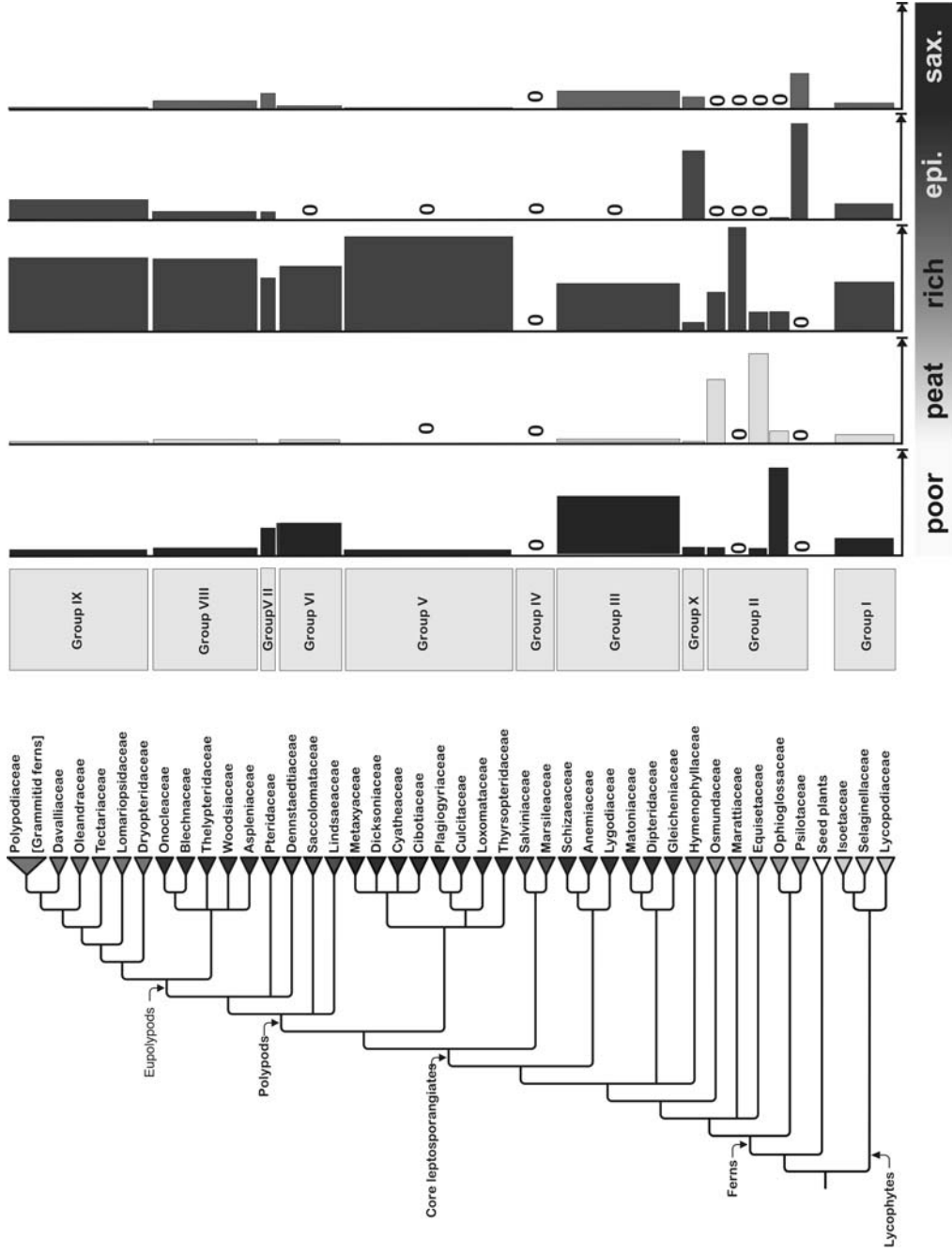


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group	poor	%*	peat	%	rich	%	saxicol	%	epiphytic	%	aquatic	%	rheophytic	%	Total/subtotal
<b>I. Lycophytes</b>	213	16	114	9	680	52	69	5	202	15	133	10	0	0	1313
<i>Lycopodiaceae</i>	213	44	107	22	25	5	0	0	195	40	0	0	0	0	483
<i>Selaginellaceae</i>	0	0	0	0	<b>655**</b>	95	69	10	7	1	0	0	0	0	690
<i>Isoetaceae</i>	0	0	3	2	0	0	0	0	0	0	133	95	0	0	140
<b>II. Basal ferns</b>	91	26	28	8	212	61	0	0	2	1	0	0	7	2	347
<i>Equisetaceae</i>	1	6	14	88	3	19	0	0	0	0	2	13	0	0	16
<i>Marattiaceae</i>	0	0	0	0	<b>183**</b>	100	0	0	0	0	0	0	0	0	183
<i>Psilotaceae</i>	0	0	0	0	0	0	5	33	14	93	0	0	0	0	15
<i>Ophioglossaceae</i>	89	82	13	12	20	18	0	0	2	2	0	0	0	0	109
<i>Osmundaceae</i>	2	8	15	63	9	38	0	0	0	0	0	0	7	29	24
<b>III. Hymenophyllaceae</b>	52	7	5	1	52	7	112	16	462	65	0	0	7	1	706
<b>IV. Schizeoid Ferns</b>	221	66	7	2	100	30	22	7	0	0	0	0	2	1	333
<b>V. Tree ferns</b>	44	6	0	0	646	93	5	1	1	0	0	0	0	0	696
<b>VI. Dennstaedtioid ferns</b>	145	30	5	1	311	64	14	3	2	0	0	0	7	1	484
<b>VII. Pteridoid ferns</b>	352	28	2	0	723	58	191	15	97	8	8	0,6	29	2	1247
<b>VIII. Eupolypods I</b>	252	7	137	4	2561	71	245	7	309	9	0	0	113	3	3617
<b>IX. Eupolypods II</b>	102	4	41	2	1878	72	534	1	1752	19	3	0,1	40	2	2603
<b>X. Water ferns</b>	0	0	0	0	0	0	0	0	0	0	84	100	0	0	84
All groups	1473	13	353	3	7166	63	1192	6	2827	14	230	2	205	2	11430

\* percentage of respective group; \*\* exceptionally diverse subgroups of otherwise underrepresented groups,

Tab.2. Linear regression between species number (sp.)/abundance (abund.) of pteridophytes and increasing soil fertility measured as cation content ( $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{++}$ ,  $\text{Mg}^{++}$ ).

group	Peru (14 transects)				Ecuador (22 plots)			
	abund.	p	sp.	p	abund.	p	sp.	p
<b>I. Lycophytes</b>	-0.317	0.444	-0.217	0.456	0.032	0.888	-0.188	0.402
<b>II. Basal ferns</b>	0.940	0.001	-0.044	0.881	0.194	0.388	0.328	0.136
<b>III. Hymenophyllaceae</b>	-0.521	0.186	0.226	0.437	0.035	0.232	-0.222	0.321
<b>IV. Schizeoid Ferns</b>	-0.410	0.314	0.564	0.036	0.064	0.778	-0.061	0.787
<b>V. Tree ferns</b>	-0.219	0.602	-0.471	0.089	-0.266	0.232	-0.035	0.876
<b>VI. Dennstaedtioid ferns</b>	-0.613	0.106	0.271	0.348	-0.147	0.515	0.013	0.954
<b>VII. Pteridoid ferns</b>	0.154	0.716	-0.294	0.308	0.091	0.687	0.1	0.658
<b>VIII. Eupolypods I</b>	0.371	0.365	-0.090	0.761	0.168	0.456	0.115	0.61
<b>IX. Eupolypods II</b>	0.474	0.235	0.194	0.505	-0.04	0.861	0.185	0.41

### III.2. New insights on the mycorrhizal infections in ferns: an example from southern Ecuador

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**Abstract:** We conducted a survey on the mycorrhizal status of neotropical pteridophytes, focusing on previously neglected taxa. These include the filmy ferns (Hymenophyllaceae), grammitid ferns (Polypodiaceae), and the genus *Elaphoglossum* (Dryopteridaceae). Samples were collected at four different sites in southern Ecuador, Prov. Loja and Zamora-Chinchipec. Among the 78 investigated species (86 samples, 10 families), 19 were associated with arbuscular mycorrhizal fungi (AMF), and 27 were infected by ascomycetes, which are here considered as a kind of mycorrhiza similar to the ericoid type. The roots of 32 samples (including half of the *Elaphoglossum* species) were free of evident fungal infection.

**Keywords:** Andes, ascomycetes, *Elaphoglossum*, grammitid ferns, Hymenophyllaceae, mycorrhizae, pteridophytes, vesicular arbuscular mycorrhizae (VAM).

### Introduction

Mycorrhiza, the symbiosis between fungus and plant root, is known to enable plants to survive in the harshest environments by mediating the nutrient flux (Allen et al., 1993; Cairney & Meharg, 2003; Cooke & Lefor, 1998). Despite the evident advantage, there are conditions under which plants may dispense of a fungal partner and thrive, especially if they are growing on substrates that can be characterized as rich in nutrients. Since most plant groups have a special preference for one type of substrate, it does not surprise that mycorrhizae are unevenly distributed among the plant families (Newman & Reddell, 1987). Each new screening for fungal infections helps to reveal the patterns in the correlation between substrate type and mycorrhizae, especially if they include exceptions from the rule (e.g., Gemma et al., 1992; Motetee et al., 1996) that bring up new aspects.

One area worthy of such investigations is the Reserva Biológica San Francisco in southern Ecuador (Prov. Zamora-Chinchipe), where we conducted ecological studies on pteridophytes (lycophytes and ferns). The 1000 ha large reserve contains mature montane rain forest at 1800-3150 m and harbours 247 species of pteridophytes (Lehnert et al., submitted manuscript; chapter II.2). The rugged topography of the area creates a mosaic of different substrate properties, with nutrient deficient soils on the ridges (Gradstein et al., submitted manuscript) and slopes that receive a downhill flow of nutrients (Wilcke et al., 2001). Highly abundant and species-rich groups in this reserve are the filmy ferns (Hymenophyllaceae), grammitid ferns (Polypodiaceae), and the genus *Elaphoglossum* (Dryopteridaceae), most of them usually epiphytic species, which also often colonize the ground on the ridges (Kessler et al., in prep.).

Looking for a reference on the mycorrhizal status for these fern groups, we found that mostly reports for smaller regions outside of South America are available (e.g., Berch & Kendrick, 1982; Cooper, 1976; Gemma et al., 1992; Iqbal et al., 1981; Moteetee et al., 1996; Nadarajah & Nawawi, 1993), and the few surveys cover only a fraction of the pteridophytes worldwide (Boullard, 1958, 1979; Hepden, 1960, Newman & Reddell, 1987). No treatment for Andean ferns was found; the few studies in the Neotropics had either no overlap in the investigated species (Andrade et al., 2000; Fernández, 2005), or they had contradicting results for the same species (Lesica & Antibus, 1990; Schmid et al., 1995). Compared to the general diversity, the number of investigated species from our three focus groups (Hymenophyllaceae; grammitid ferns; *Elaphoglossum*) was very low.

Our present account aims on filling these gaps in order to have a basis for future studies. As far as we know, this is the first survey on mycorrhiza in Andean ferns sampled in situ.

### Materials and Methods

Root samples were collected at five different sites in SE Ecuador (Fig. 1): A) along the Gualaceo-Limon road at 3100-3300 m (Prov. Azuay), B) the mountain pass El Tiro between the towns of Loja and Zamora at 2600-2800 m (Prov. Loja/Zamora-Chinchipe), C) the area of Cerro Toledo, situated E of the town of Yantzatza, at 2900-3100 m (Prov. Loja), D) the Reserva Biológica San Francisco at 1800-2600 m (Prov. Zamora-Chinchipe), E) the Campamento Indígena Shaimi on the shores of Río Nangaritza at 900-1200 m (Prov. Zamora-Chinchipe). The study sites span an elevational gradient of 2400 m and range from lower montane forest to páramo vegetation. All sample areas face east and receive heavy precipitation all year round (Richter, 2003).

Sampling was focused on previously rarely investigated taxa. Thus most samples come from the families Dryopteridaceae (*Elaphoglossum*), Polypodiaceae (grammitid ferns, mainly *Melpomene*, *Terpsichore*, and *Lellingeria*), and Hymenophyllaceae (*Hymenophyllum s.l.*, *Trichomanes s.l.*). Non-grammitid Polypodiaceae were not included in this study because they are covered for the study area in a current licenciatura thesis at the Universidad Técnica Particular de Loja (UTPL).

Sample plants were carefully removed and cleaned mechanically from the substrate, then rinsed with water to remove smaller litter parts and mineral compounds. At least 10 cm of roots from each sample plant (86) were preserved in 70 % ethanol; of plants which we suspected to harbour ericoid mycorrhiza (54), 5-10 cm of the roots were preserved in 10 % aqueous glutardialdehyde for transmission electron microscopy (TEM) preparation and stored at 8-10°C.

Preparation of the ethanolic samples for light microscopy was as follows: the samples were bleached in 10 % KOH for ca. 24 h at 60°C; if the roots were still dark, the KOH was changed and the sample kept at 60°C for another 12-24 h. Then the roots were rinsed twice with water and acidified with 1 N HCl. Staining was done with methyl-blue in 90% lactic acid for at least 3 h. The stained roots were examined

with a dissecting microscope at 30-60 x; promising portions of young roots were cut out, mounted on slides in lactic acid and examined at 100-400 x. Samples and slides are stored at the Albrecht-von-Haller Institute of Plant Sciences, Department of Systematic Botany, Georg-August-University Göttingen, Germany.

Preparation of the TEM samples follows Schmid et al. (1995). We opted for the fixation with 1% osmiumtetroxid for 1 h at 20°C, then 1% uranylacetate for 1 h at 20°C. Samples and TEM slides are stored at the Eberhard-Karls-University, Tübingen, Germany (Botanisches Institut, Spezielle Botanik, Mykologie und Botanischer Garten).

In the case of the ascomycetes (Fig. 2), fungal infection was considered as mycorrhiza if the host cell was still intact and showed some response to the infection, i.e., thickening of the cell walls where the hyphae penetrated the cell and thickening of host cell cytoplasm when hyphal coils were present. Arbuscular mycorrhizal fungi (AMF) (Fig. 3) were just screened for presence, as they are not known to be pathogens or simple plant endophytes. It was also the smallest common denominator in the manner to compare our results with the data gathered from literature. However, presence of single hyphae and vesicles in the outer cortex were considered as erroneous infections and not counted.

## Results & Discussion

Among the 86 Ecuadorian fern samples studied by us, 78 species from 10 families were represented (Tab. 1). A total of 52 samples were infected by mycorrhizal fungi. Arbuscular mycorrhizal fungi (AMF) occurred in 18 species; 34 were infected by ascomycetes, which is considered here as a kind of ericoid mycorrhiza (Kottke, 2002). The roots of 32 samples (including all investigated Polypodiaceae and half of the *Elaphoglossum* species) were free of evident fungal infection. Two specimens (*Arachniodes denticulata* (Sw.) Ching, *Elaphoglossum lloense* (Hook.) T. Moore) had only a weak peripheral infection by ascomycetes and are listed as dubious.

Hymenophyllaceae are represented with 18 species in our sample and show a high percentage of mycorrhization (78 %). The mainly epiphytic species of *Hymenophyllum* were colonized by ascomycetes, whereas the predominantly terrestrial or saxicolous species of *Trichomanes* and *Abrodictium* had more cases of AMF infection. One unidentified *Trichomanes* grew epiphytically and had



ascomycetes like the epiphytic *Hymenophyllum* species. The only exception to the restriction of ascomycetes to epiphytes was the strictly terrestrial *Trichomanes dactylites* Sodiro.

Grammitid ferns, represented by 20 species, had an infection rate of 75 %. Only ascomycetes were found as fungal partner, even in terrestrial and saxicolous species. This apparent conflict with the trend observed in the Hymenophyllaceae, among which the majority of terrestrial species had AMF infections, is due to the microhabitats inhabited by the species. The investigated terrestrial grammitid ferns usually grew in thick moss cushions like their epiphytic kin and by this means under very similar ecological conditions, which may lead to maintaining the type of mycorrhiza. Furthermore, most of the species sampled as terrestrials are either potentially epiphytic or closely related to epiphytic species. Potential ascomycete-association may thus be an ancestral trait within this clade. Only the samples of *Melpomene occidentalis* Lehnert, sp. nov. ined., rooted directly in mineral soil and showed no fungal infection.

Among the 23 species of *Elaphoglossum*, we found only 12 with fungal infection. No clear correlation between the types of substrate and fungus was evident. VAM and ascomycetes occur randomly among epiphytes and terrestrials. Ascomycetes accounted for 75% of the infections.

The remainder of the investigated species shows mycorrhizal associations as expected from previous accounts; only the Gleicheniaceae show a low rate of infection (Tab. 1), although they are often cited as example for obligatorily vesicular-arbuscular mycorrhiza (Boullard, 1958). The root samples, however, were difficult to prepare because of their tough texture and the dark and persistent colorants in the cortex. Probably mycorrhizae were present but not visible in our samples of Gleicheniaceae because repeated clearing may have affected the colourability of fungal hyphae with dye and thus their visibility.

The tree ferns (Cyatheaceae and Dicksoniaceae) bear the difficulty of acquiring fine roots from the compact subterranean root system, which many species develop. Aerial roots from the trunks are easier to harvest but are expected to lack mycorrhizae because they are less likely to get in contact with inoculum of soil fungi. The plants included in this study are either small species or young plants of easily assignable larger species, which can be uprooted with most of their roots. Still our results for the Cyatheaceae (50% infected) are much lower than the results of previous

surveys (100% infected; Boullard, 1958; Hepden, 1960) but are at least congruent in the type of mycorrhiza (VAM). One explanation could be that juvenile plants of *Cyathea* are less dependent on mycorrhizae than mature plants.

All investigated samples of three species of *Asplenium* (Aspleniaceae) were free of fungal infection. The genus is not very diverse or abundant in the study sites compared to our three focus groups and occurred only on the lower slopes.

The samples of twelve terrestrial and epiphytic species of non-grammitid Polypodiaceae from the RBSF and surroundings (L. Pazmiño, pers. comm.; not included in list) are free of fungal infections, which is congruent with previous reports (Lesica & Antibus, 1992; Schmid et al., 1995).

We are aware that our sample size per species is quite low. Negative results in any species here included do not exclude the potential occurrence of mycorrhiza. We aim to widen our sample size in the future and want to include conspecific samples from sites with different substrate chemistry. This should allow us not only to distinguish between facultative and obligatory mycorrhizae but also about the conditioning factors.

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### Figure captions

- Fig. 1. Sampling area in southern Ecuador.
- Fig. 2. Mycorrhiza involving ascomycetes in ferns: septate hyphae and hyphal coils in the inner cortex of *Melpomene firma* (J. Sm.) A. R. Sm. & R. C. Moran; infection starts with penetration of the root hairs (arrows). Photo M. Lehnert.
- Fig. 3. Vesicular-Arbuscular Mycorrhiza (VAM) in ferns: aseptate hyphae and vesicles of an unidentified glomeromycete in the cortex of a fine root of *Loxomopsis pearcei* (Maxon) H. Christ. Photo M. Lehnert.
- Tab. 1. Samples investigated. Abbreviations: e = epiphyte, s = saxicol, t = terrestrial; VAM = vesicular-arbuscular mycorrhiza; EtOH = samples preserved in 70% ethanol; GA = samples preserved in glutardialdehyde. All vouchers are deposited at the herbarium GOET.

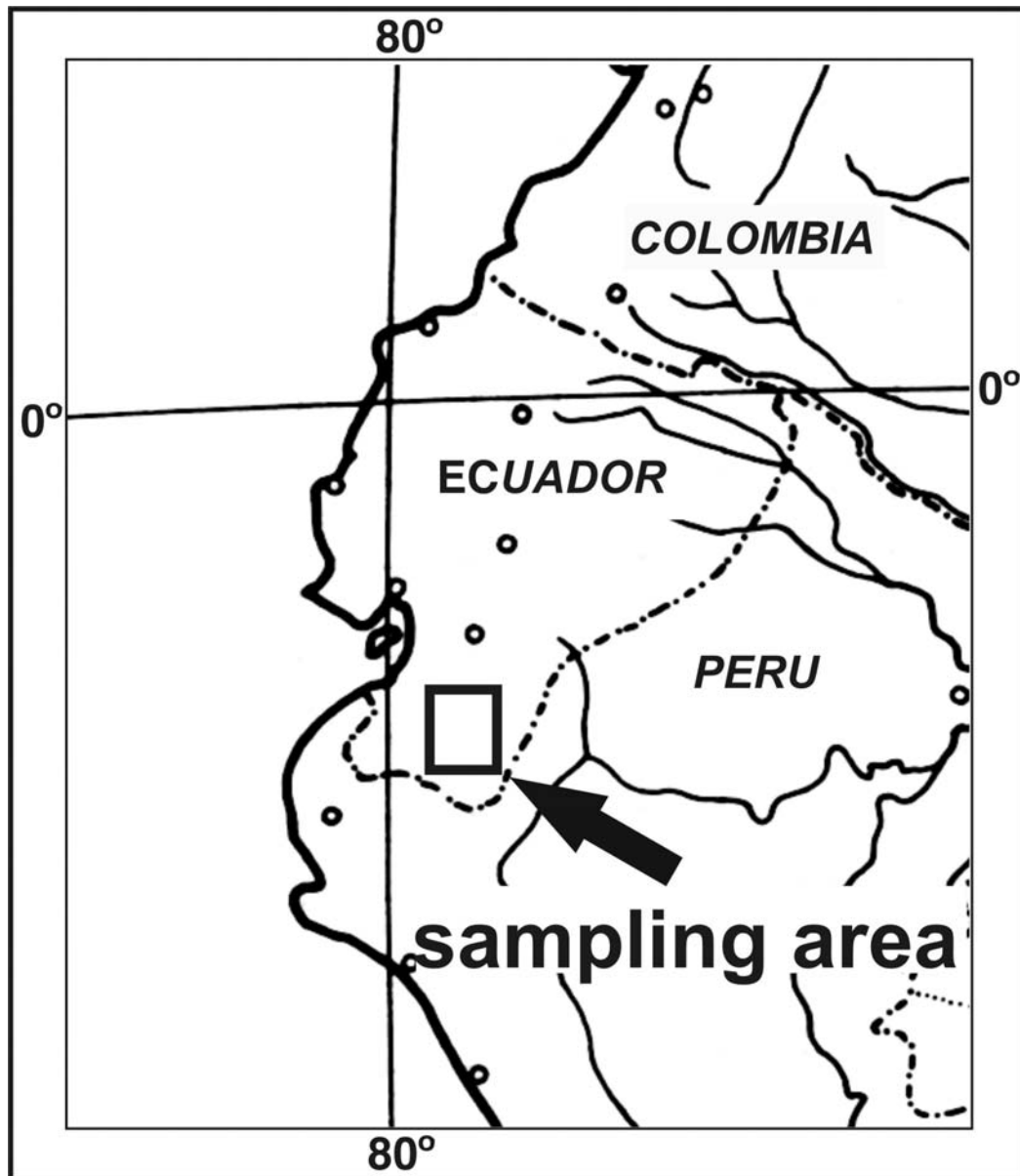


Fig. 1. Sampling area in southern Ecuador.

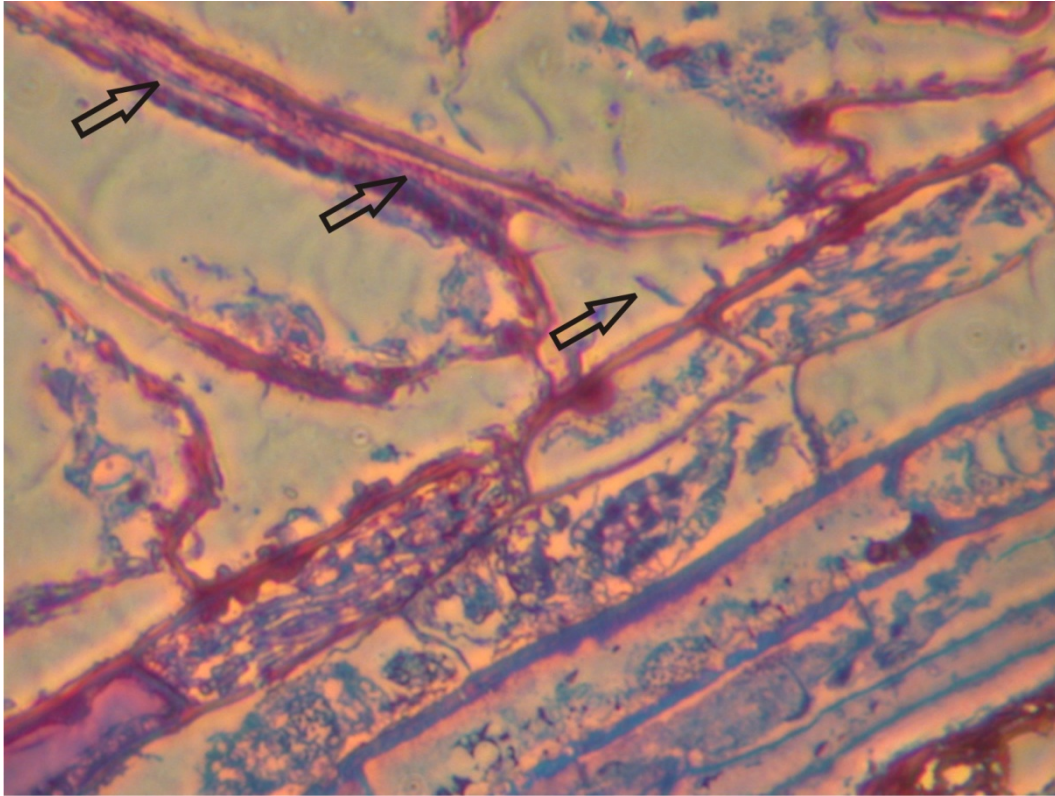


Fig. 2.



Fig. 3.

Tab. 1.

		species		substrate	fungal infection	VAM	other infection	observation	collection	EIOH	GA
<b>Aspleniaceae</b>											
Asplenium		aeritum Sw.		t	-	-	-	no infection	Lehnert M. 1473	+	+
Asplenium		hallii Hook.		t	-	-	-	no infection	Lehnert M. 1395	+	-
Asplenium		serra Langsd. & Fisch.		t	-	-	-	no infection	Lehnert M. 1394	+	-
<b>Blechnaceae</b>											
Blechnum		schomburgkii (Klotzsch) C. Chr. sp. 1		t	+	VAM	-	weak	Lehnert M. 1484	+	+
Blechnum				t	-	-	-	no infection	Lehnert M. 1440	+	+
<b>Cyatheaceae</b>											
Alsophila		conantiana Lehnert		t	+	VAM	-	abuscules	Lehnert M. 1414	+	+
Cyathea		bipinnatifida (Baker) Domin		t	+	-	-	no infection	Lehnert M. 1438	+	+
Cyathea		dudleyi R. M. Tryon		t	+	VAM	-	abuscules	Lehnert M. 1550	+	+
Cyathea		hybrid		t	-	-	-	no infection	Lehnert M. 1434	+	+
Cyathea		obnoxia Lehnert		t	-	-	-	no infection	Lehnert M. 1470	+	+
Cyathea		peladensis (Hieron.) Domin		t	+	VAM	-	abuscules	Lehnert M. 855	+	+
<b>Dryopteridaceae</b>											
Arachniodes		denticulata (Sw.) Ching		t	?	?	-	weak, root hair infection, not assignable	Lehnert M. 996	+	-
Elaphoglossum		antisanae (Sodirot) H. Christ		e	-	-	-	no infection	Lehnert M. 1485	+	+
Elaphoglossum		argyrophyllum (Sodirot) R. C. Moran, comb. ined.		e	-	-	-	no infection	Lehnert M. 1490	+	+
Elaphoglossum		deltoidum (Sodirot) H. Christ		t	-	-	-	no infection	Lehnert M. 1460	+	-
Elaphoglossum		deltoidum (Sodirot) H. Christ		t	-	-	-	no infection	Lehnert M. 1463	+	-
Elaphoglossum		dendricola (Baker) H. Christ		t	-	-	-	no infection	Lehnert M. 1458	+	-
Elaphoglossum		engelii (H. Karst.) H. Christ		t	+	-	Asco	-	Lehnert M. 1457	+	-
Elaphoglossum		erinaceum (F. e) T. Moore		e	+	-	Asco	coils, root hair infection	Lehnert M. 1387	+	+
Elaphoglossum		glossophyllum Hieron.		e	-	-	-	no infection, septate hyphae among root hairs	Lehnert M. 1551	+	+
Elaphoglossum		glossophyllum Hieron.		e	+	-	Asco	coils, root hair infection	Lehnert M. 1552	+	+
Elaphoglossum		guamanianum (Sodirot) C. Chr.		e	+	-	Asco	root hair infection, septate hyphae	Lehnert M. 1493	+	+
Elaphoglossum		heteromorphum (Klotzsch) T. Moore		t	+	VAM	-	abuscules	Lehnert M. 1462	+	-
Elaphoglossum		latifolium (Sw.) J. Sm.		e	+	VAM	-	abuscules	Lehnert M. 1492	+	+
Elaphoglossum		loense (Hook.) T. Moore		e	?	?	-	root hair infection, septate hyphae between cells	Lehnert M. 1491	+	+
Elaphoglossum		papillosum (Baker) H. Christ		t	+	-	Asco	coils	Lehnert M. 1472	+	+
Elaphoglossum		petiolosum (Desv.) T. Moore		e	+	-	Asco	septate hyphae	Lehnert M. & N. Mandl 1441	+	+
Elaphoglossum		productum Rosenst.		e	-	-	-	no infection	Lehnert M. 1553	+	+
Elaphoglossum		quiltense (Baker) C. Chr.		t	+	-	Asco	septate hyphae	Lehnert M. 1459	+	-
Elaphoglossum		sp. 1		e	+	-	Asco	root hair infection, septate hyphae	Lehnert M. 1487	+	+
Elaphoglossum		sp. 2		e	-	-	-	no infection	Lehnert M. 1486	+	+
Elaphoglossum		sp. 3		t	-	-	-	no infection, many root hairs	Lehnert M. 1502	+	-
Elaphoglossum		squarrosus (Klotzsch) T. Moore		t	+	VAM	-	abuscules	Lehnert M. 1488	+	+
Elaphoglossum		vulcanicum H. Christ		e	-	-	-	no infection	Lehnert M. 1475	+	+
Elaphoglossum		yatesii (Sodirot) H. Christ		t	+	-	Asco	weak, root hair infection, septate hyphae	Lehnert M. 1461	+	-
Elaphoglossum		kilippii (Maxon) Tindale		t	+	VAM	-	abuscules	Lehnert M. 980	+	-
Polystichum		platyphyllum (Willd.) C. Presl		t	+	VAM	-	weak	Lehnert M. 1412	+	+
<b>Gleicheniaceae</b>											
Slicherus		brevitomentosus B. Ælig. & Æstergaard		t	-	-	-	no infection	Lehnert M. 1480	+	+
Slicherus		melanoblastus Æstergaard & B. Ælig.		t	-	-	-	no infection	Lehnert M. 1476	+	+
Slicherus		melanoblastus Æstergaard & B. Ælig.		t	-	-	-	no infection	Lehnert M. 1549	+	+
Slicherus		rubiginosus (Mett.) Nakai		t	-	-	-	no infection	Lehnert M. 1268	+	+
Slicherus		rubiginosus (Mett.) Nakai		t	+	VAM	-	abuscules	Lehnert M. 1478	+	+
Slicherus		sp. 1		t	+	VAM	-	abuscules	Lehnert M. 1479	+	+
Slicherus		tomentosus (Cav. ex Sw.) A. R. Sm.		t	-	-	-	no infection	Lehnert M. 1477	+	+



Tab. 1, continued

species	substrate	fungal infection	VAM	other infection	observation	collection	EIOH	GA
<u>Hymenophyllaceae</u>								
Abrodictyum rigidum (Sw.) Ebihara & Dubuisson	t	+	VAM	-	arbuscules	Lehnert M. 1515	+	-
Hymenophyllum calodictyon Bosch	e	+	-	Asco	septate hyphae	Lehnert M. 1443	+	+
Hymenophyllum cristatum Hook. & Grev.	e	+	-	Asco	septate hyphae	Lehnert M. 1547	+	+
Hymenophyllum fucoides (Sw.) Sw.	e	+	-	Asco	septate hyphae	Lehnert M. 1444	+	+
Hymenophyllum microcarpum Desv.	t	+	-	Asco	coils, root hair infection	Lehnert M. 1494	+	+
Hymenophyllum multilatum C. V. Morton	e	+	-	Asco	septate hyphae	Lehnert M. 1447	+	+
Hymenophyllum plumieri Hook. & Grev.	e	+	-	Asco	septate hyphae	Lehnert M. 1362	+	+
Hymenophyllum polyanthos (Sw.) Sw.	e	+	-	Asco	septate hyphae	Lehnert M. 1445	+	+
Hymenophyllum sp. 1	e	-	-	-	no infection	Lehnert M. 1455	+	-
Hymenophyllum sp. 2	s	-	-	-	no infection	Lehnert M. 1566	+	-
Hymenophyllum trichomanoides Bosch	e	+	-	Asco	septate hyphae	Lehnert M. 1446	+	+
Trichomanes cellulolum Klotzsch	t	+	VAM	-	arbuscules	Lehnert M. 1481	+	+
Trichomanes dactylites Sodiro	t	+	-	Asco	coils, root hair infection	Lehnert M. 1501	+	+
Trichomanes elegans Rich.	s	+	VAM	-	arbuscules	Lehnert M. 1516	+	-
Trichomanes pellicens Kunze	t	+	VAM	-	arbuscules	Lehnert M. 1514	+	-
Trichomanes sp. 1	e	+	-	Asco	septate hyphae	Lehnert M. 1483	+	+
Trichomanes sp. 2	s	-	-	-	no infection	Lehnert M. 1546a	+	-
Trichomanes sp. 3	t	-	-	-	no infection	Lehnert M. 1482	+	+
<u>Loxomataceae</u>								
Loxomopsis pearcei (Maxon) Baker	t	+	VAM	-	arbuscules	Lehnert M. 1056	+	+
<u>Polypodaceae</u> [grammitids]								
Ceradenia glabra A. R. Smith & M. Kessler	e	+	-	Asco	root hair infection, septate hyphae	Lehnert M. 1495	+	-
Cochlidium serrulatum (Sw.) L. E. Bishop	t	+	-	Asco	root hair infection, septate hyphae	Lehnert M. 1467	+	+
Enterosora parietina (Klotzsch) L.E. Bishop	e	+	-	-	no infection	Lehnert M. 1497	+	-
Lellingeria major (Coppel) A. R. Sm. & R.C. Moran	e	+	-	Asco	septate hyphae	Lehnert M. 1498	+	-
Lellingeria major (Coppel) A. R. Sm. & R.C. Moran	t	+	-	Asco	septate hyphae	Lehnert M. 1466	+	+
Lellingeria subessilis (Baker) A. R. Sm. & R. C. Moran	e	+	-	-	no infection	Lehnert M. 1499	+	-
Meipomene assurgens (Maxon) A. R. Sm. & R. C. Moran	e	+	-	Asco	septate hyphae	Lehnert M. 1427	+	+
Meipomene erecta (C. V. Morton) A. R. Sm. & R. C. Moran	t	+	-	Asco	weak	Lehnert M. 1570	+	+
Meipomene firma (J. Sm.) A. R. Sm. & R. C. Moran	e	+	-	Asco	septate hyphae	Lehnert M. 1328	+	+
Meipomene gracilis (Hook.) A. R. Sm. & R. C. Moran	s	+	-	Asco	weak	Lehnert M. 1569	+	-
Meipomene moniliformis (Lagasca ex Sw.) A. R. Sm. & R.C. Moran	e	+	-	Asco	weak, coils	Lehnert M. 1559	+	-
Meipomene moniliformis (Lagasca ex Sw.) A. R. Sm. & R.C. Moran	t	+	-	Asco	root hair infection, septate hyphae	Lehnert M. 1510	+	-
Meipomene occidentalis Lehnert	t	-	-	-	no infection	Lehnert M. 1507	+	+
Meipomene occidentalis Lehnert	t	-	-	-	no infection	Lehnert M. 1508	+	+
Meipomene pseudonutans (Rosenst. & Christ) A.R. Smith & R.C. Moran	s	+	-	Asco	root hair infection, septate hyphae	Lehnert M. 1558	+	-
Meipomene pseudonutans (Rosenst. & Christ) A.R. Smith & R.C. Moran	t	+	-	Asco	weak, root hair infection	Lehnert M. 1464	+	+
Meipomene sklenarii Lehnert	t	+	-	Asco	septate hyphae	Lehnert M. 1465	+	+
Terpsichore lanigera (Desv.) A. R. Sm.	e	-	-	-	no infection	Lehnert M. 1496	+	-
Terpsichore leucosticta (J. Sm.) A. R. Sm.	t	+	-	Asco	coils, root hair infection	Lehnert M. 1509	+	+
Terpsichore semihirsuta (Klotzsch) A. R. Sm.	t	+	-	Asco	septate hyphae	Lehnert M. 1511	+	+
<u>Pteridaceae</u>								
Pteris muricata Hook.	t	+	VAM	-	arbuscules	Lehnert M. 1571	+	-
Pterozonium brevifrons (A. C. Sm.) Lellingier	s	+	VAM	-	weak	Lehnert M. 1435	+	-
<u>Thelypteridaceae</u>								
Thelypteris minutula C. V. Morton	s	-	-	-	no infection	Lehnert M. 1337	+	-

### III.3. Mycorrhizae and pteridophytes – a global phylogenetic perspective

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**Abstract:** We compiled a list of the known mycorrhizal status of pteridophytes worldwide. As each report was done in a different manner, we equalized the differences by restricting our summary to an absent/present enumeration of fungal infection, and distinguishing only vesicular-arbuscular mycorrhiza (VAM) from other types of infections. A total of 773 different gatherings from twelve studies were considered, which cover 675 species of 33 families. In average, 62% of all samples were infected by symbiotic fungi, which are significantly unevenly distributed among the families. In 26 families (including grammitid ferns [Polypodiaceae]) we find mycorrhizal rates of or above the average. Three families have a very low percentage of mycotrophism (22% in Equisetaceae, 23% in Polypodiaceae without grammitid ferns, and 25% in Tectariaceae). The aquatic families Salviniaceae and Marsileaceae are without fungal infection. The association with arbuscular mycorrhizal fungi (AMF) in VAM is most common, especially in terrestrial habitats. In 28 families (including Polypodiaceae without grammitid ferns), AMF contribute to 50% or more of the mycorrhizae, in 13 families even 100%. Although the record of ascomycete infections is fragmentary, it indicates that these are frequent in epiphytic ferns, which have previously been considered to mostly lack mycorrhizae. The kind of fungal partner is still undefined for many species. Future studies preferably should include ecological factors of the collections sites and should aim on the distinction between facultative and obligatory mycorrhiza, which has been neglected in the past.

Keywords: AMF, aquatic, ascomycetes, epiphytic, ericoid, mycorrhiza, pteridophytes, saxicol, terrestrial, VAM.

### **Introduction**

Mycorrhizae are one of the most important symbioses on earth, and the mutual connections between plants and soil fungi are so diverse that they epitomize the ecological web (Allen et al., 2003; Brundrett, 2004). In many aspects mycorrhizae have been intensively studied, especially among plants of economic and agricultural value (e.g. Subramanian & Charest, 1998; Greipsson & El-Mayas, 2000; Jakobsen et al., 2005). However, the record of the mycorrhizal status is still fragmentary and contradictive for many plant groups. The pteridophytes, understood here in the traditional sense including ferns and lycophytes with their ca. 12000 species worldwide (Smith et al. 2006), are among them. Partly, this is because most species are found in the tropics, which are less frequently visited by ecologically oriented botanists. For the other part, ferns are not economically important, and thus not as often the topic of ecophysiological studies as are crops. Nevertheless, over the last century several studies have included information on fungal symbionts in fern roots. Earlier works (e.g., Boullard, 1958; Hepden, 1960; Cooper, 1976; Newman & Reddell, 1987) suggested that mycotrophism occurs in all fern families, even if it may be inconsistent. More recent investigations, however, indicate a much lower percentage of ferns and fern allies to be mycorrhizal (e.g., Gemma et al., 1992). An aspect rarely considered is that the mycorrhizal status of a given species may be dependent from life stage or substrate type (Gemma et al., 1992), although already Boullard (1958, 1979) and Hepden (1960) pointed out that such correlations exists.

The purpose of the present study was mainly to estimate the frequency of mycorrhiza in ferns worldwide and to place these in a phylogenetic perspective based on recently published studies (Smith et al., 2006). The summary should also reveal underrepresented families that merit further investigation. Contradicting reports of the mycorrhizal status of certain species may indicate facultative associations correlated to abiotic factors (e.g., soil, temperature, and precipitation).

### **Materials and Methods**

Accounts of mycorrhizae in ferns and fern allies were extracted from literature (App. 1). Each different report for a species was counted as one sample and associated with one mycorrhizal condition, even if the original study included several samples of a species with different results (e.g., Gemma et al., 1992; Zhao Zhi-wei, 2000). We distinguished between general fungal infection and type of fungal infection. The latter category was further divided into

confidential reports of vesicular arbuscular mycorrhiza (VAM) and unspecified accounts (App. 1), which may contain further VAM and other kinds of mycotrophism, e.g., association with ascomycetes (Duckett & Read, 1995; Kottke, 2001) (App. 1). We distinguished between terrestrial, epiphytic, saxicolous, and aquatic plants. Gatherings of the same species from different substrates were counted as separate samples, even if they were included in the same study. Some screenings (Cooper, 1976; Zhao Zhi-wei, 2000; Zhang et al., 2003) did not specify the type of substrate the sampled species were growing in. The preferred substrate type of these species has been evaluated from literature (Edie, 1978; Brownsey & Smith-Dodsworth, 1989) and herbarium specimens at UC; Alan R. Smith (UC) provided information on New Zealand ferns, and Laine Huiet (UC) on the genus *Adiantum*. If a species can be found on more than one substrate type, the most common occurrence was considered. The results were tested for goodness of fit using the G-test (Fowler et al., 1998).

The classification of the fern families follows Smith et al. (2006). The genera and names have been changed accordingly in Tab. 2 and App. 1.; the originally published names are given in parentheses in App. 1. Names were corrected where necessary according to *IPNI* and the *Index Filicum*. Author abbreviations follow Pichi Sermolli (1996).

## Results

We found a total of 12 published studies with reliable information on mycorrhizae in ferns (Tab. 1). Boullard's work (1958, 1979) was the first general survey on fern mycorrhizae and considered many aspects often neglected in later studies, like the different life stages of the plant, life form, and substrate chemistry. The used classification of the mycorrhizae, however, is obsolete today, and many of his drawings indicate that he apparently included ascomycetes, visible as dense hyphal coils in the root cells, in his account (e.g., Boullard, 1958; plate V, fig. 2). Most of his samples were taken from cultivated plants or from herbarium specimens, which puts the confidence in his findings in question. Cultivated plants may be exposed to different fungi than in the wild, or may dispense of their mycorrhiza under optimized growth conditions. The dried condition of herbarium material leads to a diminished coloration of the fungal hyphae and possible wrong identification of the infection. Because of the uncertainty in the identity and originality of the mycorrhizae, Boullard's work, although insightful and funded on a broad basis, was not included in our survey. The study of Cooper (1976) is included in our survey because it covers only samples collected in situ, although the 101 species are unspecified regarding their infection. They were included in the VAM count

because back then only vesicular-arbuscular mycorrhiza (VAM) involving glomeromycetes (AMF) was usually considered as a true symbiosis.

In total our survey uncovered 773 individual samples involving 675 pteridophyte species from 33 families (App. 1). In most studies, the samples were screened for VAM only, and no information about other fungal infections is given. Accordingly, we can report 315 specimens (297 species) with classical mycorrhiza evident as arbuscules (AMF). Lehnert et al. (in prep. b) and Schmid et al. (1995) further found evidence of ascomycete-association in at least 52 species. Since some investigations (Berch & Kendrick, 1982; Ragupathy & Mahadevan 1993; Muthukumar & Udaiyan, 2000; Zhao et al., 2000; Zhang, 2003) looked only for infection by glomeromycetes (AMF; VAM) and may have not counted specimens with ascomycete-infections, the number of specimens free of fungal infection is between 86 and 290 specimens. Using the higher estimate, we still find mycotrophism in 62% of the investigated samples. VAM is present in 41% of the samples, comprising 66% of the infections. The comparison of the proportions shows that mycorrhizae are differently distributed among the fern families with high significance (G-test;  $df= 33$ ,  $G= 63.69$ ,  $P< 0.01$ ).

Comparing the substrate types, 762 samples (675 species) were included in the analysis; 11 species (6 *Asplenium*, 5 *Pteris*) could not be associated with one substrate type and were omitted from this comparison (Tab. 2). Mycotrophism is high in terrestrial, saxicolous, and epiphytic habitats, with 67%, 59% and 53%, respectively, while it is almost absent in aquatic ferns (9%), accounting to only one infected specimen. This distribution differed only in the last case significantly (G-test;  $df= 1$ ,  $G_{adj}= -9.06$ ,  $P< 0.01$ ) from the observed mean (62%).

Epiphytic species constitute a high percentage of the ascomycete infections (67%) (App. 1). In contrast, only 24 (8%) of 315 samples with VAM grew epiphytically; the others were predominantly terrestrial (84%) or saxicolous (7%). This distribution is significantly skewed (G-test;  $df= 6$ ,  $G= 85.60$ ,  $P< 0.01$ ).

Only two families (Marsileaceae, Salviniaceae) were completely non-mycorrhizal, but the sample size in these cases is low (3-4 species each). Similarly, the families that are listed as 100 % mycorrhizal (Davalliaceae, Dicksoniaceae, Loxomataceae, Onocleaceae, Plagiogyriaceae, and Schizeaceae) are represented by only one or two species in the analysis. The lowest percentages of fungus-associated species were found in the Polypodiaceae (without grammitid ferns) (23%; 60% VAM), Equisetaceae (22%; 100% VAM), and

Tectariaceae (25%; 50% VAM). The percentage of infected samples varies significantly between the families (Tab. 2).

### Discussion

The percentage of mycorrhizae in pteridophytes as documented by our survey, which covers ca. 6% of the extant pteridophyte diversity, averages 62% and lies between the findings of previous studies (97%, Newman & Redell, 1987; 75%, Gemma et al., 1992; 36%, Moteetee et al., 1996; 32%, Zhao 2000). Lesica and Antibus (1990), focusing on epiphytes, could not report any bona fide mycorrhiza in 12 fern species from Costa Rica.

The varying results in the percentages are partly explained by the focus on VAM in most studies. Other fungal infections are often not considered as symbiotic but as pathogenic or endobiotic. Recent studies on liverworts (Duckett & Read, 1995; Chambers et al., 1999; Kottke et al., 2003; Kottke & Nebel, 2005) and neotropical ferns (Schmid et al., 1995) suggest the existence of previously unrecognized types of mycorrhiza involving ascomycetes, akin to those forming the ericoid mycorrhiza type (Duckett & Read, 1995; Brundrett, 2002; Kottke, 2002). The simple observation of ascomycetes in living root cells may be equivocal because these fungi are very common saprophytes, and thus they may just prematurely attack the roots. Electron microscopic studies give evidence if the host cell is still intact after infection and reacting to it (Schmid et al., 1996), which is a criterion for real mycorrhiza. An association with basidiomycetes, which form most mycorrhizae with northern temperate trees (Kottke, 2002), has not yet been found in the roots of pteridophytes.

The correlations between substrate type and mycorrhiza are long known. Boullard (1958) gave the generalization that mycorrhizae are absent in ferns growing on calcareous rocks, in water, and among most epiphytes. Indeed, the aquatic habitat hosts only few mycorrhizal species. The reasons are suspected to be inhibited growth of the fungi in the low aerated medium (Boullard, 1958). Floating plants, like species of *Ceratopteris* and the members of the Salviniaceae, have all possible nutrients available in their easiest accessible form solved in the water, and do not need a costly symbiosis that mediates in nutrient-uptake. The mycorrhizae reported in *Isoetes coromandelina* L. (Ragupathy & Mahadevan, 1993) and *Pilularia globulifera* L. (Boullard, 1958; not included in analysis) apparently occur only when the plant grows not submerged, like in periodically drying water bodies. In this case, the fungi may act more as a root extension for increased uptake of water than of nutrients.

Epiphytic pteridophytes are to a comparable extend mycorrhizal as are terrestrial pteridophytes (Tab. 2), but the ratio of VAM to other fungal infections is reversed. The

dominance of ascomycetes among the mycorrhizae is likely the reason why most epiphytes have been scored as non-mycorrhizal in the past. The change of the fungal partner from the primarily soil-dwelling glomeromycetes to ascomycetes is understandable in the context of the demands by the habitat, which is disconnected from the soil, often short-lived and regularly originates *de novo*. This may be a problem because mycorrhizae have to be built up in the roots repeatedly from inoculum, i.e., spores or hyphae. Since glomeromycetes apparently are not viable without symbiosis, the establishment of a VAM in epiphytic habitats requires facultatively mycorrhizal plants, which already grow on the branches when the fungal diaspore arrives (Janos, 1993). Establishing a new mycorrhiza with an ubiquitous litter decomposer like the ascomycetes allows obligatively mycorrhizal plants with small diaspores to conquer even the outer branches of a tree and benefit from the advantages of the symbiosis from an early stage, as seen in Orchidaceae (Brundrett, 2002).

Saxicolous ferns have generally been considered to have low rates of mycorrhization (Boullard, 1958; Olsson & Tyler, 2004). Our survey, however, shows mycorrhiza in 59 % (42% VAM) of the saxicolous pteridophyte species, which is almost equal to the infection rate of the terrestrial specimens (Tab. 2, 3). A similar ratio has been previously shown in Hawaiian ferns (Gemma et al., 1992), where saxicolous ferns even surpass the terrestrial ferns in mycotrophy (86% saxicolous vs. 83% terrestrial). A reason for this may be an erroneous assessment of the substrate. Many species listed as saxicolous, e.g., *Cystopteris fragilis* (L.) Bernh, should probably rather be considered as terrestrials. Even though these species are found mainly in rock outcrops and in cracks, most of them grow only when enough soil has accumulated in fissures, thus creating rooting conditions comparable to a typical terrestrial habitat.

Comparing the fungal infections across the different pteridophyte lineages, it is striking that most families have high rates of fungal infection, ranging from 50% to 100% of the samples in 26 of the 34 recognized families. The records of fully mycorrhizal families (Davalliaceae, Dicksoniaceae, Loxomataceae, Onocleaceae, Plagiogyriaceae, and Schizeaceae) are based on very small samples sizes (1-2 samples and species) and should be treated with caution. However, a comparison with their ecologically similar but better sampled sister taxa suggests that the percentage will stay above the average if more samples are investigated (Tab. 2). Uncertainty remains in the equally underrepresented Anemiaceae. The mycorrhization of the Isoetaceae is certainly much lower than found in our survey, as the observations of older studies indicate (Boullard, 1958).



The presence of VAM (AMF infection) is generally high among fern families, even in families with low overall mycorrhization, such as Equisetaceae (100% of infected samples), Polypodiaceae (60%), and Tectariaceae (50%) (Tab. 2). A contrary trend is only seen in the grammitid ferns (Polypodiaceae) and the Hymenophyllaceae, especially the genus *Hymenophyllum*, which are mainly epiphytes with ascomycetes as fungal partner (Tab. 2). This is interesting in an evolutionary context because AMF are supposed to be the primordial partners in the symbiosis (Brundrett, 2002). There is fossil evidence of AMF from the Devonian (Taylor, 1990) and it has been hypothesised that these fungi enabled the early tracheophytes to conquer the dry land (Simon et al. 1993). The epiphytic habitat, on the other hand, as known from extent biota, is historically quite young and supposedly connected with the special architecture of angiosperm trees with open crowns and wide branches, which dominate the vegetation only since the late Cretaceous (Willis & McElwain, 1997). Gymnosperm trees, which dominated the forests prior to the radiation of the polypod ferns (sensu Smith et al., 2006), do not support an epiphytic plant community as diverse as angiosperm trees do (pers. obs.). Angiosperms are suspected to have triggered the radiation of the core leptosporangiate ferns in the late Mesozoic and early Neozoic (Schneider et al., 2004) by changing forest structure and soil properties (Lehnert et al., in prep. a [chapter III.1]). Both may have had a major impact on type and frequency of mycotrophism in ferns, as in land plants in general. The progenitors of the epiphytic taxa had to adapt to the special conditions in the tree crown like discussed above, including the infrequent availability of AMF inoculum. Loss or flexibility of mycotrophism, as seen in the Polypodiaceae, and change to a more independent fungal partner (e.g., ascomycetes), as seen in the grammitid ferns and the Hymenophyllaceae, may have favoured the development of epiphytism in ferns. On the other side, the terrestrial ferns experienced a better nutrient availability by the leaf litter of the dominant angiosperms (Lehnert et al., in prep. a), which decomposes and releases micronutrients faster than gymnosperm or fern litter (Wardle et al., 2003), probably making it possible for the plants to dispense of mycotrophism (Brundrett, 2002). Correspondingly, one should observe these trends in the phylogenies, but the correlation is quite low (Fig. 1). However, the expected trend can be observed in the gametophytes of ferns and fern allies, which often have different mycorrhizal conditions than the sporophytes (Boullard 1958, 1979). The Lycopodiaceae are a phylogenetic old lineage (Fig.1), whose prothallia are predominantly chlorophyll-free, subterranean, and obligatorily mycotrophic (Boullard, 1958, 1979; Kubitzky et al., 1997), but whose sporophytes often dispense of the symbiosis (Tab. 2). The green epigeaus prothallia of the leptosporangiate ferns show a reduction of fungal

association (Boullard, 1958, 1979) from constant in basal lineages like Gleicheniaceae to absent in the core leptosporangiate ferns (Fig. 1), which include the Cyatheaceae and Polypodiaceae in the old sense (Pryer et al., 2004; Smith et al., 2006) as cited by Boullard (1958).

The pattern may be obscured in the sporophytes by errors in the percentages due to insufficient sample size (Fig. 1), or may emerge clearer if more parameters are considered, like the differentiation between obligatory and facultative mycorrhiza. This is excluded in our analysis because of insufficient and inconsistent information, but may have major importance in this context. Since phylogenetically derived fern lineages have coevolved with improved soil conditions, they may have at least a higher frequency of facultative mycorrhizal species or lower rates of fungal infections in the roots than basal lineages.

An aspect that has to be taken into account when labelling a species as mycorrhizal or non-mycorrhizal is that mycorrhizae are present only during determined phases in the life of a root (Brundrett, 2002) and may be missed in limited samples. Furthermore, there are indications of seasonality in mycorrhizae (Boullard, 1958; Iqbal, 1981), meaning that in some regions mycorrhizal fungi are less frequent in the soil and may be not detectible in the roots of the plants during certain periods (i.e., cold and dry seasons). This is surely of importance in temperate regions, but its relevance in the humid tropics is unknown. Plants that follow the seasonal cycle of the soil fungi and are mycorrhizal during the growth seasons should be considered obligatorily mycorrhizal (Iqbal et al., 1981; Allen, 1983). Finally, information about the soil fertility is helpful for discriminating obligatory and facultative mycorrhizae. Diverse ecological studies with angiosperms have shown that mycorrhizal infection may be influenced by the fertility of the substrate (e.g., Nilsson & Wallander, 2004; Titus & Lepš, 2000; West, 1995). Some host plant species reduce the fungal infection actively if the soil is fertilized and the mycorrhizae just means a loss of assimilates (West, 1995).

The correlation between phylogenetic position of the pteridophyte and their dependence on mycorrhiza surely deserves more study.

### **Conclusions**

Mycotrophism in pteridophytes is not as prevalent as, but much more diverse than previously thought. In the course of evolution, it has been modified, lost, and regained in the individual fern lineages. Most apparent is the change of the fungal partner during the switch from the terrestrial to the epiphytic habitat. Mycorrhizal associations may be a major factor responsible

for the ecological diversity we observe in extant members of pteridophytes and contain a phylogenetic signal. Future studies preferably should aim to (a) sample fern lineages whose mycorrhizal status is little known, (b) clarify the status and ecological role of ascomycetes as mycotrophic partners of pteridophytes, (c) distinguish the several types of fungal partners and between facultative and obligatory mycorrhizae, which has been neglected in the past, and (d) test the phylogenies of ferns and mycorrhizal fungi for possible co-evolutions.

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### Figure captions

Fig. 1. Comparison of the phylogeny of pteridophytes (lycophytes and ferns) with the percentage of observed fungal infection pictured as black outline; presence of vesicular arbuscular mycorrhiza (VAM) light gray, ascomycetes in dark gray, and unspecified infections in white. Numbers behind columns are species number per family/investigated species; in brackets are investigated samples/infected samples. “d.d.” = data deficient. Phylogenetic tree altered from Pryer et al. (2004) and Smith et al. (2006).

Tab. 1. Reports used in this study, with number of investigated species and registered cases of mycorrhiza.

Tab. 2. Comparison of the mycorrhizal infections and types among the investigated samples the families according and substrate types. “Total” always refers to the number of incorporated samples. Aspleniaceae and Pteridaceae were represented with more samples in the general overview (App. 1); number shown in brackets.

Tab. 3. Summary of VAM and general infection rate distributed among the four substrate types. Values in brackets: \* undefined infections; \*\* only screened for VAM, other infections possible.

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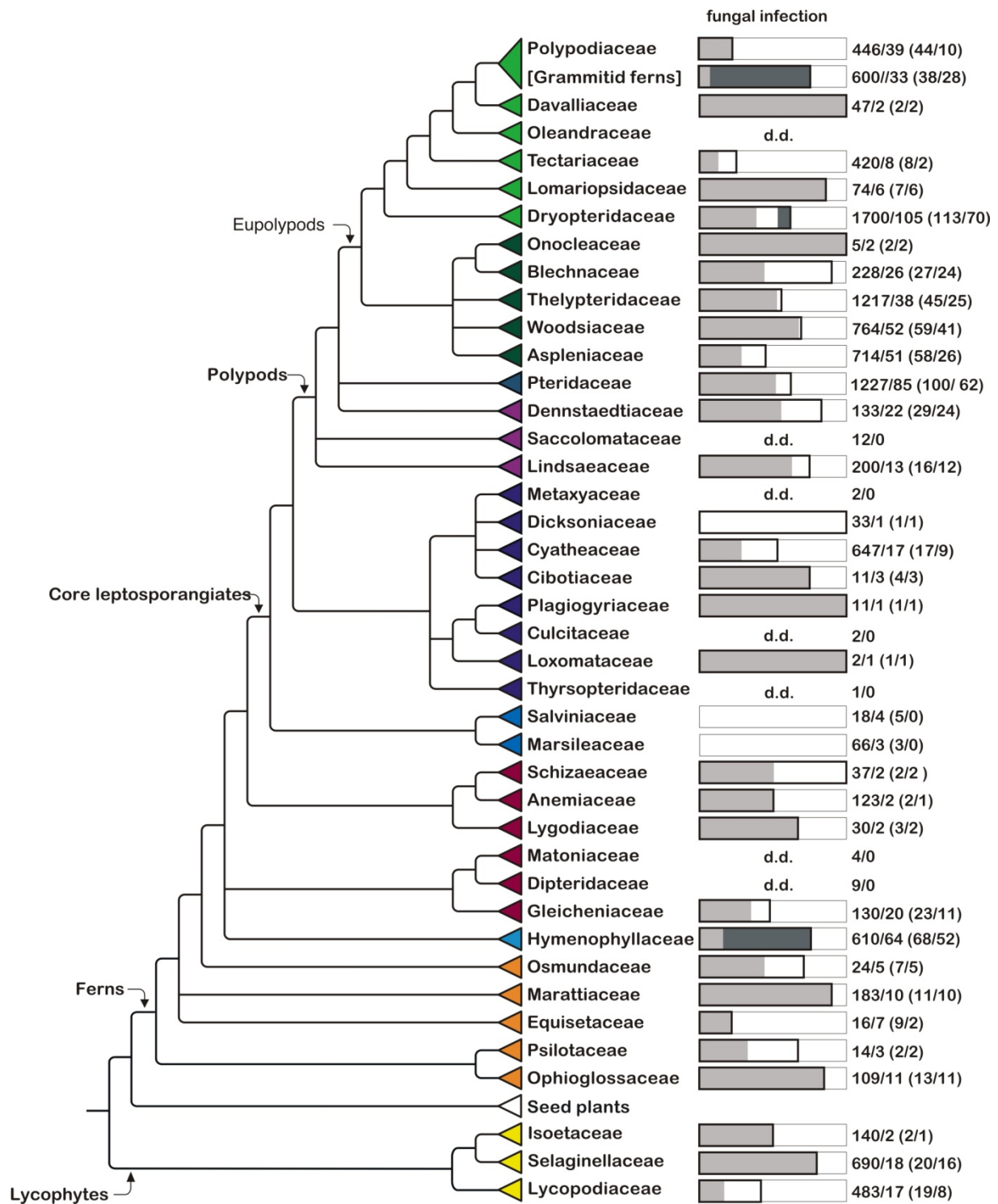


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Tab. 1. Reports used in this study, with number of investigated species and registered cases of mycorrhiza.

publication	area	investigated sp.	infected sp.
Berch & Kendrick 1982	Canada	39	26
Cooper 1976	New Zealand	101	101
Gemma et al. 1992	Hawaii	88	67
Iqbal et al. 1981	Pakistan	16	16
Lehnert et al., in prep. b	Ecuador	86	52
Lesica & Antibus, 1990	Costa Rica	10	0
Moteetee et al., 1996	Lesotho, South Africa	49	12
Muthukumar & Udaiyan, 2000	India	73	61
Ragupathy & Mahadevan 1993	India	4	1
Schmid 1995	Costa Rica	64	28
Zhang et al., 2003	China	34	27
Zhao Zhi-wei, 2000	China	202	83

Tab. 2. Comparison of the mycorrhizal infections and types among the investigated samples the families according and substrate types. "Total" always refers to the number of incorporated samples. Aspleniaceae and Pteridaceae were represented with more samples in the general overview (App. 1); number shown in brackets.

family	total of sam-plings	number of species	infected samples			epiphytic			terrestrial			saxicol			aquatic			infected	
			total	VAM	other	total	VAM	other	total	VAM	other	total	VAM	other	total	VAM	other	%	total
Anemiaceae	2	2	1	1	0	0	0	0	0	0	0	2	1	0	0	0	0	50	
Aspleniaceae (64)*	58	51	26	16	10	1	29	12	5	13	4	4	4	0	0	0	45		
Blechnaceae	27	26	24	12	12	0	25	10	12	2	2	0	0	0	0	0	89		
Cibotiaceae	4	3	3	3	0	0	4	3	0	0	0	0	0	0	0	0	75		
Cyatheaceae	17	17	9	5	4	0	17	5	4	0	0	0	0	0	0	0	53		
Davalliaceae	2	2	2	2	0	0	2	0	0	0	0	0	0	0	0	0	100		
Dennstaedtiaceae	29	22	24	16	8	0	29	16	8	0	0	0	0	0	0	0	83		
Dicksoniaceae	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	100		
Dryopteridaceae	113	105	70	44	23	13	81	37	13	0	0	0	0	0	0	0	62		
Equisetaceae	9	7	2	2	0	0	9	2	0	0	0	0	0	0	0	0	22		
Gleicheniaceae	23	20	11	8	3	0	23	8	3	0	0	0	0	0	0	0	48		
Hymenophyllaceae	68	64	52	11	41	3	29	17	6	9	2	2	0	0	0	0	76		
Isoetaceae	2	2	1	1	0	0	0	0	0	0	0	0	0	0	2	1	50		
Lindsaeaceae	16	13	12	10	0	0	16	10	0	0	0	0	0	0	0	0	75		
Lomariopsidaceae	7	6	6	6	0	0	6	6	0	0	0	0	0	0	0	0	86		
Loxomataceae	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	100		
Lycopodiaceae	19	17	8	3	5	2	13	1	4	0	0	0	0	0	0	0	42		
Lygodiaceae	3	2	2	2	0	0	3	2	0	0	0	0	0	0	0	0	67		
Marattiaceae	11	10	10	10	0	0	11	10	0	0	0	0	0	0	0	0	91		
Marsileaceae	3	3	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0		
Onocleaceae	2	2	2	2	0	0	2	2	0	0	0	0	0	0	0	0	100		
Ophioglossaceae	13	11	11	11	0	1	12	10	0	0	0	0	0	0	0	0	85		
Osmundaceae	7	5	5	3	2	0	7	3	2	0	0	0	0	0	0	0	71		
Plagiogyraceae	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	100		
Polypodiaceae	44	39	10	6	4	4	9	3	2	4	1	0	0	0	0	0	23		
Polyodiaceae (grammitids)	38	33	28	2	26	2	18	11	0	9	3	0	2	0	0	0	74		
Psilotaceae	3	3	2	1	1	1	2	0	1	1	0	0	0	0	0	0	67		
Pteridaceae (105)*	100	85	62	52	10	12	74	41	10	13	9	0	1	0	0	0	62		
Salviniaceae	5	4	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0		
Schizeaceae	2	2	2	1	1	0	2	1	1	0	0	0	0	0	0	0	100		
Selaginellaceae	20	18	16	16	0	1	17	14	0	2	1	0	0	0	0	0	80		
Tectariaceae	8	8	2	1	1	1	0	7	1	0	0	0	0	0	0	0	25		
Thelypteridaceae	45	38	25	24	1	0	44	24	1	1	0	0	0	0	0	0	56		
Woodsiaceae	59	52	41	40	1	0	55	38	0	4	2	1	0	0	0	0	55		
total	762	675	472	313	154	171	24	66	527	268	84	53	22	9	11	1	62		

Tab. 3. Summary of VAM and general infection rate distributed among the four substrate types. Values in brackets: \* undefined infections; \*\* only screened for VAM, other infections possible.

	epiphytic	saxicol	terrestrial	aquatic
samples	171	53	527	11
VAM vs. no VAM	24(+22*)/125(+22)	22(+22)/125(+22)	266(+71)/179(+71)	1/10
fungal vs. non-fungal	87(+25**)/59(+25)	32(+18)/3(+18)	352(+143)/21(+143)	1/10

Appendix 1. Samples of all used species listed alphabetically after the family according to Smith et al. (2006); reports of the same species from different reports are counted as separate samples. Originally published names are given in brackets.

species	listed as ...	region	country	publication	substrate	Fungal infect.	VAM	other
<b>Anemiaceae</b>								
1	<i>Anemia cafrorum</i> (L.), comb. ined.	Africa	Lesotho	Moteete et al., 1996	saxicol	?	-	not inv.
2	<i>Anemia hirsuta</i> (J. P. Roux), comb. ined.	Africa	Lesotho	Moteete et al., 1996	saxicol	+	VAM	not inv.
<b>Aspleniaceae</b>								
3	<i>Asplenium adiantum-nigrum</i> L.	Africa	Lesotho	Moteete et al., 1996	saxicol	+	VAM	not inv.
	<i>Asplenium adiantum-nigrum</i> L.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	
4	<i>Asplenium aethiopicum</i> (Burm. f.) Bech.	Africa	Lesotho, South Africa	Moteete et al., 1996	terrestrial, saxicol, epiphytic	+	VAM	not inv.
5	<i>Asplenium anthrophyoides</i> H. Christ	Asia	China	Zhao Zhi-wei, 2000	?	?	-	not inv.
6	<i>Asplenium auriculatum</i> Sw.	Neotr.	Costa Rica	Lesica & Antibus, 1990	epiphytic	-	-	-
	<i>Asplenium auriculatum</i> Sw.	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
7	<i>Asplenium auritum</i> Sw.	Neotr.	Costa Rica	Lesica & Antibus, 1990	epiphytic	-	-	-
	<i>Asplenium auritum</i> Sw.	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
	<i>Asplenium auritum</i> Sw. var. <i>moritzianum</i> Hieron.	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
8	<i>Asplenium bulbiferum</i> G. Forst.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
9	<i>Asplenium cheilosorum</i> Kunze ex Mett.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
10	<i>Asplenium cordatum</i> Thunb.	Africa	Lesotho	Moteete et al., 1996	saxicol	?	-	not inv.
11	<i>Asplenium crinicaule</i> Hance	Asia	India	Muthukumar & Udaiyan, 2000	saxicol	?	-	not inv.
12	<i>Asplenium dalhousiae</i> Hook.	H-Arct.	Pakistan	Iqbal et al. 1981	terrestrial	+	VAM	septate

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13	<i>Asplenium excisum</i> C. Presl	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
14	<i>Asplenium falcatum</i> Lam.	Austr.	New Zealand	Cooper 1976	epiphytic, terrestrial	+	not det.	+
15	<i>Asplenium flabellifolium</i> Cav.	Austr.	New Zealand	Cooper 1976	saxicol	+	not det.	+
16	<i>Asplenium flaccidum</i> G. Forst.	Austr.	New Zealand	Cooper 1976	terrestrial, epiphytic, saxicol	+	not det.	+
17	<i>Asplenium florentinum</i> Wagner ined.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	
18	<i>Asplenium fuscipes</i> Baker	Asia	China	Zhao Zhi-wei, 2000	?	?	-	not inv.
19	<i>Asplenium griffithianum</i> Hook.	Asia	China	Zhao Zhi-wei, 2000	epiphytic, saxicol	?	-	not inv.
20	<i>Asplenium hallii</i> Hook.	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
21	<i>Asplenium harpeodes</i> Kunze	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
22	<i>Asplenium holoplebium</i> Baker	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
23	<i>Asplenium hookerianum</i> Colenso	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
24	<i>Asplenium horridum</i> Kaulf.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial		-	
25	<i>Asplenium lucidum</i> G. Forst.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
26	<i>Asplenium lushmanense</i> C. Chr.	Asia	China	Zhao Zhi-wei, 2000	?	+	VAM	not inv.
27	<i>Asplenium lyallii</i> (Hook. f.) T. Moore	Austr.	New Zealand	Cooper 1976	terrestrial, epiphytic	+	not det.	+
28	<i>Asplenium macraei</i> Hook. & Grev.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	
29	<i>Asplenium monanthes</i> L.	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
	<i>Asplenium monanthes</i> L.	Africa	Lesotho	Moteeteete et al., 1996	terrestrial, saxicol	?	-	not inv.
30	<i>Asplenium nidus</i> L.	Ocean.	Hawaii	Gemma et al. 1992	epiphytic	?	-	not inv.
31	<i>Asplenium normale</i> D. Don.	Asia	China	Zhao Zhi-wei, 2000	epiphytic, saxicol	?	-	not inv.
	<i>Asplenium normale</i> D. Don.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
32	<i>Asplenium obtusatum</i> G. Forst.	Austr.	New Zealand	Cooper 1976	saxicol	+	not det.	+
33	<i>Asplenium pekinense</i> Hance	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	?	-	not inv.
34	<i>Asplenium platyneuron</i> (L.) Oakes	Africa	Lesotho	Moteeteete et al.,	terrestrial,	?	-	not inv.

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35	<i>Asplenium praemorsum</i> Sw.	Asia	China	1996 Zhao Zhi-wei, 2000	saxicol epiphytic	?	-	not inv.
36	<i>Asplenium prolongatum</i> Hook.	Asia	China	Zhao Zhi-wei, 2000	epiphytic, saxicol	?	-	not inv.
37	<i>Asplenium pseudofontanum</i> Koss.	H-Arct.	Pakistan	Iqbal et al. 1981	terrestrial	+	VAM	-
38	<i>Asplenium rhizophyllum</i> L.	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
39	<i>Asplenium richardii</i> Hook.	Austr.	New Zealand	Cooper 1976	saxicol, terrestrial	+	not det.	+
40	<i>Asplenium serra</i> Langsd. & Fisch.	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
41	<i>Asplenium serra</i> Langsd. & Fisch.	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
42	<i>Asplenium serricula</i> Fée	Asia	India	Muthukumar & Udaiyan, 2000	saxicol	+	VAM	not inv.
43	<i>Asplenium simonsianum</i> Hook.	Asia	China	Zhao Zhi-wei, 2000	?	?	-	not inv.
44	<i>Asplenium sphenotomum</i> Hillebr.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	
45	<i>Asplenium stoloniferum</i> Bory	Africa	South Africa	Moteetee et al., 1996	terrestrial	?	-	not inv.
46	<i>Asplenium tenuicaule</i> Hayata	Asia	China	Zhao Zhi-wei, 2000	?	?	-	not inv.
47	<i>Asplenium theciferum</i> (Kunth) Mett.	Neotr.	Costa Rica	8	epiphytic	-	-	-
48	<i>Asplenium trichomanes</i> L.	Austr.	New Zealand	Cooper 1976	saxicol	+	not det.	+
49	<i>Asplenium trichomanes</i> L.	Africa	Lesotho, South Africa	Moteetee et al., 1996	saxicol	?	-	not inv.
50	<i>Asplenium trichomanes</i> L.	Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
51	<i>Asplenium trichomanes</i> L.	H-Arct.	Pakistan	Iqbal et al. 1981	terrestrial	+	VAM	-
52	<i>Asplenium trichomanes</i> L.	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
53	<i>Asplenium unilaterale</i> Lam.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
54	<i>Asplenium unilaterale</i> Lam.	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	?	-	not inv.
55	<i>Asplenium uniseriale</i> Raddi	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
56	<i>Asplenium varians</i> Wall. ex Hook & Grev.	Asia	India	Muthukumar & Udaiyan, 2000	saxicol	+	VAM	not inv.
57	<i>Asplenium varians</i> Wall. ex Hook & Grev.	Asia	China	Zhao Zhi-wei, 2000	saxicol	?	-	not inv.
58	<i>Asplenium wrightioides</i> H. Christ	Asia	China	Zhao Zhi-wei, 2000	?	?	-	not inv.
59	<i>Asplenium yunnanense</i> Franch.	Asia	China	Zhao Zhi-wei, 2000	saxicol	?	-	not inv.
60	<i>Asplenium zenkerianum</i> Kunze	Asia	India	Muthukumar & 2000	saxicol	+	VAM	not inv.

[*Loxoscaphe theciferum* (Kunth) T. Moore]

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		Udaiyan, 2000						
<b>Blechnaceae</b>								
54	<i>Blechnum attenuatum</i> var. <i>giganteum</i> (Kaulf.) Bonap.	Africa	South Africa	Moteetee et al., 1996	saxicol	+	VAM	not inv.
55	<i>Blechnum austr. e</i> L.	Africa	Lesotho	Moteetee et al., 1996	terrestrial	+	VAM	not inv.
56	<i>Blechnum banksii</i> (Hook. f.) Mett. ex Diels	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
57	<i>Blechnum capense</i> (L.) Schildt.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
58	<i>Blechnum discolor</i> (G. Forst.) Keys.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
59	<i>Blechnum filiforme</i> (A. Cunn.) Erttingsh.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
60	<i>Blechnum fluviatile</i> (R. Br.) Salom.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
61	<i>Blechnum kunthianum</i> Gaudich.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
62	<i>Blechnum lanceolatum</i> (L.) Kaulf.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
63	<i>Blechnum membranaceum</i> (Col.) Mett.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
64	<i>Blechnum minus</i> (R. Br.) Allan	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
65	<i>Blechnum nigrum</i> (Col.) Mett.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
66	<i>Blechnum occidentale</i> L.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
67	<i>Blechnum orientale</i> L.	Asia	India	Muthukumar & Udaiyan, 2000	saxicol	+	VAM	not inv.
	<i>Blechnum orientale</i> L.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
68	<i>Blechnum patersonii</i> (R. Br.) Mett.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
69	<i>Blechnum penna-marina</i> (Poir.) Kuhn	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
70	<i>Blechnum punctulatum</i> Sw.	Africa	Lesotho	Moteetee et al., 1996	terrestrial	+	VAM	not inv.
71	<i>Blechnum schomburgkii</i> (Klotzsch) C. Chr.	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
72	<i>Blechnum</i> sp. 1	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
73	<i>Blechnum vulcanicum</i> (Blume) Kuhn	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
74	<i>Brainea insignis</i> (Hook.) J. Sm.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
75	<i>Sadleria cyatheoides</i> Kaulf.	Ocean.	Hawaii	Gemma et al.	terrestrial	+	VAM	not inv.



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76	<i>Sadleria squarrosa</i> (Gaudich.) T. Moore	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
77	<i>Woodwardia japonica</i> (L. f.) Sm.	Asia	China	Zhao Zhi-wei, 1992	terrestrial	+	VAM	not inv.
78	<i>Woodwardia orientalis</i> Sw.	Asia	China	Zhang et al., 2000	terrestrial	+	VAM	not inv.
79	<i>Woodwardia unigemmata</i> (Makino) Nakai	Asia	China	Zhao Zhi-wei, 2003	terrestrial	?	-	not inv.
80	<b>Cibotiaceae</b> <i>Cibotium barometz</i> (L.) J. Sm.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
81	<i>Cibotium chamissoi</i> Kaulf.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
82	<i>Cibotium glaucum</i> (Sm.) Hook. & Arn.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
	<i>Cibotium glaucum</i> (Sm.) Hook. & Arn.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
	[ <i>Cibotium st.-johnii</i> Krajina]							
	<b>Cyatheaceae</b>							
83	<i>Alsophila colensoi</i> Hook. f.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
84	<i>Alsophila conantiana</i> Lehnert	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
85	<i>Alsophila costularis</i> Baker	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
86	<i>Alsophila dealbata</i> Pr.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
87	<i>Alsophila dregei</i> (Kunze) R. M. Tryon	Africa	Lesotho	Motestee et al., 1996	terrestrial	?	-	not inv.
88	<i>Alsophila smithii</i> (Hook. f.) R. M. Tryon	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
89	<i>Alsophila spinulosa</i> (Hook.) R. M. Tryon	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
90	<i>Cyathea bipinnatifida</i> (Baker) Domin	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
91	<i>Cyathea dudleyi</i> R. M. Tryon	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
92	<i>Cyathea hybrid</i>	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
93	<i>Cyathea obnoxia</i> Lehnert	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
94	<i>Cyathea peladensis</i> (Hieron.) Domin	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
95	<i>Gymnosphaera gigantea</i> (Wall. ex Hook.) J. Sm.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
96	<i>Gymnosphaera podophylla</i> (Hook.) Copel.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
97	<i>Sphaeropteris brunoniana</i> (Hook.) R. M.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.

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198	Tryon Sphaeropteris cooperi (F. Muell.) R. M.	[Cyathea cooperi (Hook. & Arnott) Domin]	Ocean.	Hawaii	2000 Gemma et al. 1992	terrestrial	+	VAM	not inv.
199	Tryon Sphaeropteris medullaris (G. Forst.) Bernh.	[Cyathea medullaris (Forst.) Sw.]	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
200	<b>Davalliaceae</b> Arastegia pulchra (D. Don.) Copel.		Asia	India	Muthukumar & Udaiyan, 2000	epiphytic	+	VAM	not inv.
201	Davallia bullata Wall. ex Hook.		Asia	India	Muthukumar & Udaiyan, 2000	epiphytic	+	VAM	not inv.
202	<b>Dennstaedtiaceae</b> Dennstaedtia melanostipes Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
203	Dennstaedtia scabra (Wall.) Moore		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
204	Histiopteris incisa (Thunb.) J. Sm.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
205	Histiopteris incisa (Thunb.) J. Sm.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
206	Hypolepis distans Hook.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
207	Hypolepis millefolium Hook.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
208	Hypolepis punctata (Thunb.) Mett.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
209	Hypolepis rugulosa (Labill.) J. Sm.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
210	Hypolepis tenuifolia (Forst. f.) Bernh.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
211	Leptolepia novae-zealandiae (Colenso) Kuhn		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
212	Microlepia callescens C. Presl	[Microlepia "marginata var. callescens"]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
213	Microlepia hookeriana (Wall.) C. Presl		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
214	Microlepia marginata (Houtt.) C. Chr.		Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
215	Microlepia marginata (Houtt.) C. Chr.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
216	Microlepia pilosissima Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
217	Microlepia platyphylla (D. Don.) J. Sm.		Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	
218	Microlepia platyphylla (D. Don.) J. Sm.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
219	Microlepia rhomboidea (Wall.) C. Presl		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
220	Microlepia strigosa (Thunb.) C. Presl		Ocean.	Hawaii	Gemma et al.	terrestrial	+	VAM	not inv.

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118	<i>Microlepia trapeziformis</i> (Roxb.) Kuhn	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
119	<i>Monachosorum henryi</i> H. Christ	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
120	<i>Paesia scaberula</i> (A. Rich.) Kuhn	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
121	<i>Pteridium aquilinum</i> (L.) Kuhn	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
	<i>Pteridium aquilinum</i> (L.) Kuhn	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
	<i>Pteridium aquilinum</i> (L.) Kuhn	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
	<i>Pteridium aquilinum</i> (L.) Kuhn	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
	<i>Pteridium aquilinum</i> (L.) Kuhn	Africa	Lesotho	Moteetee et al., 1996	terrestrial	?	-	not inv.
122	<i>Pteridium decompositum</i> Gaudich.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
123	<i>Pteridium revolutum</i> (Blume) Nakai	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
	<b>Dicksoniaceae</b>							
124	<i>Dicksonia squarrosa</i> (G. Forst.) Sw.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
	<b>Dryopteridaceae</b>							
125	<i>Acrophorus stipellatus</i> T. Moore	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
126	<i>Acromohra globisora</i> (Hayata) Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
127	<i>Acromohra sporadosora</i> (Kunze) Ching	Asia	China	9	terrestrial	?	-	not inv.
128	<i>Arachniodes aristata</i> (G. Forst.) Tindale	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
	<b>Arachniaceae</b>							
129	<i>Arachniodes denticulata</i> (Sw.) Ching	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	?	?	-
130	<i>Arachniodes festina</i> (Hance) Ching	Asia	China	Zhang et al., 2003	terrestrial	?	-	not inv.
131	<i>Arachniodes rhomboidea</i> (Wall.) C. Presl	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
132	<i>Arachniodes simplicior</i> (Makino) Ohwi	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
133	<i>Ctenitis ferruginea</i> (Bedd.) Ching	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	
134	<i>Ctenitis mariformis</i> (Rosenst.) Ching	Asia	China	Zhang et al., 2003	terrestrial	?	-	not inv.
135	<i>Ctenitis membranifolia</i> Ching & C. H. Wang	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
136	<i>Cyrtomium caryotideum</i> (Wall. ex Hook.	Asia	India	Muthukumar &	terrestrial	+	VAM	not inv.

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	& Grev.) C. Presl <i>Cyrtomium caryotideum</i> (Wall. ex Hook & Grev.) C. Presl	Asia	China	Udaiyan, 2000 Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
137	<i>Cyrtomium falcatum</i> (L. f.) C. Presl	Asia	China	Zhang et al., 2003	terrestrial	?	-	not inv.
138	<i>Cyrtomium fortunei</i> J. Sm.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
139	<i>Cyrtomium scabrosa</i> (Kunze) Ching	Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
140	<i>Dryopteris basisora</i> H. Christ	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
141	<i>Dryopteris caroli-hopei</i> Fraser-Jenk.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
142	<i>Dryopteris chrysocoma</i> (H. Christ) C. Chr.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
143	<i>Dryopteris cochleata</i> (D. Don.) C. Chr.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
144	<i>Dryopteris cristata</i> A. Gray	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
145	<i>Dryopteris diffracta</i> (Baker) C. Chr.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
146	<i>Dryopteris dilatata</i> A. Gray	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
147	<i>Dryopteris frutuosa</i> H. Christ	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
148	<i>Dryopteris fuscipes</i> C. Chr.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
149	<i>Dryopteris fusco-atra</i> (Hillebr.) Robinson	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
150	<i>Dryopteris glabra</i> (Brack.) Kuntze	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
151	<i>Dryopteris hendersonii</i> (Bedd.) C. Chr.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
152	<i>Dryopteris inaequalis</i> (Langsd. & Fisch.) Kuhn	Africa	Lesotho	Moteete et al., 1996	terrestrial	?	-	not inv.
153	<i>Dryopteris intermedia</i> A. Gray	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
154	<i>Dryopteris intermedia</i> x <i>venulosa</i> Wherry	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
155	<i>Dryopteris leptopoda</i> Hayata	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
156	<i>Dryopteris marginalis</i> (L.) A. Gray	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
157	<i>Dryopteris marginata</i> (Wall. ex C. B. Clarke) H. Christ	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
158	<i>Dryopteris odontoloma</i> (T. Moore) C. Chr.	H-Arct.	Pakistan	Iqbal et al. 1981	terrestrial	+	VAM	septate
	<i>Dryopteris odontoloma</i> (T. Moore) C.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.

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159	Chr. Dryopteris parasitica (L.) Kuntze	H-Arct. Asia	Pakistan China	Iqbal et al. 1981 Zhao Zhi-wei, 2000	2000	+ +	VAM VAM	- not inv.
160	Dryopteris sparsa (D. Don) Kuntze							
161	Dryopteris spinulosa Watt	H-Arct.	Canada	Berch & Kendrick 1982		+	VAM	not inv.
162	Dryopteris stenolepis (Baker) C. Chr.	Asia	China	Zhao Zhi-wei, 2000		?	-	not inv.
163	Dryopteris sublacera H. Christ	Asia	China	Zhao Zhi-wei, 2000		+	VAM	not inv.
164	Dryopteris unidentata (Hook. & Arn.) C. Chr.	Ocean.	Hawaii	Gemma et al. 1992		+	VAM	
165	Dryopteris urophylla (Wall.) C. Chr.	H-Arct. Ocean.	Pakistan Hawaii	Iqbal et al. 1981 Gemma et al. 1992		+	VAM VAM	- not inv.
166	Dryopteris wallichiana (Spreng.) Hyl.							
167	Elaphoglossum acrostichoides (Hook. & Grev.) Scheupe	Africa	Lesotho	Moteetee et al., 1996		?	-	not inv.
168	Elaphoglossum aemulum (Kaulf.) Brack.	Ocean.	Hawaii	Gemma et al. 1992		+	VAM	not inv.
169	Elaphoglossum alatum Gaudich.	Ocean.	Hawaii	Gemma et al. 1992		+	VAM	not inv.
170	Elaphoglossum antisanae (Sodirol) H. Christ	Neotr.	Ecuador	Lehnert et al., in prep.		-	-	
171	Elaphoglossum argyrophyllum (Sodirol) R. C. Moran, comb. ined.	Neotr.	Ecuador	Lehnert et al., in prep.		-	-	
172	Elaphoglossum beddomei Sledge	Asia	India	Muthukumar & Udaiyan, 2000		-	-	not inv.
173	Elaphoglossum crassifolium (Gaud.) Anderson & Crosby	Ocean.	Hawaii	Gemma et al. 1992		+	VAM	not inv.
174	Elaphoglossum cuspidatum (Willd.) T. Moore	Neotr.	Costa Rica	Wäckers 1998		+	-	Asco
175	Elaphoglossum deltoideum (Sodirol) H. Christ	Neotr.	Ecuador	Lehnert et al., in prep.		-	-	
	Elaphoglossum deltoideum (Sodirol) H. Christ	Neotr.	Ecuador	Lehnert et al., in prep.		-	-	
176	Elaphoglossum dendricola (Baker) H. Christ	Neotr.	Ecuador	Lehnert et al., in prep.		-	-	
177	Elaphoglossum engelii (H. Karst.) H. Christ	Neotr.	Ecuador	Lehnert et al., in prep.		+	-	Asco
178	Elaphoglossum erinaceum (Fée) T. Moore	Neotr.	Ecuador	Lehnert et al., in prep.		+	-	Asco
	Elaphoglossum erinaceum (Fée) T. Moore	Neotr.	Costa Rica	Wäckers 1998		+	-	Asco
179	Elaphoglossum eximium (Mett.) H. Christ	Neotr.	Costa Rica	Wäckers 1998		+	-	Asco
180	Elaphoglossum fourmieranum L. D. Gómez	Neotr.	Costa Rica	Wäckers 1998		+	-	Asco
181	Elaphoglossum glossophyllum Hieron.	Neotr.	Ecuador	Lehnert et al., in prep.		-	-	

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182	Elaphoglossum glossophyllum Hieron. Elaphoglossum guamanianum (Sodiroti) C. Chr.	Ecuador	Neotr.	Lehnert et al., in prep.	epiphytic	+	-	Asco
183	Elaphoglossum heteromorphum (Klotzsch) T. Moore	Ecuador	Neotr.	Lehnert et al., in prep.	epiphytic	+	-	Asco
184	Elaphoglossum hirtum (Sw.) C. Chr.	Ecuador	Neotr.	Lehnert et al., in prep.	terrestrial	+	VAM	-
185	Elaphoglossum latifolium (Sw.) J. Sm. Elaphoglossum latifolium (Sw.) J. Sm.	Hawaii Costa Rica Ecuador	Ocean. Neotr. Neotr.	Gemma et al. 1992 Wäckers 1998 Lehnert et al., in prep.	epiphytic epiphytic epiphytic	- + +	- - VAM	Asco - -
186	Elaphoglossum lingua Raddi	Costa Rica	Neotr.	Wäckers 1998	epiphytic	+	-	Asco
187	Elaphoglossum iloense (Hook.) T. Moore	Ecuador	Neotr.	Lehnert et al., in prep.	epiphytic	?	?	-
188	Elaphoglossum nilgiricum Krajina & Sledge	India	Asia	Muthukumar & Udaiyan, 2000	epiphytic	+	VAM	-
189	Elaphoglossum papillosum (Baker) H. Christ	Ecuador	Neotr.	Lehnert et al., in prep.	terrestrial	+	-	Asco
190	Elaphoglossum pellucidum Gaudich.	Hawaii	Ocean.	Gemma et al. 1992	epiphytic	+	VAM	not inv.
191	Elaphoglossum peltatum (Sw.) Urb.	Costa Rica	Neotr.	Lesica & Antibus, 1990	epiphytic	-	-	-
192	Elaphoglossum peltatum (Sw.) Urb.	Costa Rica	Neotr.	Wäckers 1998	epiphytic	+	-	Asco
193	Elaphoglossum petiolatum Urb. Elaphoglossum petiolosum (Desv.) Moore	Costa Rica Ecuador	Neotr. Neotr.	Wäckers 1998 Lehnert et al., in prep.	epiphytic epiphytic	+	- -	Asco Asco
194	Elaphoglossum productum Rosenst.	Ecuador	Neotr.	Lehnert et al., in prep.	epiphytic	-	-	-
195	Elaphoglossum quitense (Baker) C. Chr.	Ecuador	Neotr.	Lehnert et al., in prep.	terrestrial	+	-	Asco
196	Elaphoglossum sp. 1	Ecuador	Neotr.	Lehnert et al., in prep.	epiphytic	+	-	Asco
197	Elaphoglossum sp. 2	Ecuador	Neotr.	Lehnert et al., in prep.	epiphytic	-	-	-
198	Elaphoglossum sp. 3	Ecuador	Neotr.	Lehnert et al., in prep.	terrestrial	-	-	-
199	Elaphoglossum squarrosum (Klotzsch) T. Moore	Ecuador	Neotr.	Lehnert et al., in prep.	terrestrial	+	VAM	-
200	Elaphoglossum stigmatolepis (Fée) T. Moore	India	Asia	Muthukumar & Udaiyan, 2000	epiphytic	-	-	not inv.
201	Elaphoglossum vulcanicum H. Christ	Ecuador	Neotr.	Lehnert et al., in prep.	epiphytic	-	-	-
202	Elaphoglossum wawrae (Luer) C. Chr.	Hawaii	Ocean.	Gemma et al. 1992	epiphytic	+	VAM	-
203	Elaphoglossum yatesii (Sodiroti) H. Christ	Ecuador	Neotr.	Lehnert et al., in prep.	terrestrial	+	-	Asco
204	Hypodematum crenatum (Forssk.) Kuhn	India	Asia	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	-

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	Hypodematum crenatum (Forssk.) Kuhn	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
205	Lastreopsis decomposita (R. Br.) Tindale	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
206	Lastreopsis glabella (A. Hunn. in Hook.) Tindale	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
207	Lastreopsis hispida (Sw.) Tindale	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
208	Lastreopsis kilippii (Maxon) Tindale	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
209	Lastreopsis velutina (A. Rich.) Tindale	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
210	Peranema christensenae (Ching), comb. ined	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
211	Polystichum acrostichoides Schott	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
212	Polystichum alteruatum Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
213	Polystichum alticola Scheelpe & N. C. Anthony	Africa	Lesotho	Moteetee et al., 1996	terrestrial	?	-	not inv.
214	Polystichum biaristatum (Blume) T. Moore	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
215	Polystichum chingae Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
216	Polystichum cystostegia (Hook.) Cheesem.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
217	Polystichum dielsii H. Christ	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
218	Polystichum eximium (Mett. ex Kuhn) C. Chr.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
219	Polystichum jishushanense Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
220	Polystichum luctuosum (Kunze) T. Moore	Africa	Lesotho	Moteetee et al., 1996	terrestrial	?	-	not inv.
221	Polystichum monticola N. C. Anthony & Scheipe	Africa	Lesotho	Moteetee et al., 1996	terrestrial	?	-	not inv.
222	Polystichum platyphyllum (Willd.) C. Presl	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
223	Polystichum pycnopterum (Christ) Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
224	Polystichum richardii (Hook.) J. Sm.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
225	Polystichum sylvaticum (Colenso) Diels	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
226	Polystichum transvaalense N. C. Anthony	Africa	Lesotho	Moteetee et al., 1996	terrestrial	?	-	not inv.
227	Polystichum tsus-simense (Hook.) J. Sm.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
228	Polystichum vestitum (G. Forst.) C.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not	+

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229	Presl Rumohra adiantiformis (G. Forst.) Ching	Austr.	Zealand New Zealand	Cooper 1976	terrestrial, epiphytic	+	det. not det.	+
230	<b>Equisetaceae</b> Equisetum arvense L.	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
231	Equisetum debile Roxb.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
232	Equisetum diffusum D. Don	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
233	Equisetum hyemale L.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
	Equisetum hyemale var. affine Eaton	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
	Equisetum hyemale var. elatum Morton	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
234	Equisetum ramosissimum Desf.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
235	Equisetum ramosissimum Desf.	Africa	Lesotho, South Africa	Moteetee et al., 1996	terrestrial	?	-	not inv.
236	Equisetum scirpoides Michx.	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
	<b>Gleicheniaceae</b>							
237	Dicranopteris dichotoma (Thunb.) Bernh.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
238	Dicranopteris gigantea Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
239	Dicranopteris linearis (Burm.) Underw.	Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
	Dicranopteris linearis (Burm.) Underw.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
240	Dicranopteris pedata (Houtt.) Nakai	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
241	Dicranopteris splendida (Hand.-Mazz.) Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
242	Diplopterygium giganteum (Wall. ex Hook.) Nakai	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
243	Diplopterygium glaucoides (Ching) Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
244	Diplopterygium glaucum (Houtt.) Nakai	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
245	Diplopterygium pinnatum (Kunze) Ching	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
246	Gleichenia circinnata Sw.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
247	Gleichenia microphylla (R. Br.) H. Christ	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
248	Gleichenia umbraculifera (Kunze) T.	Africa	Lesotho	Moteetee et al.,	terrestrial	+	VAM	not inv.



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249	Moore Sticherus brevitomentosus B. Øllg. & Østergaard	Neotr.	Ecuador	1996 Lehnert et al., in prep.	terrestrial	-	-	-
250	Sticherus cunninghamii (Hook.) H. St. John	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
251	Sticherus laevigatus (Willd.) C. Presl	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
252	Sticherus melanoblastus Østergaard & B. Øllg.	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
253	Sticherus melanoblastus Østergaard & B. Øllg.	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
253	Sticherus owhyhensis (Hook.) Nakai	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
254	Sticherus rubignosus (Mett.) Nakai	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
254	Sticherus rubignosus (Mett.) Nakai	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
255	Sticherus sp.	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
256	Sticherus tomentosus (Cav. ex Sw.) A. R. Sm.	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
257	<b>Hymenophyllaceae</b> Abrodictyum rigidum (Sw.) Ebihara & Dubuisson	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
258	Abrodictyum strictum (Menzies ex Hook. & Grev.) Ebihara & K. Iwats.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
259	Crepidomanes latealatum (Bosch) Copel.	Asia	China	Zhao Zhi-wei, 2000	epiphytic	?	-	not inv.
260	Hymenophyllum atrovirens Fée & L'Herm.	Austr.	New Zealand	Cooper 1976	terrestrial, saxicol	+	not det.	+
261	Hymenophyllum badium Hook. & Grev.	Asia	China	Zhao Zhi-wei, 2000	epiphytic, saxicol	?	-	not inv.
262	Hymenophyllum bivalve (G. Forst.) Sw.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
263	Hymenophyllum blumeanum Spreng.	Asia	China	Zhao Zhi-wei, 2000	epiphytic	?	-	not inv.
264	Hymenophyllum calodictyon Bosch	Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
265	Hymenophyllum costaricanum Bosch	Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
266	Hymenophyllum cristatum Hook. & Grev.	Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
267	Hymenophyllum demissum (G. Forst.) Sw.	Austr.	New Zealand	Cooper 1976	terrestrial, epiphytic	+	not det.	+
268	Hymenophyllum dilatatum (G. Forst.) Sw.	Austr.	New Zealand	Cooper 1976	epiphytic	+	not det.	+
269	Hymenophyllum elegans Rich.	Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
270	Hymenophyllum exsertum Wall. ex Hook.	Asia	India	Muthukumar & Udayan, 2000	epiphytic	?	-	not inv.

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	Hymenophyllum exsertum Wall. ex Hook.	[Mecodium exsertum (Wall. ex Hook.) Copel.]	Asia	India	Muthukumar & Udayan, 2000	saxicol	+	VAM	not inv.
271	Hymenophyllum ferrugineum Colla		Austr.	New Zealand	Cooper 1976	epiphytic	+	not det.	+
272	Hymenophyllum flabellatum Labill.		Austr.	New Zealand	Cooper 1976	epiphytic, terrestrial	+	not det.	+
273	Hymenophyllum flexuosum A. Cunn.		Austr.	New Zealand	Cooper 1976	saxicol	+	not det.	+
274	Hymenophyllum fucoides (Sw.) Sw.		Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
275	Hymenophyllum hirsutum (L.) Sw.		Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
276	Hymenophyllum lanceolatum Hook. & Arn.	[Sphaerocionium lanceolatum (Hook. & Arn.) Copel.]	Ocean.	Hawaii	Gemma et al. 1992	epiphytic	+	VAM	not inv.
277	Hymenophyllum malingii (Hook.) Mett.		Austr.	New Zealand	Cooper 1976	epiphytic	+	not det.	+
278	Hymenophyllum microcarpum Desv.		Neotr.	Costa Rica	Lesica & Antibus, 1990	epiphytic	-	-	-
	Hymenophyllum microcarpum Desv.		Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
	Hymenophyllum microcarpum Desv.		Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	-	Asco
279	Hymenophyllum minimum A. Rich.		Austr.	New Zealand	Cooper 1976	saxicol, epiphytic	+	not det.	+
280	Hymenophyllum multialatum C. V. Morton		Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
281	Hymenophyllum multifidum (G. Forst.) Sw.		Austr.	New Zealand	Cooper 1976	terrestrial, epiphytic, saxicol	+	not det.	+
282	Hymenophyllum peltatum (Poir.) Desv.		Austr.	New Zealand	Cooper 1976	epiphytic, saxicol	+	not det.	+
283	Hymenophyllum plumierii Hook. & Grev.		Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
284	Hymenophyllum plumosum Kaulf.		Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
285	Hymenophyllum polyanthos (Sw.) Sw.		Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
286	Hymenophyllum pulcherrimum Col.		Austr.	New Zealand	Cooper 1976	epiphytic, saxicol	+	not det.	+
287	Hymenophyllum rarum R. Br.		Austr.	New Zealand	Cooper 1976	epiphytic, saxicol	+	not det.	+
288	Hymenophyllum recurvum Gaud.	[Mecodium recurvum (Gaud.) Copel.]	Ocean.	Hawaii	Gemma et al. 1992	epiphytic	+	VAM	
289	Hymenophyllum revolutum Col.		Austr.	New Zealand	Cooper 1976	epiphytic	+	not det.	+
290	Hymenophyllum rufescens Kirk		Austr.	New Zealand	Cooper 1976	epiphytic, saxicol	+	not det.	+
291	Hymenophyllum sanguinolentum (G. Forst.) Sw.		Austr.	New Zealand	Cooper 1976	epiphytic, saxicol	+	not det.	+
292	Hymenophyllum scabrum A. Rich.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+

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293	<i>Hymenophyllum</i> sp. 1		Neotr.	Zealand Ecuador	Lehnert et al., in prep.	epiphytic epiphytic	-	det.	-
294	<i>Hymenophyllum</i> sp. 2		Neotr.	Ecuador	Lehnert et al., in prep.	saxicol	-	-	-
295	<i>Hymenophyllum trichomanoides</i> Bosch		Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
296	<i>Hymenophyllum tunbrigense</i> (L.) Sm.		Africa	Lesotho	Moteetee et al., 1996	saxicol	?	-	not inv.
297	<i>Hymenophyllum villosum</i> Colenso		Austr.	New Zealand	Cooper 1976	epiphytic	+	not det.	+
298	<i>Polyphlebium angustatum</i> (Carmich.) Ebihara & Dubuisson	[ <i>Trichomanes angustatum</i> Carm.]	Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
299	<i>Polyphlebium capillaceum</i> (L.) Ebihara & Dubuisson	[ <i>Trichomanes capillaceum</i> L.]	Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	VAM	-
300	<i>Polyphlebium diaphanum</i> (Kunth) Ebihara & Dubuisson	[ <i>Trichomanes diaphanum</i> Kunth]	Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
301	<i>Polyphlebium hymenophylloides</i> (Bosch) Ebihara & K. Iwats.	[ <i>Trichomanes hymenophylloides</i> Bosch]	Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
302	<i>Polyphlebium venosum</i> (R. Br.) Copel.	[ <i>Trichomanes venosum</i> R. Br.]	Austr.	New Zealand	Cooper 1976	epiphytic, saxicol	+	not det.	+
303	<i>Trichomanes cellulosum</i> Klotzsch		Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
304	<i>Trichomanes dactylites</i> Sodiro		Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	-	Asco
305	<i>Trichomanes diversifrons</i> (Bory) Mett.		Neotr.	Costa Rica	Wäckers 1998	terrestrial	+	VAM	-
306	<i>Trichomanes elegans</i> Rich.		Neotr.	Ecuador	Lehnert et al., in prep.	saxicol	+	VAM	-
307	<i>Trichomanes elegans</i> Rich. <i>Trichomanes melanotrichum</i> Schltidl.		Neotr. Africa	Costa Rica Lesotho	Wäckers 1998 Moteetee et al., 1996	terrestrial saxicol	+	VAM -	- not inv.
308	<i>Trichomanes pellucens</i> Kunze		Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
309	<i>Trichomanes pinnatum</i> Hedw.		Neotr.	Costa Rica	Wäckers 1998	terrestrial	+	VAM	-
310	<i>Trichomanes pyxidiferum</i> L.		Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
311	<i>Trichomanes reniforme</i> Forst.		Austr.	New Zealand	Cooper 1976	terrestrial, saxicol	+	not det.	+
312	<i>Trichomanes</i> sp. 1		Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
313	<i>Trichomanes</i> sp. 2		Neotr.	Ecuador	Lehnert et al., in prep.	saxicol	-	-	-
314	<i>Trichomanes</i> sp. 3		Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
315	<i>Vandenboschia auriculata</i> (Blume) Copel.	[ <i>Trichomanes auriculatum</i> Blume]	Asia	China	Zhao Zhi-wei, 2000	epiphytic, saxicol	?	-	not inv.
316	<i>Vandenboschia colensoi</i> (Hook. f. in Hook) Copel.	[ <i>Trichomanes colensoi</i> Hook. f. in Hook.]	Austr.	New Zealand	Cooper 1976	saxicol, terrestrial	+	not det.	+
317	<i>Vandenboschia collarata</i> (Bosch)	[ <i>Trichomanes collaratum</i> Bosch]	Neotr.	Costa Rica	Wäckers 1998	terrestrial	-	-	-

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318	Ebihara & K. Iwats. Vandenboschia cyrtotheca (Hillebr.) Copel.	Ocean.	Hawaii	Gemma et al. 1992	epiphytic	?	-	not inv.
319	Vandenboschia davallioides (Gaudich.) Copel.	Ocean.	Hawaii	Gemma et al. 1992	epiphytic	?	-	not inv.
320	Vandenboschia rupestris (Raddi) Ebihara & K. Iwats. [Trichomanes rupestre (Raddi) Bosch]	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
321	<b>Isoetaceae</b> Isoetes coromandelina L.	Asia	India	Ragupathy & Mahadevan 1993	aquatic	+	VAM	not inv.
322	Isoetes transvaalensis Jermy & Schelpe	Africa	Lesotho	Moteete et al., 1996	aquatic	?	-	not inv.
323	<b>Lindsaeaceae</b> Lindsaea cultrata (Willd.) Sw.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
324	Lindsaea ensifolia Sw.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
325	Lindsaea ensifolia Sw. var. ensifolia	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
326	Lindsaea heterophylla Dryand.	Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
327	Lindsaea javanensis Blume	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
328	Lindsaea linearis Sw.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
329	Lindsaea odorata Roxb.	Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
330	Lindsaea orbiculata (L.) Mett.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
331	Lindsaea trichomanoides Dryand.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
332	Lindsaea odorata Roxb.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
333	Lindsaeaosoria flynnii W. H. Wagner	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
334	Odontosoria chinensis (L.) Maxon	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
335	Schizoloma heterophyllum (Dryand.) J. Sm.	Asia	China	Zhang et al., 2003	terrestrial	?	-	not inv.
336	Sphenomeris chinensis (L.) Maxon	Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
337	Stenoloma chusana (L.) Ching	Asia	China	Zhang et al., 2003	terrestrial, saxicol	+	VAM	not inv.
338	Stenoloma chusana (L.) Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	+	VAM	not inv.
339	<b>Lomariopsidaceae</b> Lomariopsis fendleri D. C. Eaton	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-

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337	<i>Nephrolepis cordifolia</i> (L.) C. Presl	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
	<i>Nephrolepis cordifolia</i> (L.) C. Presl	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
338	<i>Nephrolepis exaltata</i> (L.) Schott	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
	<i>Nephrolepis exaltata</i> (L.) Schott	Ocean.	Hawaii	Gemma et al. 1992	terrestrial, geothermic	+	VAM	not inv.
339	<i>Nephrolepis falcata</i> (Cav.) C. Chr.	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
340	<i>Nephrolepis multiflora</i> (Roxb.) Jairrett ex C. V. Morton	Ocean.	Hawaii	Gemma et al. 1992	terrestrial, saxicol	+	VAM	not inv.
341	<i>Loxomopsis pearcei</i> (Maxon) Baker	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-
	<b>Lycopodiaceae</b>							
342	<i>Huperzia billardierei</i> (Spring) Rothm.	Austr.	New Zealand	Cooper 1976	epiphytic	+	not det.	+
346	<i>Huperzia henryi</i> Baker	Asia	China	Zhao Zhi-wei, 2000	epiphytic	?	-	not inv.
343	<i>Huperzia phyllantha</i> (Hook. & Arnott) Holub	Ocean.	Hawaii	Gemma et al. 1992	epiphytic	+	VAM	not inv.
347	<i>Huperzia saururus</i> (Lam.) Rothm.	Africa	Lesotho	Moteete et al., 1996	terrestrial	?	-	not inv.
348	<i>Huperzia serrata</i> (Thunb.) Trev. f. longipetiolata (Spring) Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
349	<i>Huperzia verticillata</i> (L. f.) Rothm.	Africa	South Africa	Moteete et al., 1996	epiphytic	?	-	not inv.
344	<i>Lycopodiella cernua</i> (L.) Pich. Serm.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
	<i>Lycopodiella cernua</i> (L.) Pich. Serm.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	
350	<i>Lycopodium casuarinoides</i> Spring	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	?	-	not inv.
351	<i>Lycopodium clavatum</i> L.	Africa	South Africa	Moteete et al., 1996	terrestrial	?	-	not inv.
352	<i>Lycopodium complanatum</i> L.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
353	<i>Lycopodium fastigiatum</i> R. Br.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
354	<i>Lycopodium flabelliforme</i> (Fernald) Blanchard	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
355	<i>Lycopodium japonicum</i> Thunb.	Asia	India	Muthukumar & Udayan, 2000	epiphytic	-	-	-
	<i>Lycopodium japonicum</i> Thunb.	Asia	China	Zhao Zhi-wei, 2000	epiphytic	+	VAM	not inv.
345	<i>Lycopodium laterale</i> R. Br.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
356	<i>Lycopodium scariosum</i> G. Forst.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+

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357	<i>Lycopodium tristachyum</i> Pursh		H-Arct.	Zealand Canada	Berch & Kendrick 1982	terrestrial	?	det. -	not inv.
358	<i>Lycopodium volubile</i> G. Forst.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
359	<b>Lygodiaceae</b> <i>Lygodium conforme</i> C. Chr.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
360	<i>Lygodium japonicum</i> (Thunb.) Sw.		Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
	<i>Lygodium japonicum</i> (Thunb.) Sw.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
	<b>Marattiaceae</b>								
361	<i>Angiopteris bipinnata</i> (Ching) J. M. Carnus	[ArchAngiopteris bipinnata Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
362	<i>Angiopteris caudatifolmis</i> Hieron.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
363	<i>Angiopteris evecta</i> (G. Forst.) Hofm.		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	
364	<i>Angiopteris henryi</i> (H. Christ & Gies)	[ArchAngiopteris henryi H. Christ & Gies]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
365	<i>Angiopteris hokouensis</i> Ching	[ArchAngiopteris hokouensis Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
	<i>Angiopteris hokouensis</i> Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
366	<i>Angiopteris subtundata</i> (Ching), comb. ined.	[ArchAngiopteris subtundata Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
367	<i>Angiopteris wangii</i> Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
368	<i>Angiopteris yunnanensis</i> Hieron.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
369	<i>Christensenia assamica</i> (Griff.) Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
370	<i>Marattia douglasii</i> (C. Presl) Baker		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
	<b>Marsileaceae</b>								
371	<i>Marsilea minuta</i> L.		Asia	India	Muthukumar & Udaivan, 2000	aquatic	-	-	
372	<i>Marsilea quadrifolia</i> L.		Asia	India	Ragupathy & Mahadevan 1994	aquatic	?	-	not inv.
373	<i>Marsilea</i> sp.		Africa	Lesotho	Moteetee et al., 1996	aquatic	?	-	not inv.
	<b>Onocleaceae</b>								
374	<i>Matteuccia struthiopteris</i> (L.) Tod. var. <i>pennsylvanica</i> (Willd.) C. V. Morton	[Matteuccia pennsylvanica (Willd.) Raymond]	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
375	<i>Onoclea sensibilis</i> L.		H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
	<b>Ophioglossaceae</b>								

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376	<i>Botrychium lanuginosum</i> Wall. ex Hook. & Grev.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
377	<i>Botrychium oneidense</i> House	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
378	<i>Botrychium ternatum</i> (Thunb.) Sw.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
379	<i>Botrychium virginianum</i> Sw.	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
380	<i>Ophioglossum concinnum</i> Brack.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	
381	<i>Ophioglossum lancifolium</i> C. Presl	Africa	Lesotho	Moteetee et al., 1996	terrestrial	?	-	not inv.
382	<i>Ophioglossum pendulum</i> L.	Ocean.	Hawaii	Gemma et al. 1992	epiphytic	+	VAM	not inv.
383	<i>Ophioglossum petiolatum</i> Hook.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
	<i>Ophioglossum petiolatum</i> Hook.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial		-	
384	<i>Ophioglossum reticulatum</i> L.	Asia	India	Muthukumar & Udaayan, 2000	terrestrial	+	VAM	
	<i>Ophioglossum reticulatum</i> L.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
385	<i>Ophioglossum thermale</i> Komarov	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
386	<i>Ophioglossum vulgatum</i> L.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
	<b>Osmundaceae</b>							
387	<i>Osmunda cinnamomea</i> L.	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
388	<i>Osmunda japonica</i> Thunb.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
	<i>Osmunda japonica</i> Thunb.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
389	<i>Osmunda regalis</i> L.	Asia	India	Muthukumar & Udaayan, 2000	terrestrial	-	-	-
	<i>Osmunda regalis</i> L.	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
390	<i>Todea hymenophylloides</i> A. Rich.	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
391	<i>Todea superba</i> Colenso	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
	<b>Plagiogyriaceae</b>							
392	<i>Plagiogyria adnata</i> (Blume) Bedd.	Asia	China	5	terrestrial	+	VAM	not inv.
	<b>Polyodiaceae</b>							
393	<i>Campyloneurum amphostenon</i> (Kunze ex Klotzsch) Fée var. <i>irregularis</i> (Lellinger) B. León	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
394	<i>Campyloneurum angustifolium</i> (Sw.)	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-

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	Fée																					
395	Campyloneurum brevifolium Link								Neotr.	Costa Rica	Wäckers 1998		-									-
396	Campyloneurum repens (Aubl.) C. Presl							Neotr.	Costa Rica	Wäckers 1998		-										-
397	Christopteris hemionitidea (Wall. ex Mett.) C. Presl							Asia	India	Muthukumar & Udayan, 2000		+	VAM									not inv.
398	Colysis hemitoma (Hance) Ching							Asia	China	Zhang et al., 2003		?										not inv.
399	Dicranoglossum panamense (C. Chr.) L. D. Gómez							Neotr.	Costa Rica	Wäckers 1998		-										-
400	Dicranoglossum polypodioides (Hook.) Lellinger							Neotr.	Costa Rica	Lesica & Antibus, 1990		-										-
	Dicranoglossum polypodioides (Hook.) Lellinger							Neotr.	Costa Rica	Wäckers 1998		-										-
401	Drynaria quercifolia (L.) J. Sm.							Asia	India	Muthukumar & Udayan, 2000		?										not inv.
402	Loxogramme sp.							Austr.	New Zealand	Cooper, 1976		+	not det.									+
403	Metapolydium membranaceum (D. Don) Ching							Asia	India	Muthukumar & Udayan, 2000		+	VAM									not inv.
404	Microgramma lycopodioides (L.) Copel.							Neotr.	Costa Rica	Wäckers 1998		-										-
405	Microgramma percussa (Cav.) E. R. de la Sota							Neotr.	Costa Rica	Wäckers 1998		-										-
406	Microgramma reptans (Cav.) A. R. Sm.							Neotr.	Costa Rica	9		-										-
407	Microsorium hymenoides (Kunze) Ching							Asia	India	Muthukumar & Udayan, 2000		+	VAM									not inv.
408	Microsorium spectrum (Kaulf.) Copel.							Ocean.	Hawaii	Gemma et al., 1992		-										not inv.
409	Niphidium crassifolium (L.) Lellinger							Neotr.	Costa Rica	Wäckers 1998		-										-
410	Pecluma alfredii (Rosenst.) M. G. Price							Neotr.	Costa Rica	Wäckers 1998		-										-
411	Pecluma pectinata (L.) M. G. Price							Neotr.	Costa Rica	Lesica & Antibus, 1990		-										-
412	Phlebodium aureum (L.) J. Sm.							Ocean.	Hawaii	Gemma et al., 1992		-										not inv.
413	Phymatosorus diversifolius (Willd.) Pic. Serm.							Austr.	New Zealand	Cooper 1976		+	not det.									+
414	Phymatosorus scandens (C. Presl) Pic. Serm.							Austr.	New Zealand	Cooper 1976		+	not det.									+
415	Phymatosorus scolopendria (Burm. f.) Pichi-Sermolli							Asia	India	Muthukumar & Udayan, 2000		?										not inv.
	Phymatosorus scolopendria (Burm. f.) Pichi-Sermolli							Ocean.	Hawaii	Gemma et al., 1992		?										not inv.
416	Pleopeltis bradeorum (Rosenst.) comb. ined.							Neotr.	Costa Rica	Wäckers 1998		-										-
417	Pleopeltis furfuraceum Schtidl. & Cham.							Neotr.	Costa Rica	Lesica & Antibus, 1990		-										-
	Pleopeltis furfuraceum Schtidl. & Cham.							Neotr.	Costa Rica	Wäckers 1998		-										-



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418	<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.		Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
	<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.	[ <i>Polypodium macrocarpum</i> (Willd.) Ching]	Asia	India	Muthukumar & Udayan, 2000	epiphytic	+	VAM	not inv.
	<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.		Africa	Lesotho, South Africa	Moteetee et al., 1996	saxicol, epiphytic	?	-	not inv.
419	<i>Pleopeltis polyodioides</i> (L.) E. G. Andrews & Windham subsp. ecklonii (Kunze) Schelpe	[ <i>Polypodium polyodioides</i> (L.) Hitchk. subsp. ecklonii (Kunze) Schelpe]	Africa	South Africa	Moteetee et al., 1996	epiphytic	?	-	not inv.
420	<i>Pleopeltis thunbergiana</i> Kaulf.		Ocean.	Hawaii	Gemma et al. 1992	epiphytic	?	-	not inv.
421	<i>Polypodium nigropaleaceum</i> (H. Christ) Diels		H-Arct.	Pakistan	Iqbal et al. 1981	terrestrial	+	VAM	-
422	<i>Polypodium pellucidum</i> Kaulf.		Ocean.	Hawaii	Gemma et al. 1992	terrestrial, saxicol	?	-	not inv.
423	<i>Polypodium virginianum</i> L.		H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
424	<i>Polypodium vulgare</i> L.		Africa	Lesotho	Moteetee et al., 1996	saxicol	?	-	not inv.
425	<i>Pyrosia heterophylla</i> (L.) M. G. Price	[ <i>Drymoglossum heterophyllum</i> (L.) Trimen]	Asia	India	Muthukumar & Udayan, 2000	epiphytic	+	VAM	not inv.
426	<i>Pyrosia serpens</i> (G. Forst.) Ching		Austr.	New Zealand	Cooper 1976	terrestrial, epiphytic	+	not det.	+
427	<i>Serpocaulon dissimile</i> (L.) A. R. Sm.	[ <i>Polypodium dissimile</i> L.]	Neotr.	Costa Rica	9	epiphytic	-	-	-
428	<i>Serpocaulon fraxinifolium</i> (Jacq.) A. R. Sm.	[ <i>Polypodium fraxinifolium</i> Jaq.]	Neotr.	Costa Rica	9	epiphytic	-	-	-
429	<i>Serpocaulon loriforme</i> (Rosenst.) A. R. Sm.	[ <i>Polypodium loriforme</i> Rosenst.]	Neotr.	Costa Rica	9	epiphytic	-	-	-
430	<i>Serpocaulon ptilorhizon</i> (H. Christ) A. R. Sm.	[ <i>Polypodium ptilorhizon</i> H. Christ]	Neotr.	Costa Rica	9	epiphytic	-	-	-
431	<i>Serpocaulon triseriale</i> (Sw.) A. R. Sm.	[ <i>Polypodium triseriale</i> Sw.]	Neotr.	Costa Rica	9	epiphytic	-	-	-
432	<b>Polyodiaceae [grammitids]</b> <i>Adenophorus abietinus</i> (D. C. Eaton) K. A. Wilson		Ocean.	Hawaii	Gemma et al. 1992	epiphytic	?	-	not inv.
433	<i>Adenophorus tamariscinus</i> (Kaulf.) Hook. ex Grev.		Ocean.	Hawaii	Gemma et al. 1992	epiphytic	+	VAM	not inv.
434	<i>Adenophorus tenellus</i> (Kaulf.)	[ <i>Grammitis tenella</i> Kaulf.]	Ocean.	Hawaii	Gemma et al. 1992	epiphytic	+	VAM	not inv.
435	<i>Ceradenia glabra</i> A. R. Smith & M. Kessler		Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
436	<i>Cochlidium serrulatum</i> (Sw.) L. E. Bishop		Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	-	Asco
437	<i>Enterosora parietina</i> (Klotzsch) L. E. Bishop		Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	-	-	-
438	<i>Grammitis baldwinii</i> (Baker) Copel.		Ocean.	Hawaii	Gemma et al. 1992	epiphytic	?	-	not inv.
439	<i>Grammitis billardieri</i> Willd.		Austr.	New Zealand	Cooper 1976	epiphytic	+	not det.	+
440	<i>Grammitis crassa</i> Fée		Austr.	New Zealand	Cooper 1976	epiphytic	+	not det.	+

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441	<i>Grammitis heterophylla</i> Labill.	Austr.	Zealand New Zealand	Cooper 1976	epiphytic	+	det.	+
442	<i>Grammitis pumila</i> J. B. Armstr.	Austr.	Zealand New Zealand	Cooper 1976	epiphytic	+	det.	+
443	<i>Lellingeria limula</i> (H. Christ) A. R. Sm. & R. C. Moran	Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
444	<i>Lellingeria major</i> (Copel.) A. R. Sm. & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
445	<i>Lellingeria major</i> (Copel.) A. R. Sm. & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	-	Asco
446	<i>Lellingeria saffordii</i> (Maxon) A. R. Sm. & R. C. Moran	Ocean.	Hawaii	Gemma et al. 1992	epiphytic	?	-	not inv.
447	<i>Lellingeria subsessilis</i> (Baker) A. R. Sm. & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	-	-	-
448	<i>Lellingeria suprasculpta</i> (H. Christ) A. R. Sm. & R. C. Moran	Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
449	<i>Melpomene assurgens</i> (Maxon) A. R. Sm. & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
450	<i>Melpomene erecta</i> (C. V. Morton) A. R. Sm. & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	-	Asco
451	<i>Melpomene firma</i> (J. Sm.) A. R. Sm. & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
452	<i>Melpomene flabelliformis</i> (Poir.) A. R. Sm. & R. C. Moran	Africa	Lesotho	Moteetee et al., 1996	saxicol	?	-	not inv.
453	<i>Melpomene gracilis</i> (Hook.) A. R. Sm. & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	saxicol	+	-	Asco
454	<i>Melpomene moniliformis</i> (Lagasca ex Sw.) A. R. Sm. & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	+	-	Asco
	<i>Melpomene moniliformis</i> (Lagasca ex Sw.) A. R. Sm. & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	-	Asco
	<i>Melpomene moniliformis</i> (Lagasca ex Sw.) A. R. Sm. & R. C. Moran	Neotr.	Costa Rica	Wäckers 1998	terrestrial	+	-	Asco
455	<i>Melpomene occidentalis</i> Lehnert	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
	<i>Melpomene occidentalis</i> Lehnert	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	-	-	-
456	<i>Melpomene pseudonutans</i> (Rosenst. & Christ) A. R. Smith & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	saxicol	+	-	Asco
	<i>Melpomene pseudonutans</i> (Rosenst. & Christ) A. R. Smith & R. C. Moran	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	-	Asco
457	<i>Melpomene sklenarii</i> Lehnert	Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	-	Asco
458	<i>Melpomene xiphopteroides</i> (Liebm.) A. R. Sm. & R. C. Moran	Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
459	<i>Micropolypodium blepharodes</i> (Maxon)	Neotr.	Costa Rica	Lesica & Antibus,	epiphytic	-	-	-

	A. R. Sm.	Seymour]	Neotr.	Costa Rica	1990 Wäckers 1998	epiphytic	+	-	Asco
	Micropolypodium blepharodes (Maxon) Seymour								
460	Terpsichore asplenifolia (Sw.) A. R. Sm.		Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
461	Terpsichore lanigera (Desv.) A. R. Sm.		Neotr.	Ecuador	Lehnert et al., in prep.	epiphytic	-	-	-
462	Terpsichore leucosticta (J. Sm.) A. R. Sm.		Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	-	Asco
463	Terpsichore semihirsuta (Klotzsch) A. R. Sm.		Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	-	Asco
464	Terpsichore turrialbae (H. Christ) A. R. Sm.		Neotr.	Costa Rica	Wäckers 1998	epiphytic	+	-	Asco
<b>Psilotaceae</b>									
465	Psilotum complanatum Sw.		Ocean.	Hawaii	Gemma et al. 1992	epiphytic	?	-	not inv.
466	Psilotum nudum L.		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
467	Tmesipteris tannensis Bernh.		Austr.	New Zealand	Cooper 1976	epiphytic	+	not det.	+
<b>Pteridaceae</b>									
468	Actiniopteris radiata (Sw.) Link		Asia	India	Muthukumar & Udaiyan, 2000	saxicol	+	VAM	not inv.
469	Adiantum bonatianum Brause		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
470	Adiantum capillus-veneris L.		Ocean.	Hawaii	Gemma et al. 1992	saxicol	+	VAM	not inv.
	Adiantum capillus-veneris L.		Africa	Lesotho	Moteetee et al., 1996	saxicol	?	-	not inv.
	Adiantum capillus-veneris L.		Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
471	Adiantum capillus-veneris L. Adiantum caudatum L.		H-Arct. Asia	Pakistan India	Iqbal et al. 1981 Muthukumar & Udaiyan, 2000	terrestrial terrestrial	+	VAM VAM	- not inv.
472	Adiantum cuneipinnulum Nair & Gosh		Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
473	Adiantum cunninghamii Hook.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
474	Adiantum diaphanum Blume		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
475	Adiantum edgeworthii Hook.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
476	Adiantum flabellulatum L.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
477	Adiantum fulvum Raoul		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
478	Adiantum hispidulum Sw.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
479	Adiantum hispidulum Sw.		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	?	-	not inv.

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480	<i>Adiantum incisum</i> Forssk. <i>Adiantum lunulatum</i> Burm. f.		H-Arct. Asia	Pakistan India	Iqbal et al. 1981 Muthukumar & Udayan, 2000 Zhao Zhi-wei, 2000	terrestrial terrestrial	+ +	VAM VAM	- not inv.
481	<i>Adiantum lunulatum</i> Burm. f.	[ <i>Adiantum philipense</i> L.]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
482	<i>Adiantum malesianum</i> Ghatak <i>Adiantum pedatum</i> L.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
483	<i>Adiantum poiretii</i> Wikstr.		H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
484	<i>Adiantum venustum</i> D. Don.		Africa	Lesotho, South Africa	Moteetee et al., 1996	terrestrial	?	-	not inv.
485	<i>Aleuritopteris albomarginata</i> (C. B. Clarke) Ching		H-Arct. Asia	Pakistan China	Iqbal et al. 1981 Zhao Zhi-wei, 2000	terrestrial terrestrial	+ +	VAM VAM	- not inv.
486	<i>Aleuritopteris argentea</i> (S. G. Gmel.) Fee		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
487	<i>Aleuritopteris duclouxii</i> (H. Christ) Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
488	<i>Aleuritopteris grevilleoides</i> (H. Christ), comb. ined	[ <i>Sinopteris grevilleoides</i> (H. Christ) C. Chr. & Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	?	-	not inv.
489	<i>Aleuritopteris pseudofarinosa</i> Ching & S. K. Wu		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
490	<i>Aleuritopteris subvillosa</i> (Hook.) Ching	[ <i>Leptolepidium subvillosum</i> (Hook.) Hsing & S. H. Wu]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
491	<i>Ananthacorus angustifolius</i> (Sw.) Underw. & Maxon		Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
492	<i>Anetium citrifolium</i> (L.) Splitg.		Neotr. Asia	Costa Rica China	Wäckers 1998 Zhao Zhi-wei, 2000	epiphytic epiphytic	- ?	- -	- not inv.
493	<i>Antrophyum henryi</i> H. Christ		Ocean.	Hawaii	Gemma et al. 1992	aquatic	-	-	-
494	<i>Ceratopteris thalictroides</i> (L.) Brongn.		Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
495	<i>Cheilanthes anceps</i> Blanf.		Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
496	<i>Cheilanthes bullosa</i> Kunze		Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
497	<i>Cheilanthes distans</i> (R. Br.) Mett.		Austr.	New Zealand	Cooper 1976	terrestrial, saxicol	+	not det.	+
498	<i>Cheilanthes eckloniana</i> (Kunze) Mett.		Africa	Lesotho	Moteetee et al., 1996	saxicol	?	-	not inv.
499	<i>Cheilanthes farinosa</i> (Forssk.) Kaulf.		H-Arct. Asia	Pakistan China	Iqbal et al. 1981 Zhao Zhi-wei, 2000	terrestrial saxicol	+	VAM	-
500	<i>Cheilanthes hancockii</i> Baker		Asia	China	Zhao Zhi-wei, 2000	saxicol	+	VAM	not inv.
501	<i>Cheilanthes hirta</i> Sw.		Africa	Lesotho	Moteetee et al., 1996	terrestrial	?	-	not inv.
502	<i>Cheilanthes quadripinnata</i> (Forssk.) Kuhn		Africa	Lesotho	Moteetee et al., 1996	terrestrial	?	-	not inv.
503	<i>Cheilanthes sieberi</i> Kunze		Austr.	New Zealand	Cooper 1976	terrestrial, saxicol	+	not det.	+

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504	<i>Cheilanthes swartzii</i> Webb. & Benth.	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
505	<i>Cheilanthes viridis</i> (Forssk.) Kuhn	Africa	Lesotho	Moteetee et al., 1996	terrestrial	?	-	not inv.
506	<i>Coniogramme intermedia</i> Hieron.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
507	<i>Coniogramme pilosa</i> (Brack.) Hieron.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
508	<i>Coniogramme rosthomi</i> Hieron.	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	?	-	not inv.
509	<i>Coniogramme simillima</i> Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
510	<i>Cryptogramma stelleri</i> (J. F. Gmel.) Prantl	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
511	<i>Doryopteris concolor</i> (Langsd. & Fisch.) Kuhn	Africa	South Africa	Moteetee et al., 1996	terrestrial	?	-	not inv.
512	<i>Doryopteris decipiens</i> (Hook.) J. E. Sm.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
513	<i>Doryopteris decora</i> Brack.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
514	<i>Gymnopteris bipinnata</i> H. Christ var. <i>auriculata</i> (Franch.) Ching	Asia	China	Zhao Zhi-wei, 2000	saxicol	?	-	not inv.
515	<i>Gymnopteris vestita</i> (Wall.) Underw.	Asia	China	Zhao Zhi-wei, 2000	saxicol	+	VAM	not inv.
516	<i>Haplopteris elongata</i> (Sw.) E. H. Crane	Asia	India	Muthukumar & Udayan, 2000	epiphytic	+	VAM	not inv.
517	<i>Haplopteris elongata</i> (Sw.) E. H. Crane	Ocean.	Hawaii	Gemma et al. 1992	epiphytic	+	VAM	not inv.
518	<i>Haplopteris flexuosa</i> (Fée) E. H. Crane	Asia	China	Zhao Zhi-wei, 2000	epiphytic	?	-	not inv.
519	<i>Hecistopteris pumila</i> (Spreng.) J. Sm.	Neotr. Asia	Costa Rica	Wäckers 1998	epiphytic	-	-	-
520	<i>Hemionitis arifolia</i> (Burm.) T. Moore	Asia	India	Muthukumar & Udayan, 2000	saxicol	+	VAM	not inv.
521	<i>Onychium angustifrons</i> Ching	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	?	-	not inv.
522	<i>Onychium contiguum</i> Wall. ex. Hope	H-Arct. Asia	Pakistan	Iqbal et al. 1981	terrestrial	+	VAM	-
523	<i>Onychium contiguum</i> Wall. ex. Hope	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	+	VAM	not inv.
524	<i>Onychium japonicum</i> (Thunb.) Kuntze	H-Arct. Asia	Pakistan	Iqbal et al. 1981	terrestrial	+	VAM	septate
525	<i>Onychium japonicum</i> (Thunb.) Kuntze var. <i>lucidum</i> (D. Don) H. Christ	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	?	-	not inv.
526	<i>Onychium lucidum</i> (D. Don) Spring	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	+	VAM	not inv.
527	<i>Pellaea calomelanos</i> (Bory ex Willd.) J. E. Burrows	Africa	Lesotho	Moteetee et al., 1996	saxicol	?	-	not inv.
528	<i>Pellaea falcata</i> (R. Br.) Fée	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+

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526	<i>Pellaea glabella</i> Mett.		H-Arct.	Canada	Berth & Kendrick 1982	terrestrial	+	VAM	not inv.
527	<i>Pellaea mairei</i> Brause		Asia	China	Zhao Zhi-wei, 2000	saxicol	+	VAM	not inv.
528	<i>Pellaea rotundifolia</i> (G. Forst.) Hook.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det. VAM	+
529	<i>Pellaea ternifolia</i> (Cav.) Link		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
530	<i>Pityrogramma austroamericana</i> Domin		Ocean.	Hawaii	Gemma et al. 1992	terrestrial, saxicol	+	VAM	not inv.
531	<i>Pityrogramma calomelanos</i> (L.) Link		Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
532	<i>Polytaenium lanceolatum</i> (L.) Benedict	[Anthrophyum lanceolatum (L.) Kaulf.]	Neotr.	Costa Rica	Lesica & Antibus, 1990	epiphytic	-	-	-
533	<i>Polytaenium lineatum</i> Sw.	[Anthrophyum lineatum (Sw.) Kaulf.]	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
534	<i>Pteris aspericaulis</i> Wall.		Asia	China	Zhang et al., 2003	?	+	VAM	not inv.
	<i>Pteris aspericaulis</i> Wall. var. <i>tricolor</i> T. Moore		Asia	China	Zhao Zhi-wei, 2000	?	?	-	not inv.
535	<i>Pteris cretica</i> L.		Africa	Lesotho	Moteete et al., 1996	saxicol	+	VAM	not inv.
	<i>Pteris cretica</i> L.		Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
	<i>Pteris cretica</i> L.		H-Arct.	Pakistan	Iqbal et al. 1981	terrestrial	+	VAM	septate
	<i>Pteris cretica</i> L.		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
536	<i>Pteris cretica</i> L. var. <i>laeta</i> C. Chr. & Tardieu		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
	<i>Pteris cretica</i> L. var. <i>nervosa</i> (Thunb.) Ching & S. H. Wu		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
	<i>Pteris dissitifolia</i> Baker		Asia	China	Zhao Zhi-wei, 2000	?	?	-	not inv.
537	<i>Pteris ensiformis</i> Burm.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
538	<i>Pteris esquirolii</i> H. Christ		Asia	China	Zhao Zhi-wei, 2000	?	?	-	not inv.
539	<i>Pteris excelsa</i> Gaudich.		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
	<i>Pteris excelsa</i> Gaudich.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
540	<i>Pteris irregularis</i> Kaulf.		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
541	<i>Pteris linearis</i> Poir.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
542	<i>Pteris macilentia</i> A. Rich.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det. VAM	+
543	<i>Pteris muricata</i> Hook.		Neotr.	Ecuador	Lehnert et al., in prep.	terrestrial	+	VAM	-

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544	<i>Pteris quadriaurita</i> Retz.		Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
545	<i>Pteris semipinnata</i> L.		Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	?	-	not inv.
546	<i>Pteris setulosocostulata</i> Hayata		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
547	<i>Pteris tremula</i> R. Br.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
548	<i>Pteris vittata</i> L.		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
	<i>Pteris vittata</i> L.		Africa	Lesotho	Moteete et al., 1996	saxicol	+	VAM	not inv.
	<i>Pteris vittata</i> L.		Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
	<i>Pteris vittata</i> L.		Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
	<i>Pteris vittata</i> L.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
549	<i>Pteris wangiana</i> Ching		Asia	China	Zhao Zhi-wei, 2000	?	?	-	not inv.
550	<i>Pterozonium brevifrons</i> (A. C. Sm.) Lellinger		Neotr.	Ecuador	Lehnert et al., in prep.	saxicol	+	VAM	-
551	<i>Radiovittaria minima</i> (Baker) E. H. Crane	[ <i>Vittaria minima</i> (Baker) Benedict]	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
552	<i>Radiovittaria remota</i> (Fée) E. H. Crane	[ <i>Vittaria remota</i> Fée]	Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
553	<i>Vittaria costaricensis</i> Lellinger		Neotr.	Costa Rica	Wäckers 1998	epiphytic	-	-	-
	<b>Salvinaceae</b>								
554	<i>Salvinia cucullata</i> Roxb.		Asia	India	Ragupathy & Mahadevan 1996	aquatic	?	-	not inv.
555	<i>Azolla filiculoides</i> Lam.		Ocean.	Hawaii	Gemma et al. 1992	aquatic	-	-	not inv.
556	<i>Azolla pinnata</i> R. Br.		Asia	India	Muthukumar & Udayan, 2000	aquatic	-	-	not inv.
	<i>Azolla pinnata</i> R. Br.		Asia	India	Ragupathy & Mahadevan 1995	aquatic	-	-	not inv.
557	<i>Salvinia natans</i> (L.) All.		Asia	India	Muthukumar & Udayan, 2000	aquatic	-	-	not inv.
	<b>Schizeaceae</b>								
558	<i>Schizea fistulosa</i> Labill.		Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
559	<i>Schizea robusta</i> Baker		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
	<b>Selaginellaceae</b>								
560	<i>Selaginella arbuscula</i> Spring		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	-
561	<i>Selaginella biformis</i> A. Br.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
562	<i>Selaginella bryopteris</i> (L.) Baker		Asia	India	Muthukumar &	epiphytic	+	VAM	not inv.

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	<i>Selaginella bryopteris</i> (L.) Baker	Asia	India	Udaiyan, 2000 Muthukumar & Udaiyan, 2000	saxicol	+	VAM	not inv.	
563	<i>Selaginella caffrorum</i> (Milde) Hieron.	Africa	Lesotho	Moteetee et al., 1996	terrestrial	+	VAM	not inv.	
564	<i>Selaginella chrysochaulos</i> (Hook. & Grev.) Spring	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.	
565	<i>Selaginella davidii</i> Franch.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.	
	<i>Selaginella davidii</i> Franch.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.	
566	<i>Selaginella delicatula</i> (Desv.) Alston	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.	
567	<i>Selaginella frondosa</i> Warb.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.	
568	<i>Selaginella helferi</i> Warb.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.	
569	<i>Selaginella involvens</i> (Sw.) Spring	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.	
570	<i>Selaginella mettenii</i> Baker	Africa	Lesotho	Moteetee et al., 1996	terrestrial	+	VAM	not inv.	
571	<i>Selaginella moellendorffii</i> Hieron.	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.	
572	<i>Selaginella monospora</i> Spring	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	?	-	not inv.	
573	<i>Selaginella picta</i> (Griff.) A. Braun ex Baker	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.	
574	<i>Selaginella pulvinata</i> (Hook. & Grev.) Maxim.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.	
575	<i>Selaginella remotifolia</i> Spring	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	+	VAM	not inv.	
576	<i>Selaginella sanguinolenta</i> (L.) Spring	Asia	China	Zhao Zhi-wei, 2000	terrestrial, saxicol	+	VAM	not inv.	
577	<i>Selaginella</i> sp.	Asia	India	Muthukumar & Udaiyan, 2000	saxicol	?	-	not inv.	
<b>Tectariaceae</b>									
578	<i>Arthropteris tenella</i> (G. Forst.) J. Sm. in Hook. f.	Austr.	New Zealand	Cooper 1976	epiphytic, saxicol	+	not det.	+	
579	<i>Pleocnemia winitii</i> Holttum	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.	
580	<i>Tectaria devexa</i> (Kunze) Copel.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.	
581	<i>Tectaria gaudichaudii</i> (Mett.) Maxon	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.	
582	<i>Tectaria glabra</i> (Ching & Wang), comb. ined.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.	
583	<i>Tectaria sagenioides</i> (Mett.), comb. ined.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.	



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584	<i>Tectaria setulosa</i> (Baker) Holttum	[ <i>Ctenitopsis setulosa</i> (Baker) C. Chr. & Tardieu]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
585	<i>Tectaria subsageniacea</i> (H. Christ), comb. ined.	[ <i>Ctenitopsis subsageniacea</i> (H. Christ) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
586	<b>Thelypteridaceae</b> <i>Cyclosorus acuminatus</i> (Panz.) Nakai		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
587	<i>Cyclosorus auriculatus</i> (J. Sm.) C. M. Kuo	[ <i>Cyclogramma auriculata</i> (J. Sm.) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
588	<i>Cyclosorus cyatheoides</i> (Kaufl.) Farw.	[ <i>Thelypteris cyatheoides</i> (Kaufl.) Fosberg]	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
589	<i>Cyclosorus dentatus</i> (Forssk.) Ching	[ <i>Christella dentata</i> (Forssk.) Brownsey & Jermy]	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
	<i>Cyclosorus dentatus</i> (Forssk.) Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
590	<i>Cyclosorus erubescens</i> (Wall. ex Hook.) C. M. Kuo	[ <i>Glaphylopteridopsis erubescens</i> (Wall.) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
591	<i>Cyclosorus esquirolii</i> (Christ) C. M. Kuo	[ <i>Pseudocyclosorus esquirolii</i> (Christ) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
592	<i>Cyclosorus griffithii</i> (T. Moore) C. M. Kuo	[ <i>Dictyocline griffithii</i> T. Moore]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
593	<i>Cyclosorus gymnopteridifrons</i> (Hayata) C. M. Kuo	[ <i>Pronephrum gymnopteridifrons</i> (Hayata) Holtt.]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
594	<i>Cyclosorus hokouensis</i> Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
595	<i>Cyclosorus interruptus</i> (Willd.) H. Ito	[ <i>Cyclosorus gogglodes</i> (Schkuhr) Link]	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
	<i>Cyclosorus interruptus</i> (Willd.) H. Ito		Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
	<i>Cyclosorus interruptus</i> (Willd.) H. Ito		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	?	-	not inv.
596	<i>Cyclosorus molliusculus</i> (Kuhn) Ching	[ <i>Thelypteris interrupta</i> (Willd.) Iwats.]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
597	<i>Cyclosorus nudatus</i> (Roxb.) B. Nayar & Kaur	[ <i>Pronephrum nudatum</i> (Roxb.) Holtt.]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
598	<i>Cyclosorus ochthodes</i> (Kunze), comb. ined.	[ <i>Pseudocyclosorus ochthodes</i> (Kunze) Holttum]	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
599	<i>Cyclosorus parasiticus</i> (L.) Farw.	[ <i>Cyclosorus parasiticus</i> (L.) Farw.]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
	<i>Cyclosorus parasiticus</i> (L.) Iwats.		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
600	<i>Cyclosorus pennigerus</i> (G. Forst.) Ching	[ <i>Thelypteris pennigera</i> (G. Forst.) Allan]	Austr.	New Zealand	Cooper 1976	terrestrial	+	not det.	+
601	<i>Cyclosorus proliferus</i> (Retz.) Tardieu ex Tardieu & C. Chr.	[ <i>Ampelopteris proliferata</i> (Retz.) Copel.]	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
602	<i>Cyclosorus proliferus</i> (Retz.) Tardieu ex Tardieu & C. Chr.	[ <i>Ampelopteris proliferata</i> (Retz.) Copel.]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
603	<i>Cyclosorus sandwicensis</i> (Brack.)	[ <i>Thelypteris sandwicensis</i> (Brack.)	Ocean.	Hawaii	Gemma et al.	terrestrial	?	-	not inv.

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604	Copel. Cyclosorus simplex (Hook.) Copel.	W.H. Wagner [Pronephrium simplex (Hook.) Holtt.]	Asia	China	1992 Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
605	Cyclosorus subnigrescens Ching & S. H. Wu		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
606	Cyclosorus subochthodes (Ching), comb. ined.	[Pseudocyclosorus subochthodes (Ching) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
607	Cyclosorus terminans (J. Sm. ex Hook.) Panigrahi	[Amphineurom terminans (Hook.) Holtt.]	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
608	Cyclosorus truncatus (Poir.) Farw.		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
609	Cyclosorus wilfordii (J. Sm.), comb. ined.	[Dictyocline wilfordii J. Sm.]	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
610	Macrothelypteris torresiana (Gaudich.) Ching		Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	
	Macrothelypteris torresiana (Gaudich.) Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
611	Phegopteris hexangonoptera (Michx.) Fée		H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
612	Pseudophegopteris pyrrochachis (Kunze) Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
613	Pseudophegopteris yunkweiensis Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
614	Thelypteris beddomei (Baker) Ching	[Parathelypteris beddomei (Baker) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
615	Thelypteris flaccida (Blume) Ching	[Macrothelypteris flaccida (Blume) Ching]	Asia	India	Muthukumar & Udayan, 2000	terrestrial	+	VAM	not inv.
	Thelypteris flaccida (Blume) Ching	[Metathelypteris flaccida (Blume) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
616	Thelypteris globulifera (Brack.) Reed		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
617	Thelypteris hattori (H. Ito) comb. ined.	[MetaThelypteris hattori (H. Ito) Ching]	Asia	China	Zhang et al., 2003	terrestrial	?	-	not inv.
618	Thelypteris hirsutipes (C. B. Clarke) Ching	[ParaThelypteris hirsutipes (Clarke) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
619	Thelypteris hudsoniana (Brack.) C. F. Reed		Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
620	Thelypteris japonica (Baker) Ching	[ParaThelypteris japonica (Baker) Ching]	Asia	China	Zhang et al., 2003	terrestrial	?	-	not inv.
621	Thelypteris minutula C. V. Morton		Neotr.	Ecuador	Lehnert et al., in prep.	saxicol	-	-	-
622	Thelypteris novoboracensis Nieuw.		H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
623	Thelypteris palustris Schott		H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
	Thelypteris palustris var. pubescens Fernwald		H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
	<b>Woodsiaceae</b>								

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624	<i>Acystopteris tenuisecta</i> (Blume) Tagawa	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
625	<i>Athyrium angustum</i> C. Presl	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
626	<i>Athyrium anisopterum</i> H. Christ	Asia	India	Muthukumar & Udaiyan, 2000	saxicol	+	VAM	not inv.
	<i>Athyrium anisopterum</i> H. Christ	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
627	<i>Athyrium biserrulatum</i> H. Christ	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
628	<i>Athyrium delicatulum</i> Ching & S. H. Wu	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
629	<i>Athyrium dissitifolium</i> (Baker) C. Chr.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
630	<i>Athyrium esculentum</i> (Retz.) Copel.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
631	<i>Athyrium falcatum</i> Bedd.	Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
632	<i>Athyrium filix-femina</i> (L.) Roth	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
633	<i>Athyrium filix-femina</i> (L.) Roth	H-Arct.	Pakistan	Iqbal et al. 1981	terrestrial	+	VAM	septate
	<i>Athyrium mackinnonii</i> (Hope) C. Chr.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
634	<i>Athyrium macraei</i> (Hook. & Grev.) Copel.	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
635	<i>Athyrium macrocarpum</i> (Blume) Bedd.	Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
636	<i>Athyrium mengtzeense</i> Hieron.	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
637	<i>Athyrium microphyllum</i> (Sm.) Alston	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
638	<i>Athyrium nipponicum</i> (Mett.) Hance	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
639	<i>Athyrium sandwichianum</i> C. Presl	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
640	<i>Athyrium schimperii</i> Moug. ex Fée	Africa	Lesotho, South Africa	Moteetee et al., 1996	terrestrial	?	-	not inv.
641	<i>Athyrium solenopteris</i> (Kunze) T. Moore	Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
642	<i>Athyrium stigmatosum</i> T. Moore	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
643	<i>Athyrium thelypteroides</i> Desv.	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
644	<i>Athyrium wardii</i> (Hook.) Makino	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
645	<i>Cystopteris bulbifera</i> (L.) Bernh.	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
646	<i>Cystopteris bulbifera</i> x <i>fragilis</i>	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.

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647	<i>Cystopteris fragilis</i> (L.) Bernh.		Austr.	New Zealand Lesotho	Cooper 1976	saxicol	+	not det.	+
	<i>Cystopteris fragilis</i> (L.) Bernh.		Africa		Moteetee et al., 1996	saxicol	+	VAM	not inv.
	<i>Cystopteris fragilis</i> (L.) Bernh.		H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
648	<i>Cystopteris fragilis</i> var. <i>laurentiana</i> Weatherby		H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
649	<i>Cystopteris pellucida</i> (Franch.) Ching		Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
650	<i>Deparia boyana</i> (Willd.) M. Kato	[ <i>Dryoathyrium boryanum</i> (Willd.) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
651	<i>Deparia dolosa</i> (H. Christ), comb. ined.	[ <i>Lunathyrium dolosum</i> (H. Christ) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
652	<i>Deparia edentula</i> (Kunze), comb. ined.	[ <i>Dryoathyrium edentulum</i> (Kunze) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
653	<i>Deparia japonica</i> (Thunb.) M. Kato	[ <i>Athyrium japonica</i> (Thunb.) Copel.]	Ocean.	Hawaii	Gemma et al. 1992	terrestrial	+	VAM	not inv.
654	<i>Deparia lancea</i> (Thunb.) R. Sano in Fraser-Jenk.	[ <i>Diplazium lanceum</i> (Thunb.) C. Presl]	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
655	<i>Deparia longipes</i> (Ching), comb. ined.	[ <i>Athyriopsis longipes</i> Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
656	<i>Deparia petersenii</i> (Kunze) M. Kato	[ <i>Athyriopsis petersenii</i> (Kunze) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
657	<i>Diplazium alatum</i> (H. Christ), comb. ined.	[ <i>Allantodia alata</i> (Christ) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
658	<i>Diplazium chinense</i> (Baker) C. Chr.	[ <i>Allantodia chinensis</i> (Baker) Ching]	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
659	<i>Diplazium dilatatum</i> Blume		Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
	<i>Diplazium dilatatum</i> Blume	[ <i>Allantodia dilatata</i> (Blume) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
660	<i>Diplazium doederleinii</i> (Luer.) Makino	[ <i>Allantodia doederleinii</i> (Luer.) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
661	<i>Diplazium donianum</i> (Mett.) Tardieu		Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.
	<i>Diplazium donianum</i> (Mett.) Tardieu		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
662	<i>Diplazium esculentum</i> (Retz.) Sw.	[ <i>Callipteris esculenta</i> (Retz.) J. Sm.]	Asia	China	Zhang et al., 2003	terrestrial	+	VAM	not inv.

Chapter III.3: Mycorrhizal status of pteridophytes

	Diplazium esculentum (Retz.) Sw.	[Callipteris esculenta (Retz.) J. Sm.]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
663	Diplazium lasiopteris Kunze		Asia	India	Muthukumar & Udaiyan, 2000	terrestrial	+	VAM	not inv.
664	Diplazium laxifrons Rosenst.	[Allantodia laxifrons (Rosenst.) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
665	Diplazium megaphyllum (Baker) H. Christ	[Allantodia megaphylla (Baker) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
666	Diplazium polypodioides Blume	[Diplazium polypodioides Blume]	H-Arct.	Pakistan	Iqbal et al. 1981	terrestrial	+	VAM	septate
667	Diplazium pullingeri (Baker) J. Sm. var. daweshannicolum W. M. Ching	[Monomelangium pullingeri (Baker) Tagawa var. daweshannicolum W. M. Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
668	Diplazium spectabile (Wall. ex Mett.)	[Allantodia spectabilis (Wall. ex Mett.) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
669	Diplazium splendens Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	+	VAM	not inv.
670	Diplazium stenochlamys (C. Chr.)	[Allantodia stenochlamys (C. Chr.) Ching]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
671	Gymnocarpium dryopteris (L.) Newman		H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	+	VAM	not inv.
672	Hemidictyum finlaysonianum Wall. ex Hook.	[Asplenium finlaysonianum Wall. ex Hook.]	Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
673	Homalosorus pycnocarpos (Spreng.) Pic. Serm	[Athyrrium pycnocarpon (Spreng.) Tidestrom]	H-Arct.	Canada	Berch & Kendrick 1982	terrestrial	?	-	not inv.
674	Pseudocystopteris atkinsonii (Bedd.) Ching		Asia	China	Zhao Zhi-wei, 2000	terrestrial	?	-	not inv.
675	Woodсия montevicensis (Spreng.) Hieron.		Africa	Lesotho	Moteetee et al., 1996	saxicol	?	-	not inv.



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Ausbildung

1995. Abitur, Freiherr-v.-Stein Schule, Gymnasium Oldenburg in Holstein. Note 1.6.
1998. Vordiplom, Biologie (Hauptfächer Botanik und Zoologie; Nebenfächer Chemie und Physikalische Chemie), Georg-August-Universität, Göttingen. Note "sehr gut".
2002. Diplom, Biologie (Hauptfach Botanik, Nebenfächer Zoologie & Chemie), Georg-August-Universität, Göttingen. Thema der Arbeit: "Die Baumfarne Boliviens (Familien Cyatheaceae & Dicksoniaceae)". Betreuer: Prof. Dr. S.R. Gradstein. Note "sehr gut".
- Februar 2002-Juli 2007. Promotionsstudent an der Georg-August-Universität, Göttingen.  
Thema der Arbeit: „Diversity and evolution of pteridophytes, with emphasis on the Neotropics“. Betreuer: apl. Prof. Dr. M. Kessler.
- August 2006-Mai 2007. *Grad student* an der University of California, Berkeley.

Derzeitige Stellung

Anwärter auf den Dokortitel an der Georg-August-Universität, Göttingen. Abgabe der Doktorarbeit am 30.05.2007; letzte Prüfung am 04.07.2007.

Lehrerfahrungen

Alle Lehrerfahrungen wurden als studentische Hilfskraft an der Georg-August-Universität Göttingen gesammelt. Folgende Tätigkeiten wurden ausgeübt:

- |                                |   |
|--------------------------------|---|
| WS 1998/99                     | Aufbereitung der Vorlesungsthemen in allgemeiner Cytologie und Pflanzenphysiologie. |
| WS 1999/2000, 2000/01, 2001/02 | Kursbetreuung <i>Pflanzenanatomisches Grundpraktikum</i> .                          |
| SS 2000, 2001                  | Kursleiter in botanischen Bestimmungsübungen.                                       |
| WS 2001/02                     | Kursbetreuung <i>Biologie für Mediziner</i> .                                       |

### Forschungserfahrung

- Juli-Oktober 2000. Erste Exkursion nach Bolivien (10 Wochen). Feldarbeit für die Diplomarbeit.
- Juli 2002–Mai 2003. Zweite Exkursion nach Bolivien (1 Jahr) mit Ausflügen nach Ecuador, Peru, Argentinien und Brasilien. Feldarbeit für das Promotionsprojekt „Revision of the fern genus *Melpomene* (Grammitidaceae/Pteridophyta)“. DAAD-Jahresstipendium für Doktoranden. Gastinstitut: Instituto de Ecología, Universidad Mayor de San Andres, La Paz-Bolivia.
- August 2003-Juli 2006. Hilfwissenschaftler im DFG-Projekt der Teilgruppe A4 “Cryptogamic plant diversity of the *Purdiaea nutans* forest in southern Ecuador and its relationship to soil, climate, and vegetation structure“ der Forschergruppe FOR402.
- August-Dezember 2003/2004. Feldforschungsaufenthalte (je 4 Monate) auf der Estación Científica San Francisco nahe Loja, Ecuador, Prov. Loja.
- Dezember 2004. Besuch des Herbariums COL (2 Wochen) in Bogotá, Colombia
- Mai 2005. Besuch der University of Colorado, Boulder, (1 Monat) auf Einladung von Dr. Tom A. Ranker. Durchführung molekularer Analysen an der Farngattung *Melpomene* (Grammitidaceae).
- August 2006-Mai 2007. Herbararbeit für die Revision der neotropischen Baumfarne der Familie Cyatheaceae an der University of California, Berkeley, auf Einladung von Dr. Alan R. Smith.
- Oktober 2006. Besuch der Herbarien in New York (NY) und Washington (US) für die Revision der neotropischen Baumfarne der Familie Cyatheaceae (3 Wochen).

### Berufliche Affiliationen

American Society of Plant Taxonomists.

### Interessensgebiete

Biodiversität und Evolutionsforschung; Biogeographie; Systematik der Farne; basale Gruppen der Angiospermen; frühe Diversifikation der Landpflanzen; Koevolution von Landpflanzen und Böden; Mykorrhiza.

### Sprachen

Deutsch (fließend), Englisch (fließend), Spanisch (gut), Latein (gut), Französisch (Grundkenntnisse).

### Publikationen

#### Eingereicht und in Vorbereitung

Mandl, N., M. Lehnert, S.R. Gradstein, M. Kessler, F. Makeshin, & M. Richter. (im Druck). The unique *Purdiaea nutans* forest of southern Ecuador: abiotic characteristics and cryptogamic diversity. Ecological Studies.



- Gradstein, S.R., M. Kessler, M. Lehnert, F. Makeschin, N. Mandl, M. Abyi, & M. Richter. (eingereicht). Vegetation, climate, and soil of the unique *Purdiaea* forest of southern Ecuador. *Flora*.
- Kessler, M. & M. Lehnert. (eingereicht). Are ridge habitats special sites for endemic plants in tropical montane rain forests? A case study of pteridophytes in Ecuador. *Journal of Vegetation Science*.
- Kessler, M., M. Lehnert, N. Mandl & S.R. Gradstein. (eingereicht). The contribution of ridge habitats to pteridophyte diversity in tropical montane forests of southeastern Ecuador. *Landscape Ecology*.
- Lehnert, M. (eingereicht). New developments on Neotropical Cyatheaceae. Proceedings of the conference *Ferns for the 21st Century*, 2004, Edinburgh, U.K.
- Lehnert, M. (eingereicht). Cyatheaceae. In: Valencia, R. et al. (Eds.). *Libro Rojo de las Plantas Vasculares Endémicas del Ecuador 2005*. Pontificia Univ. Católica del Ecuador, Quito.
- Lehnert, M. (eingereicht). Cyatheaceae, Dicksoniaceae. In: Jørgensen, P.M. et al. (Eds.). *Catalogue of the Vascular Plants of Bolivia*. Missouri Botanical Garden, St. Louis, U.S.A.
- Lehnert, M. (eingereicht). Cyatheaceae. In: Zuloaga, F.O. et al. (Eds.). *Catálogo de las plantas vasculares del Cono Sur*. Instituto Darwinion, Buenos Aires, Argentina.
- Lehnert, M., M. Kessler, L.I. Salazar, H. Navarrete, F. Werner & S. R. Gradstein. (eingereicht). Checklist to the Pteridophytes of the Reserva Biológica San Francisco (Prov. Zamora-Chinchipec, Ecuador). *Ecotropica*.
- Lehnert, M. (in Vorbereitung a). Resolving the *Cyathea caracasana*-complex: First results.
- Lehnert, M. (in Vorbereitung b). On the typification of *Cyathea pallescens* (Sodirol) Domin: the truth and its consequences.
- Lehnert, M., M. Kessler, A. N. Schmidt-Lebuhn, S. A. Klimas, S. Fehlberg, & Tom A. Ranker. (in Vorbereitung a). Phylogeny of the fern genus *Melpomene* (Polypodiaceae) inferred from morphology and chloroplast DNA analysis.
- Lehnert, M., I. Kottke, S. Setaro, L. Pazmiño, P. Lozano, & M. Kessler. (in Vorbereitung b). New insights on the mycorrhizal infections in ferns: an example from southern Ecuador.

## 2007

- Kessler, M., A. R. Smith, & M. Lehnert (2007). Ten new species of *Blechnum* (Blechnaceae, Pteridophyta) from Bolivia. *Amer. Fern. J.* 97: 66-80.

## 2006

- Kessler M., A. R. Smith, & M. Lehnert (2006). Four new species of *Selaginella* (Selaginellaceae – Pteridophyta) from Bolivia. *Edinburgh J. Bot.* 63: 85-93.
- Lehnert, M. (2006). Two new species of tree ferns (Cyatheaceae) from Ecuador. *Brittonia* 58: 4-9.
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2005

Smith, A.R., B. León, H. Tuomisto, H. van der Werff, R.C. Moran, M. Lehnert & M. Kessler. (2005). New records of pteridophytes for the Flora of Peru. *SIDA* 21: 2321-2341.

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Lehnert, M. (2004). *Cyathea bettinae*, a new tree fern from Bolivia. *Brittonia* 56: 210-212.

2003

Lehnert, M. (2003). Six new species of tree ferns from the Andes. *Amer. Fern J.* 93: 169-183.

2001

Lehnert, M., M. Mönnich, T. Pleines, A. Schmidt-Lebuhn & M. Kessler (2001). The Relictual Fern Genus *Loxsomopsis*. *Amer. Fern J.* 91: 13-24.

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Lehnert, M., N. Mandl, M. Kessler, L. I. Salazar, H. Navarrete & S. R. Gradstein. (2006). Biogeography and ecology of the pteridophytes in the Reserva Biológica San Francisco (Ecuador, Prov. Zamora-Chinchipec). 19<sup>th</sup> annual conference of the Society for Tropical Ecology, University of Kaiserslautern, Germany.

2004

Lehnert, M. (2004). New Developments on Neotropical Cyatheaceae. Pteridology conference *Ferns for the 21st Century*, Edinburgh, U.K.

Poster

2005

Lehnert, M., M. Kessler, & H. Schneider. (2005). The influence of soil evolution on pteridophyte diversification. 17<sup>th</sup> International Botanical Congress, Vienna, Austria.

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2004

Janssen, J. & M. Lehnert. (2004). How to deal with bulky ferns? – Towards a standardized method for tree fern collections. Pteridology conference *Ferns for the 21st Century*, Edinburgh, U.K.

2003

Gradstein, S. R., M. Kessler, M. Lehnert, N. Mandl, H. J. Sipman, F. Makeschin, K. Rubitzki, & M. Richter. (2003). Cryptogamic plant diversity of the *Purdiaea nutans* forest in southern Ecuador and its relationship to soil and climate. 4. Congreso Ecuatoriano de Botanica, Loja, Ecuador.