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TAXONOMIC STUDY OF THE ELAPHOGLOSSUM APODUM COMPLEX (ELAPHOGLOSSACEAE)

City University of New York Ph.D. 1983

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TAXONOMIC STUDY OF THE ELAPHOGLOSSUM APODUM COMPLEX
(ELAPHOGLOSSACEAE)

by

LUCIA ATEHORTUA

A dissertation submitted to the Graduate Faculty in Biology in partial fulfilment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1983

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

TAXONOMIC STUDY OF THE ELAPHOGLOSSUM APODUM COMPLEX (ELAPHOGLOSSACEAE)

by

LUCIA ATEHORTUA

Adviser: Dr. J.T. Mickel

The section *Polytrichia* subsection *Apoda* Mickel & Atehortúa comprises eight species, all of which are Neotropical in distribution (West Indies, Central America and northern South America). Results of morphological and chemical investigations of the *Elaphoglossum apodum* complex are presented. The comparative research is summarized in a diagram showing the probable evolutionary relationships within the subsection. A taxonomic revision is presented including keys, descriptions, illustrations and discussion of the taxa. Two new species *Elaphoglossum amazonicum* and *Elaphoglossum latum* are described.

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AAU	Aarhus: Herbarium Jutlandicum, Botanical Institute, University of Aarhus.
B	Berlin: Botanischer Garten und Botaniches Museum, Berlin-Dahlem, Königin-Luis Strasse.

BM	London: Herbarium, British Museum (Natural History).
CGE	Cambridge: Herbarium, Botany School, University of Cambridge.
COL	Bogotá: Herbario Nacional Colombiano, Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional.
F	Chicago: John G. Searle Herbarium, Field Museum of Natural History.
GH	Cambridge: Gray Herbarium of Harvard University.
K	Kew: The Herbarium, Royal Botanic Gardens, England, Great Britain.
MO	Saint Louis: Herbarium, Missouri Botanical Garden.
NY	New York: Herbarium, New York Botanical Garden.
P	Paris: Muséum National d' Historie Naturalle, Laboratorie de Phanérogamie.
PR	Praha: Botanické oddĕleni Přírodovĕd. muzea Národnibo muzea v Praze (Department of Botany, National Museum in Praga).
UC	Berkeley: Herbarium, Department of Botany, University of California, Berkely.
US	Washington: Unites States National Herbarium, Department of Botany, Smithsonian Institution.

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Introduction

The genus Elaphoglossum is composed of nearly 600 species, all of which are tropical or subtropical in distribution. About 70% of the species occur in the Neotropics. Because of their remarkable uniformity and simplicity in gross morphology, the species are often overlooked in the field, and consequently the group has been poorly collected. The great similarity among certain species complexes has led to serious difficulties in delimitation of the taxa; therefore, names have often been misapplied and many have been created for previously known species. The genus has long been very problematic to pteridologists from the taxonomic and phylogenetic points of view. Alston (1956), Holttum (1966), Pichi Sermolli (1968), and Mickel (1980), have emphasized the need for a taxonomic revision of this genus.

The author decided to undertake a study of subsection Apoda Mickel & Atehortúa. The members of this small complex are extremely similar in their gross morphology and therefore taxonomically very difficult. The purpose of this study was to define the species in question and to examine their relationships within and without the subsection. An attempt has been made to integrate comparative morphological and chemical evidence and to apply recent techniques and methods of analysis to study the variation and speciation within subsect. Apoda.

Historical Background

In the early days of fern taxonomy all ferns with sporangia covering the abaxial lamina surface were placed in the genus Acrostichum (the sorus condition being termed acrostichoid).

The first species of Elaphoglossum was described by Linnaeus (1753) as Acrostichum crinitum. Schott (1834) proposed the name Elaphoglossum but unfortunatly did not provide any description. John Smith (1841) described the genus as having "veins simple or forked, internal, venules paralleled, their apices free or clavate, terminating within a thickened margin. Fronds simple, entire, oblong or linear-lanceolate, smooth or squamose; margin fertile, frond usually membranous."

Fée (1845) kept Elaphoglossum within Acrostichum but divided the elaphoglossoids into two groups: Oligolepidea and Polylepidea, each of which were subdivided into smaller, mostly unnamed groups. Fée (1852) revised his classification and recognized four primary groups without further subdivisions: Oligolepidea, Polylepidea, Pilosella and Chromatolepidea (Table I).

Table I

Classification schemes for the genus *Elaphoglossum* (1852-1899)

Fée (1852)		Sodiro (1897)		Diels (1899)	
Group I.	Oligolepidea *	I.	Glabra	I.	Eu-Elaphoglossum *
Group II.	Polylepidea	II.	Setosa	II.	Hymenodium
Group III.	Pilosella		A. Oligotrichia		
Group IV.	Chromatolepidea		B. Polytrichia *		
		III.	Squamosa		
			A. Oligolepidea		
			B. Laciniata		
		IV.	Polylepidea		

* where some known species of subsect. *Apoda* where placed.

Moore (1857-1862) was the first to consistently recognize *Elaphoglossum* at the generic level. In it he made many new combinations. His subgroup *Oligolepideum* contained species with fronds naked or with few scales, and *Polylepideum* those with fronds clothed with numerous scales.

Hooker (1863-1864) described 94 species of *Acrostichum* under subgenus *Elaphoglossum* together with other subgenera, such as *Lomariopsis*, *Polybotrya*, *Stenochlaena*, *Rhipidopteris*, and *Egenolfia*. Smith (1896) accepted *Elaphoglossum* as a genus in a strict sense, referring it to the tribe Acrostichae. He excluded the genera *Rhipidopteris* and *Microstaphyla*, considering them as belonging to section *Polybotryae*. Kuhn (1868) indiscriminately mixed species of *Acrostichum* and *Elaphoglossum*, creating considerable taxonomic confusion. As late as 1892 Baker was describing species within *Acrostichum* subgenus *Elaphoglossum*, but the subgenus was subdivided into smaller groups based on the scales and hairs of the lamina.

Sodiro (1893) followed the model proposed by Hooker and described 81 species as *Acrostichum* (*Elaphoglossum*), separating them into two groups based on vein characters and creating more subgroups based on scales (Table I).

Diels (1899) recognized two subsections: *Eu-Elaphoglossum* for the bulk of the species and *Hymenodium* for the distinct, broad, net-veined *E. crinitum* (Table I). However, his subsectional groups largely followed those of Sodiro. In the same year Christ (1899) published his classic *Monographie des Genus Elaphoglossum*, which stands as the most detailed treatment of this genus covering 142 species in 32 groups. The primary division was based on venation: *Ordo Stenoneura* with veins running all the way to the margin without thickened ends and *Ordo Condyleoneura* with veins ending just short of the margin with swollen ends (hydathodes). Christ further subdivided these into sections, subsections, and divisions (Table II) using characters such as blade scales, frond size, stipe articulation, and rhizome habit and thickness. Basically his species groups were natural and recognizable but unfortunately he placed what are now believed to be unrelated divisions and subsections together and did not provide a usable key to the groups.

Christ placed some of the species with black, marginal, subulate scales in each of the two ordos when in fact they now seem to be closely related based on anatomical and chemical studies. By the same token, his *Condyloneura* subdivisions *Dimorpha*, *Petiolosa*, *Pilosa*, and *Ovata* have no hydathodes and belong with close relatives in *Ordo Stenoneura*.

Table II

Christ's scheme of the genus Elaphoglossum (1899)

Ordo Stenoneura	Ordo Condyloneura
1. Sectio Craspedoglossa	1. Sectio Gymnoglossa
A. Subsectio Platyglossa	A. Subsectio Dimorpha
-Divisio Latifolia	B. Subsectio Feeana
-Divisio Melanolepidea	C. Subsectio Coespitosa
-Divisio Decorata	D. Subsectio Amygdalifolia
B. Subsectio Pachyglossa	2. Sectio Polytrichia
-Divisio Conformia	A. Subsectio Hymenodium
-Divisio Micradenia	B. Subsectio Hybrida
-Divisio Squamipedia	C. Subsectio Setosa *
-Divisio Rhipidopteris	D. Subsectio Petiolosa
C. Subsectio Flaccida	E. Subsectio Pilosella
D. Subsectio Herminieriana	F. Subsectio Pilosa
2. Sectio Lepidoglossa	-Divisio Gardneriana
A. Subsectio Polylepidea	-Divisio Boraginea
-Divisio Muscosa	G. Subsectio Ovata
-Divisio Bellermaniana	3. Sectio Undulata
-Divisio Argyrophylla	
-Divisio Fimbriata	
-Divisio Stipitata	
B. Subsectio Microlepidea	
C. Subsectio Glossoidea	

* where known species of subsect. Apoda were placed.

Schummann (1915) was the first to recognize Elaphoglossum and related genera as clearly distinct from other acrostichoid ferns. Following this example, Bower (1928) divided the ferns with acrostichoid sori, placing them in several different groups. He suggested that Elaphoglossum belonged to his metaxyoid ferns, of which Metaxya was thought to be the most primitive, Syngramma taking an intermediate position, and Elaphoglossum the most advanced.

In contrast, Christensen (1938) placed Elaphoglossum in a separate subfamily, Elaphoglossoideae, within the Polypodiaceae. He remarked on its uncertain taxonomic position and suggested that this subfamily had reached a more advanced evolutionary condition than most other subfamilies of Polypodiaceae. Thus he placed it at the end of his scheme. Ching (1940) and Herter (1940, 1949) raised Elaphoglossum to family level, although the family was not validly published at that time. Copeland (1947) placed Elaphoglossum and related genera into the family Aspidiaceae and pointed out that it did not have near relatives among other genera of this family. In the same year, Holttum (1947) reviewed all the arguments to place Elaphoglossum in different groups, and, based on his field experience and observations, included the genus in the subfamily Lomariopsidoideae of his broad family

Dennstaedtiaceae. He gave interesting arguments against Christensen, Bower, and Copeland's views and suggested that the genus most closely related to Elaphoglossum was Lomariopsis. His arguments were based on the dorsiventral rhizome, venation, soriation and spore morphology. He also suggested the possibility that Elaphoglossum had a polyphyletic origin within the genus Lomariopsis. In his work on Elaphoglossum of Malaysia, Holttum (1966) suggested a tentative subdivision of the genus based on scale characters and remarked about the importance of these structures as the only possible basis for further subdivision of this complex genus.

Pichi Sermolli (1968), considering several aspects of morphology and relationships of Elaphoglossum, described a separate family Elaphoglossaceae belonging to the stock of the Aspidiales, similar to Copeland's view.

Relationships of the Genus

The relationships of the elaphoglossoid ferns to other ferns are still unclear. Elaphoglossum is placed close to Lomariopsis by some authors (Holttum 1966; Kaur, 1974, Crabbe, Jermy & Mickel 1975; Lovis 1977) because of the acrostichoid sori, largely epiphytic habitat, monolete spores and chromosome number of *n*= 41. Christensen (1938) gave it its own subfamily Elaphoglossoideae in the Polypodiaceae but could not determine its relationships with certainty. Holttum (1947) placed it in the Lomariopsidioideae of his Dennstaedtiaceae and Alston (1956a) placed it in the Lomariopsidaceae together with *Lomariopsis*, *Egenolfia*, *Bolbitis*, *Teratophyllum* and *Lomagramma*. Pichi-Sermolli (1968) erected a new family for it. Kaur (1974) also placed it in the Lomariopsidaceae. Crabbe, Jermy & Mickel (1975) placed it in the Elaphoglossoideae of the Aspleniaceae close to Lomariopsidoideae. Lovis (1977) placed it between the dryopteroid and davallioid ferns. Holttum (1947) and Sporne (1975) have suggested a davallioid relationship because of its similarities in stele and chromosome number, whereas Kaur (1974), suggested a tectarioid origin from the stock of the Aspidiales.

In spite of the controversial points of view, it seems that the majority of pteridologists more or less agree that *Elaphoglossum* belongs close to or in the Lomariopsidaceae.

Within the last three decades, taxonomic treatments of the genus have been published for Brazil (Alston, 1956b); Hawaii (Anderson & Crosby, 1966); India (Sledge, 1967); tropical Africa (Schelpe, 1969); continental Africa (Pichi-Sermolli, 1975);

Malesia (Holttum, 1978); Guatemala (Mickel, 1981a); Chiapas, Mexico (Mickel,1981b); and South Africa (Roux, 1982).

Although they did not provide any conspectus of the genus as a whole, these treatments have increased our knowledge and improved our understanding of the characters on which species discrimination is based. Holttum (1978) summarized his own observations in the field and related morphological and ecological information. He emphasized the importance of scale characters as the main basis for subdividing the genus and suggested a tentative division based on that character. His observations and discussion of these relationships have provided the background for a more careful study of those structures, which have been very helpful in solving some of the problems in the subsection herein treated. For example, scale characters such as shape, size, color, cellular pattern and distribution have been overlooked in the earliest proposed division.

Mickel & Atehortúa (1980) divided the genus into nine sections and 21 subsections based mainly on scale characters, characters as was proposed by Holttum (1947), and on additional characters such as hydathodes, resin dots, glandular hairs, phyllopodia, blade texture and shape (Table III).

Subsection Apoda

Historical background

In the first treatment of the genus Elaphoglossum (Fée, 1845, under the genus name Acrostichum) the only known species of this subsection were A. apodum Kaulf. and its synonym A. platyneuron Fée. However, Fée placed them into his group Oligolepidea together with some of the glabrous species (i.e. A. conforme and related species).

Sodiro (1893) only cited those Elaphoglossum species growing in Ecuador, including only one species of the E. apodum complex, Acrostichum apodum, which was included in group Oligotrichia together with some of the subulate and pseudo-subulate species (i.e., A. villosum and A. dendricolum, respectively). He did not mix scaly and glabrous species together.

Christ (1899) in his monographic treatment of the genus (with only 142 species known at his time) rearranged the species of subsection Apoda -- E. apodum, E. cubense, and E.procurrens-- into his subsectio Setosa together with some of the known subulate-scaly species (i.e., E. villosum, E. plumieri and E. setosum), but he did not include E. backhousianum as a part of this subsection; it was only listed in his desiderata.

Table III

Mickel and Atehortúa classification scheme of the genus _Elaphoglossum_ (1980)

---

1. Section Elaphoglossum

    Subsection Pachyglossa
    Subsection Tenuifolia

2. Section Squamipedia

    Subsection Squamipedia
    Subsection Peltapteris
    Subsection Feeana *

3. Section Decorata

4. Section Lepidoglossa

    Subsection Polylepidea
    Subsection Microlepidea
    Subsection Pilosa
    Subsection Petiolosa
    Subsection Huacsaro
    Subsection Muscosa

5. Section Polytrichia

    Subsection Hymenodium
    Subsection Hybrida *
    Subsection Apoda *

6. Section Setosa

    Subsection Setosa
    Subsection Pilosella
    Subsection Alpestria
    Subsection Plumeriana

7. Section Eximia

    Subsection Eximia
    Subsection Cardenasiana

8. Section Undulata

9. Section Amygdalifolia

---

* where some of the known species of subsect. _Apoda_ were placed.

Mickel & Atehortúa (1980) included only three species in their subsect. Apoda: E. apodum, E. cubense and E. siliquoides. This low number was in large part due to the poor knowledge of the characters on which species discrimination was based, the large amount of material to deal with, and the nomenclatural chaos of the species involved in that study (Table IV).

As a result of increased understanding I decided to undertake a study of subsection Apoda because I was aware of the characters on which species discrimination were based in this group and had a good picture of the geographical variability in some populations. One of the most fascinating aspects of this group is the remarkable similarity between species in terms of their gross morphological appearance making it almost impossible to superficially distinguish one species from another. The problem was to find characters that more clearly define the species. These included rhizome scales, (overall frond shape, spore ornamentation, geographical distribution, and flavonoid distribution patterns).

I went beyond our previous treatment looking for possible relationships to other groups and surprisingly found one species, E. procurrens, that did not satisfy me, although it seemed to fill the requirements for sect. Squamipedia. Elaphoglossum pro-

Table IV

Classification schemes of subsect. *Apoda*

Christ (1899)	Mickel & Atehortúa (1980)	Atehortúa (1983)
Ordo Condyloneura	Section Polytrichia	Section Polytrichia
Sectio Polytrichia	Subsection Apoda	Subsection Apoda
Subsectio Setosa	1. E. apodum	1. E. amazonicum
1. E. apodum	2. E. cubense	2. E. apodum
2. E. cubense	3. E. siliquoides	3. E. auripilum
3. E. procurrens		4. E. backhousianum
		5. E. cubense
		6. E. latum
		7. E. procurrens
		8. E. raywaense

currens was originally included in subsect. *Feeana* Christ based on its frond shape, slender creeping rhizome, inconspicuous phyllopodium, absence of hydathodes, and spore shape with narrow crests. However, its frond appearance and scale indumentum were extraordinarily similar to those of *E. cubense*, which also shares a similar geographical distribution. Furthermore, the presence of subulate scales covering its oblanceolate fronds, short stipe and long decurrent base formed a good syndrome of characters that were shared by almost all the species in subsect. *Apoda*. Finally, its spore ornamentation gave me clues to possible relationship within this subsection, i. e., they are very similar to those found in *E. raywaense*. Consequently, it was removed from the previous group *Squamipedia* and included in subsect. *Apoda*.

Although Christ (1899) was accurate in including *E. procurrens* with *E. apodum* and *E. cubense* in his sectio *Polytrichia* subsect. *Setosa* he failed to distinguish the *E. apodum* complex from the *E. Setosa* complex. These two groups are related but are distinct in their vein ending, flavonoid distribution pattern, and to a lesser extent in spore ornamentation.

Elaphoglossum siliquoides, which was originally in our subsect. *Apoda*, has been removed to sect. *Setosa* subsect. *Pilosella* This change is based mainly on the presence of inconspicuous hydathodes in adult fronds, inconspicuous phyllopodium, rounded fertile frond, flavonoid distribution pattern (which diverges greatly from the common pattern found in almost all species of this subsection), and spore ornamentation.

Elaphoglossum auripilum was removed from subsect. Hybrida to subsect. Apoda because of its extraordinary similarity with E. apodum, E. cubense, and E. rayawaense in rhizome habit, short stipe, spore ornamentation, and flavonoid distribution pattern. These features were considered important enough to support its inclusion in subsect. Apoda.

Also four species were added to subsection Apoda: E. amazonicum, E. backhousianun, E. latum, and E. raywaense.

During the current study, one specimen found in Cuba and others from Cocos Island (Costa Rica) seemed to be part of this subsection and closely related to E. apodum, E. auripilum, E. cubense, and E. latum. Unfortunatly, the specimen from Cuba is sterile as are most of the specimens from Cocos. It was decided that until new material is available they will remain unidentified and be classed as Species incertae."

Characterization of Subsection *Apoda*

Elaphploglossum subsect. *Apoda* Mickel & Atehortúa is a relatively homogeneous group of eight species which exhibit strong similarities in their ecological, morphological, and anatomical characters, and are further characterized by their relatively uniform flavonoid distribution (Fig. 17).

Subsection *Apoda* has been aligned with two other subsections, *Hymenodium* (Fée) Christ and *Hybrida* Christ, within section *Polytrichia* Christ, based on their external morphology, such as scale characters and distribution, absence of hydathodes, vein endings, anatomy, and flavonoid patterns.

Although members of subsect. *Apoda* closely resemble those of sect. *Setosa* in their orange-yellow to brown subulate blade scales and in their general appareance, they have been included in sect. *Polytrichia* Christ on the absence of hydathodes (vein endings) and the spore sculpturing which is characterized by the presence of low ridges and often perforated crests (Fig. 7: a-b).

Since this study was initiated important new information has been gathered through the observation of living material.

It was observed that leaves of *E. cubense* and *E. crinitum* have hydathodes in their juvenile stages which disappear with age. This observation was also made by Bell (1955) in some plants of *E. apodum*. Perhaps the hydathodes play an important physiological role during the early developmental stages and may have some function related to the microhabitat in which the species grow. Consequently, our previous definition of subsect. *Apoda* must be modified, adding that hydathodes may be present in juvenile stages though lacking in adult leaves.

As a part of the morphological syndrome of this subsection, I would add that the fronds are often characterized by a long, gradually decurrent base, acute to acuminate apex, and long and thin glandular hairs which are associated with long and delicate subulate blade scales.

Morphologoy and Anatomy

Christ (1899) made the first morphological study of the genus Elaphoglossum. This study included characters such as vein endings, scale morphology, hydathodes, glandular hairs, and frond size and shape. Holttum (1947), on the basis of field observations, emphazised the importance of the scales as taxonomically reliable characters among the species.

Bell (1950, 1951a, 1951b, 1955, and 1956) made an anatomical survey of the genus based on species collected in Jamaica and Ecuador. He included three species of subsect. Apoda -- E. apodum, E. cubense, and E. procurrens--, but did not provide specific detailed observations of these species. Nevertheless, his general observations and descriptions are consistent with those of the present study and with the study of Roux (1982) on some Elaphoglossum species of South Africa.

Stokey & Atkinson (1957) studied the gametophytes of some neotropical species of Elaphoglossum, but did not include any species of the E. apodum complex. My own observations on this group have not shown significant differences from the species observed by them.

Van Cotthem (1970a), in his survey of stomatal patterns in the ferns, studied five species of Elaphoglossum, none of which were members of subsect. Apoda. Nevertheless, his observations are similar to those of Bell (1955), Roux (1982), and myself in sections Setosa and Polytrichia (including subsect. Apoda).

Lloyd (1970), in his study of several morphological features in relation to the habitat, included one of the species of this subsection -- E. auripilum. I discuss some of his conclusions in the ecology chapter (Chapter V)

Although the spore morphology of the genus was surveyed by Mickel & Atehortúa (1980), more detailed studies on spore ornamentation using Scanning Electron Microscope (SEM) are presented and analyzed here.

Materials and Methods

Rhizomes, petioles, fronds, spores, and gametophytes of species in *Elaphoglossum* subsect. *Apoda* were examined during this study. About 3000 herbarium specimens of subulate-scaled *Elaphoglossum* species have been studied including nearly 600 specimens of the *E. apodum* complex. These were supplemented by studies of living plants cultivated at the New York Botanical Garden.

Initial inspection of the specimens was made with a dissecting scope (30X magnification). Pieces of fronds, entire scales, and spore samples were removed as needed, mounted in Hoyer's solution (Anderson, 1954), and viewed with a light microscope. The clearing action of Hoyer's solution enhanced examination of the cellular detail of the scales, frond surfaces, and gametophytes. Other leaf clearings were made by placing dried leaf segments into 5% aqueous NaOH solution for 2-5 days, bleaching with chlorox solution, and staining with tannic acid and ferric chloride in 50% alcohol (modified from Foster, 1934). The stained segments were mounted in piccolite or canadian balsam. Using fresh material, cross-sections of the rhizome, root, petiole, and frond were made on a sliding microtome at thickness of 20-35 μm, stained in 1% safranin and counterstained 0.5% fast green.

Rhizome and petiole samples from herbarium specimens and living material were softened in a solution of glycerine-alcohol (1:1) for 3-5 weeks and then placed in 10% Aerosol OT solution forseveral days. Before fixation, air bubbles were removed by placing the material in a vacuum for several minutes. The samples were then fixed in FAA, dehydrated in an ethanol-TBA series, embedded in Paraplast Plus (melting point 56-57°C), and serially sectioned at 5-15 µm on a rotary microtome. These sections were also stained with safranin and counterstained with fast green and then mounted according to the techniques described by Johansen (1940).

Sporangia and spore studies were based primarily on clearing and SEM techniques. For the clearing procedures the samples were placed in a drop of 85% lactic acid with cover slip and placed on a warming plate for several hours until the oil droplets had been driven out. Measurements of the sporangia and spores were made using 20 spores/sporangia per species. Measurements were made at 400X magnification using an ocular micrometer.

In addition to observations by light microscope, representative specimens were chosen for further examination with the SEM. Samples of spores were mounted on standard aluminum SEM studs using doublesided adhesive tape. The prepared studs were vacuum coated with gold-palladium for 2 minutes. The spores were viewed with a JEOL JSM-U3 SEM and pictures were taken with an leration voltage of 25 KV, using a polaroid type 55/ positive-negative film.

Viable spores for gametophyte studies were obtained from living plants in the greenhouses of the New York Botanical Garden. After several attempts at germination on different media, sphagnum moss was selected as the best substrate for germination. Fresh sphagnum was placed in petri dishes of 9.5 cm diam. Spores were sown on this medium and sterilized water was added to maintain the humidity. The petri dishes were sealed with parafilm "M" tape and placed under fluorescent light for seven months and then changed to indirect daylight. The stages of germination were observed under the light microscope.

Rhizome

All species investigated were collected in the rain forest or cloud forest zone at elevations of 20-2400 m. The general habit for the entire complex is epiphytic on tree trunks or with rare exceptions on wet, rocky banks.

Holttum (1964) stated that ferns with creeping or climbing rhizomes are biologically specialized and in most cases the rhizome is dorsiventral in structure. This is the case for *Elaphoglossum*. He argued that the creeping, dorsiventral, solenostelic rhizome does not represent a stage in the evolutionary development of leptosporangiate ferns, but is more probably derived from an ancestral stock having a radially organized rhizome.

External morphology

The rhizomes of the members of subsect. *Apoda* are dorsiventral densely scaly, and similar in both outward appearance and internal structure. The rhizome diameter and length of internodes are variable. In most of the species the rhizomes are obliquely ascendant or horizontal without internodes. The fronds are borne in several orthostichies crowded together on the dorsal side of the rhizome, the whole plant having a caespitose appearance. In *E. amazonicum*, *E. apodum*, *E. auripilum*, *E. latum*, and *E. raywaense* the rhizome is short-creeping, stout, and often has four rows of fronds. Buds, if present, are only associated with those petioles nearest the ventral surface of the rhizomes, just below the petiole base. Bell (1950) and Roux (1982) reported that in _Elaphoglossum_ branches arise from these buds which could survive as independent plants after the parent rhizome died. In subsect. _Apoda_ I found buds to be conspicuous in _E. procurrens_, inconspicuous in _E. backhousianum_ and _E. cubense_, and not visible in the other species.

The roots are scattered and most of them are located on the ventral side of the rhizome. It is very difficult to evaluate root and bud association due to the proximity of the leaf bases.

Most of the species in this complex have polystichous phyllotaxis with the exception of _E. backhousianum_, _E. cubense_, and _E. procurrens_. The latter in particular has a very slender, creeping rhizome which bears fronds 0.6-1.5 cm apart in an alternate pattern. Also at each petiole base in _E. procurrens_ there is a conspicuous bud which contributes to a poorly developed branch system. In _E. backhousianum_, which is also distichous, the rhizome is more stout, compact, and short-creeping. It is obliquely ascendant and the distance between the insertion of the petioles is shorter (0.5-1.0 cm) than in *E. procurrens*. Buds are associated with the petiole bases but seem to remain dormant. *Elaphoglossum cubense* appears intermediate between distichous and polystichous, although Bell (1955) considered it as distichous. In some specimens it appears to have two whereas in others appear to have three rows of fronds which are also very compact. The rhizome of this fern is stout with short internodes (0.5-0.8 cm). The remaining species have a short-creeping rhizome (0.5-1.5 cm diam. including the scale cover). The rhizome is ascendant with polystichous phyllotaxis, and buds are very difficult to detect due to the proximity of the leaf bases. The rhizome in all species is densely covered with scales (Fig. 1: a-d).

Internal anatomy

The rhizome is dictyostelic and consists mainly of parenchymatous ground tissue (Fig. 2:d-e). The parenchyma cells are thick-walled, isodiametric, and contain many starch granules, especially those cells surrounding the stele (Fig. 3: c). In *E. backhousianum*, the rhizome is densely sclerified through the outer cortex. Imbedded in the ground tissue are the vascular bundles organized in a broad ventral amphicribal vascular bundle and one or two smaller dorsal amphicribal vascular bundles. Each amphicribal vascular bundle of the stem is surrounded by an endo-

Fig. 1. Habit and leaf features of Elaphoglossum latum

a. General appearance of the plant

b. Juvenile leaves

c. Leaf vernation

d. Rhizome scales

e. Sterile lamina

f. Subulate scales on midvein

Figure 1

Fig. 2. Features of the rhizopodium and root of the _Elaphoglossum apodum_ complex.

a. Rhizome habit of _E. procurrens_ showing the rhizopodium

b. Cross-section of the root showing rhizopodium cells

c. Cross-section of the root above the rhizopodium level

d. Cross-section of the stem showing the root emergence

e. Cross-section of the stem showing root and rhizopodium

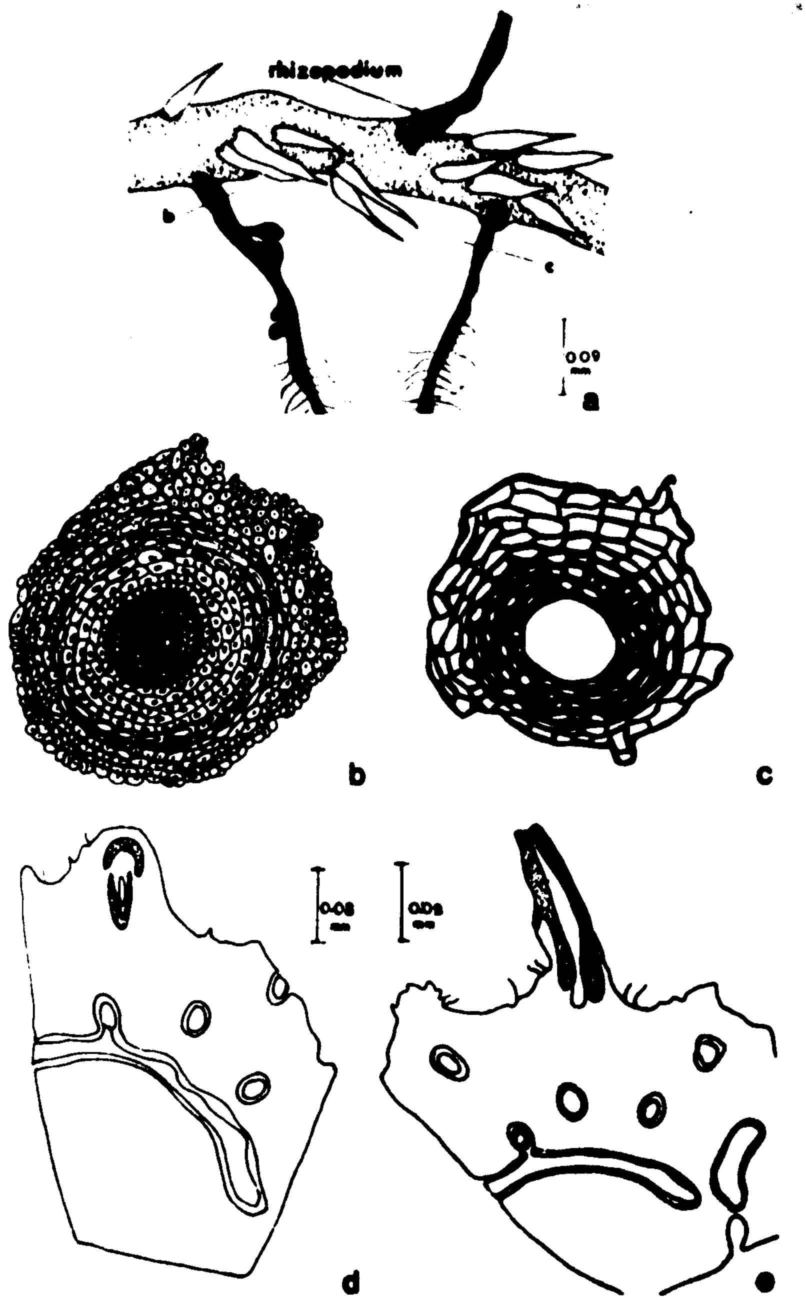


Figure 2

Fig. 3. Some sporophyte characters of the Elaphoglossum apodum complex.

a. Cross-section of the stem showing root traces near its emergence

b. Cross-section of the stem showing root emergence

c. Cross-section of the stem showing the stele type

d. Cross-section of the phyllopodium in the transition zone

e. Cross-section of an aerophore

f. Cross-section of the petiole showing one of the vascular bundles surrounded by prosenchyma cells

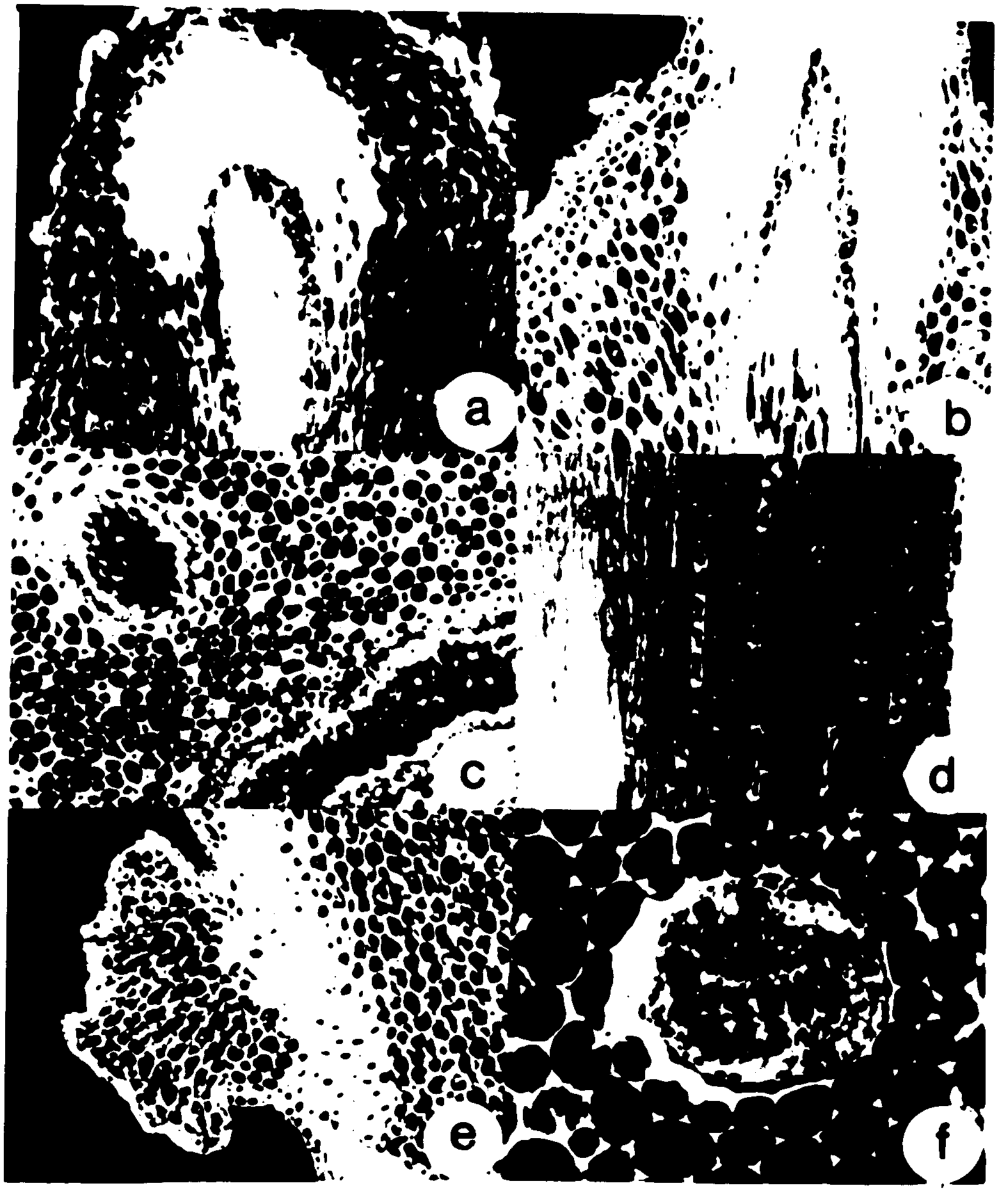


Figure 3

dermis and pericycle usually one cell layer thick. The distribution of xylem, phloem, parenchyma, leaf gaps, and root traces correspond to the same pattern described by Bell (1950) for *E. latifolium* and by Roux (1982) for *E. angustatum*.

According to Bell (1955, 1956), *Elaphoglossum* has four forms of stelar symmetry. In subsect. *Apoda* three of these forms are present: *E. backhousianum* and *E. procurrens* possess "grade alpha (1)", consisting of a dorsiventral two-leaf position and with bud traces posterior to each leaf trace. The dorsal part consists of one or two cylindrical or irregularly shaped strands (Bell, 1950; Roux, 1982). *Elaphoglossum cubense* possesses a "grade alpha (2)", consisting of a dorsiventral three leaf position and bud traces associated with the marginal ventral leaf traces. Finally, the "grade alpha (3)" consists of a dorsiventral three or multi-leaf position and bud traces associated with the marginal dorsal leaves; it is present in the remaining species *E. amazonicum*, *E. apodum*, *E. auripilum*, *E. latum*, and *E. raywaense*. The bud traces are less conspicuous in these species. Branching has been not observed in the species with this type of symmetry and stelar structure. The situation is similar to the condition found in *E. muscosum* (Bell, 1950) which has a dorsiventral rhizome with ventral and dorsal bundles and bud traces arising from the margins of the ventral bundle. The dorsal bundle is much dissected by the departure of leaf traces as was also observed in *E. pallidum* (sect. *Polytrichia* subsect. *Hybrida*) by Bell (1950). However, Bell (1956) listed *E. apodum* as having alpha (2) like *E. cubense*.

Bell (1956) suggested that the states of stelar symmetry could be arranged in a morphological series of increasing complexity, where the dorsiventral two-ranked condition of *E. backhousianum* and *E. procurrens* is the simplest, this is followed by the dorsiventral two-ranked condition of *E. cubense* in which the bud traces are found only in association with the ventral marginal rows of leaves; and finally the three- or multi-ranked condition found in *E. amazonicum*, *E. apodum*, *E. auripilum*, *E. latum*, and *E. raywaense*.

Root

In this complex group the roots are generally fibrous, black, wiry and produced on the ventral side of the rhizome. Root hairs appear throughout much of their length and are fine, brownish or yellow-brown, up to 1 mm long, linear and unicellular. Old roots have lost most or all their root hairs, and are black or dark brown in color (0.1-0.3 mm diam).

One interesting feature that seems to occur throughout the genus is a small, light-colored tissue around the base of the root (Fig. 2: a-c). This tissue appears to be a proliferation of the rhizome cortex that has been ruptured by the emerging root (Fig. 2: d-e; Fig. 3: a-b) and is variable in size and shape, up to 0.7 mm long and 0.5 mm in diam. In external morphology it looks like a swollen base which sharply contrasts with the dark surface of the root and rhizome. This "rhizopodium" is especially conspicuous in E. procurrens in which the rhizome is long-creeping and consequently the leaves do not obscure the root bases. This small amount of tissue somewhat resembles the phyllopodium but the color of the tissue of the rhizopodium is translucent or light-yellow in fresh or rehydrated tissue of herbarium specimens. The length of the rhizopodium varies with each species, i.e., 0.6-1.0 mm in E. procurrens, 0.2-0.5 mm in E. auripilum. The general appearance is rather variable. In E. auripilum, the rhizopodium is a broad, orange mammiferous structure, whereas in other species of subsect. Apoda it is more slender.

In some members of the closely related sect. Setosa subsect. Alpestria this tissue forms a scale-like sheath. Apparently this tissue was overlooked by Bell (1951) in his anatomical studies of the genus.

The internal structure of the root does not differ appreciably from that commonly found in other leptosporangiate ferns (Ogura, 1972). Bell (1951) stated that the roots in Elaphoglossum show a diarch xylem strand (Fig. 2: b). Although this is true for most species, in E. procurrens there is a monarch strand with exarch protoxylem.

The endodermal cells are narrow and thin-walled with or without suberized walls (Fig. 2: b). Sometimes the endodermis is poorly developed or may appear disintegrated in dried specimens as in E. procurrens, but by contrast is very well developed in E. auripilum. The inner sclerenchymatous cortex is well developed in all taxa and consists of more than three layers, as in E. procurrens, or of 7-8 cell layers in E. auripilum (Fig. 2: b). The outer cortex which composes most of the rhizopodium is several cells thick but is not lignified (Fig. 2: b; Fig. 4: c).

Fig. 4. Anatomical sections of leaf, root, and aerophore.

a. Cross-section of the leaf showing the epidermal cells

b. Cross-section of the leaf at the margin level showing the undifferentiated mesophyll

c. Cross-section of the root at the rhizopodium level

d. Cross-section of the aerophore showing the epidermal cells

e. Close up of the root showing the inner sclerenchymatic cortex

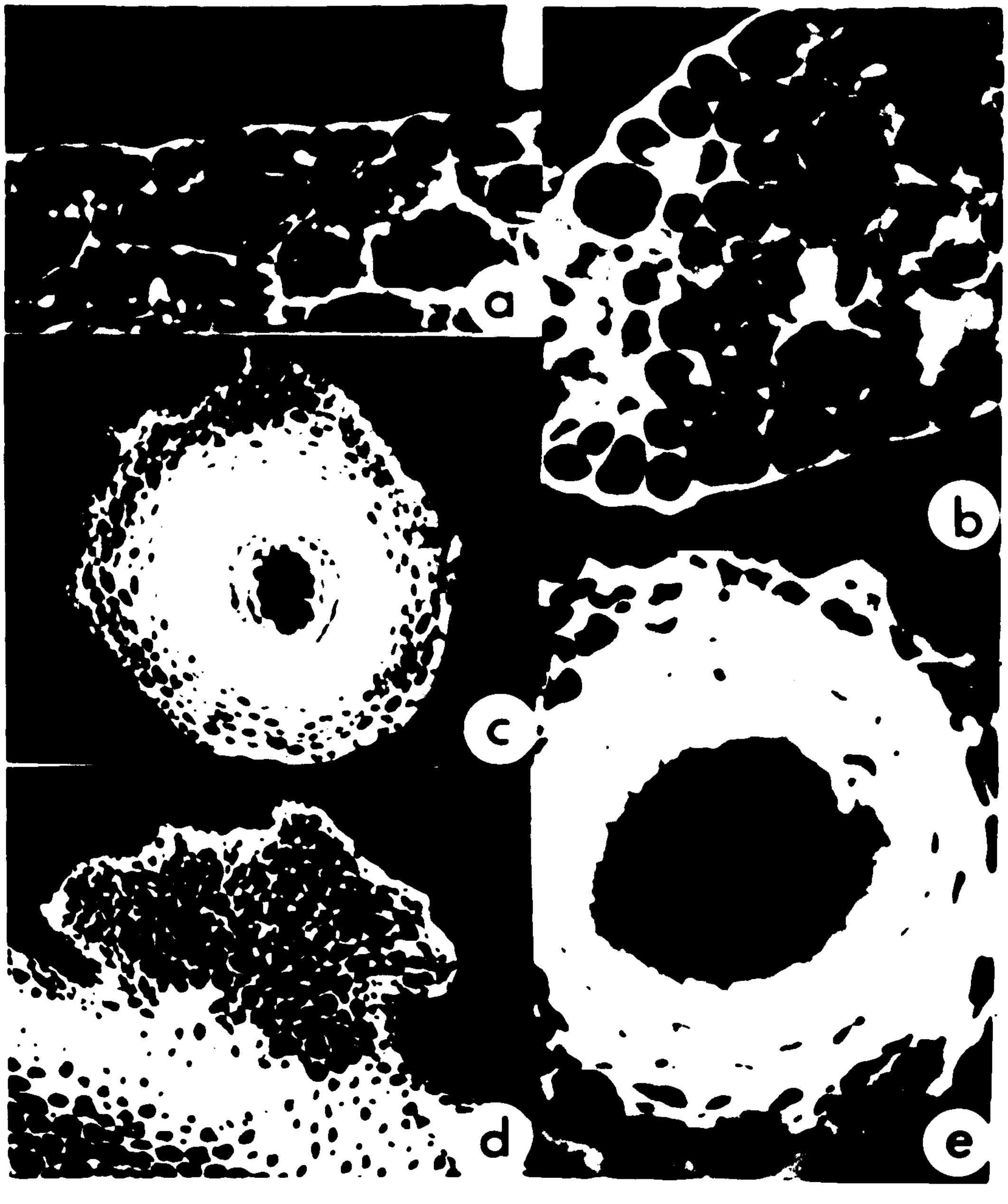


Figure 4

The number of cells ranges from two to five and the cellular content is very dense. The epidermis of the root above the rhizopodium is highly lignified (Fig. 2: c) with the outer cortex very narrow and consists of two cell layers (Fig. 4: e).

Although the anatomy of the root is relatively uniform throughout the entire genus, the presence of the rhizopodium could be used in phylogenetic interpretations. Comparative work must be done with representative species of other sections.

Leaf

In species of subsect. Apoda the fronds are short-petiolate, obliquely ascending, oblanceolate, and marginally scaly (Fig. 1: a,e,f). Frond length is quite variable, from 1-12 cm long in E. procurrens, to 45-95 cm long in E. amazonicum .

The fronds are dimorphic, entire, and lack hydathodes (Figs. 22-29). Elaphoglossum has a very sharp distinction between the trophophylls (sterile leaves) and the sporophylls (fertile leaves). The trophophylls are always larger and short-petiolate to almost sessile; the sporophylls are shorter, narrower, and more conspicuously petiolate. Most of the trophophylls have a long-decurrent base, but apex shape is quite variable.

Juvenile fronds of some species observed in the greenhouse showed a tendency to be obovate with an obtuse apex and a conspicuously decurrent base (Fig. 1: b). This was also noted by Christ (1899) and illustrated by Roux (1982).

The sporangia are borne abaxially on the sporophylls and nearly cover the surface.

Petiole

As stated above, the fronds of most members of this complex are short-petiolate. The petioles (stipes) are semiterete and sulcate or bisucalte on the abaxial side, 0.5-6.0 mm in diameter, and articulate with the phyllopodia. The stipes vary from slender in _E. procurrens_ (0.5-1 mm diam.) to very stout and fibrous in _E. auripilum_, _E. latum_, _E. cubense_, and _E. raywaense_ the stipes are shallowly sulcate on the ventral surface with two furrows running collaterally along the midvein. In _E. backhousianum_ the stipe is very stout, fibrous, dull brown, and has a deep central furrow on the abaxial side. _Elaphoglossum amazonicum_ is also very stout, fibrous, dull yellow, and has two deep furrows on the abaxial side.

The amount of indument present on the stipe is variable. Although most species are densely clothed with subulate scales and glandular hairs, some have diciduous scales which give the impression that the frond is naked (_E. cubense_ and _E. procurrens_), or they lack the glandular hairs (_E. backhousianum_).

Phyllopodium

As in most of the species in the genus, the petiole base is differentiated into a phyllopodium (Fig. 5: c). The phyllopodia are variable in length (0.2-2.0 cm). This region remains after the frond dies and is easy to recognize because its darker color contrasts sharply with the rest of the petiole, which is generally stramineous to orange or rarely brown (E. backhousianum). Phyllopodia are conspicuous in all species other than E. procurrens, in which the phyllopodia may or may not be well differentiated.

The disarticulation zone at the end of the phyllopodium abruptly changes color (Fig. 3: d), but there is not a distinctive swollen area as was previously reported by Bell (1951) for other species of Elaphoglossum (Fig. 5: c).

A cross section of the phyllopodium and petiole show that they are nearly circular. In the articulation zone the epidermis consists of rectangular cells which are very rich in starch and organelles content and are unpigmented. Adjacent to the epidermis there is a zone of compact, fibrous-like cells which gradually increase in length from the base to the apical part. They are strongly pigmented by phlobaphene (Bell, 1951), and thickly walled with many fine lateral pits. Microscopically these cells gradually lose the pigmentation near the transition zone (Fig. 3: d; Fig. 5: a-b). No changes in dimensions of the cells were observed at this level, although the outward appearance of the transition zone between pigmented and unpigmented is very sharp.

Fig. 5. Phyllopodium and blade scale

- a. Longitudinal-section of the phyllopodium showing the epidermal cells and fibrous area with lateral fine canals
- b. Longitudinal-section of the phyllopodium showing the prosenchyma cells that surround the vascular tissue
- c. External appearance of the phyllopodium and the aerophore in *E. auripilum*
- d. Typical subulate scale present on the blade of the species of subsect. *Apoda*

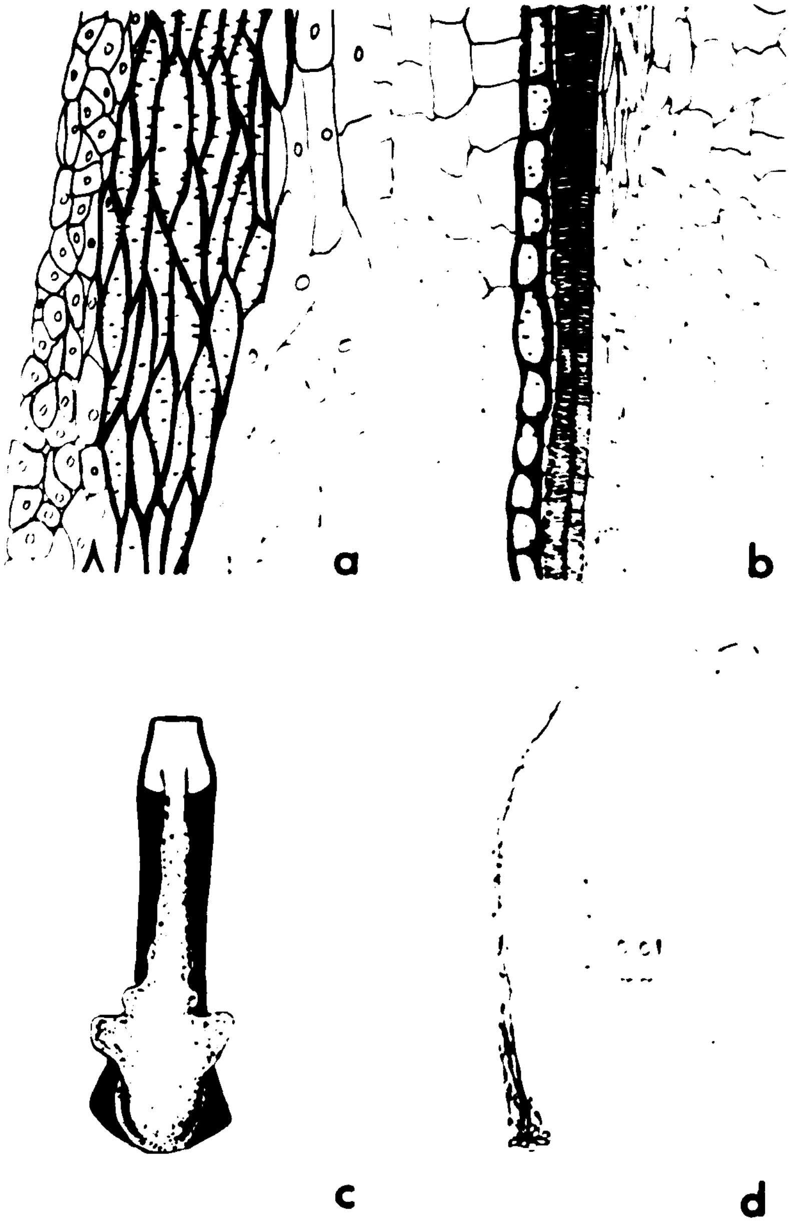


Figure 5

A little farther from the transition zone these fibrous cells become highly lignified. Inmediately interior to this lignified tissue is the parenchymatous cortex that consists of isodiametric, thick-walled cells that are conspicously nucleated and very rich in cellular content. At the transition zone the parenchymatous cells become wider and the walls thinner (Fig. 3: d). Above this zone the parenchyma cells are markedly thinner, slightly elongated and the nucleus as well as the cellular starch content is conspicuous. Surrounding the vascular bundles is a layer of parenchyma cells whose walls are perforated with conspicuous canals or pits (Fig. 3: f). A. R. Smith (1967), in his studies of stipe anatomy in "Aspidaceae", referred to them as a solid cylinder of blackened sclerenchyma tissue and also suggested that this thickening was correlated with the dissection of vascular tissue for some structural reasons, which he did not specify. He found there sclerotic sheets in most aspidioid ferns. Other anatomists have called it prosenchyma (Esau, 1953). Although there is no abscission layer between the phyllopodium and the petiole proper, the physiological changes as well as the death of transverse cell layers could account for disarticulation. Bell (1951) believed that "the sharp transition from pigmented to unpigmented cells, due the presence of phlobaphene together with the thickness changes of the parenchyma cells, indicates a metabolic discontinuity and may provide a line of weakness."

The phyllopodium is often associated with an epiphytic habitat, but Lloyd (1970) found that in Elaphoglossum it was more consistently present in terrestrial species than in the epiphytic ones (91.6% terrestrial vs. 80.4% epiphytes). On the other hand, Holttum (1966) and Roux (1982) argued the contrary.

Petiole Anatomy

The number of vascular bundles of the petiole varies among the species and also within the plnats according to the size and age of the fronds. In subsect. Apoda there are usually 3-7 strands at the base.

The bundles consist of an inner almost elliptical xylem strand with polar protoxylem elements surrounded by parenchyma and phloem which is more widely developed on the outside than the inside of the bundle (Fig. 3: f). The bundle is surrounded by a distinct endodermis. Outside of the endodermis there is a prominent and asymmetrial layer of thickened cells which partially surround the vascular bundle. This semi-ring of cells with thick walls is strongly pigmented, probably with phlobaphene. A cross-section of these cells shows a series of transverse pits or canals and the lumen seems is filled with a gummy brown substance.

For some unexplained reason, these cells are conspicuously developed along the interior side of the vascular bundles. Adjacent to this semi-ring of thickened cells there is a ring of very regular, almost symmetrical cells which are surrounded by the cortex. The cortex consists of several layers of thin-walled parenchyma cells which are prominently rich in starch content. Outside the cortex is another ring of 5-7 layers of sclerenchyma cells which are variable in size and shape and may have some comparative value (e.g., in *E. backhousianum* the ring of cells is almost complete, and a little wider than in the other species). Outside of this band of sclerenchyma cells is the epidermis which consists of a row of rectangular or almost symmetrical, thin-walled cells (Fig. 6: a).

At the base of the petiole where the phyllopodium meets the rhizome there are two undulate ridges or aerophores along the flanges of the phyllopodium, passing through the transition zone and disappearing gradually at the wings of the decurrent lamina (Fig. 5: c). This structure is present in most species of subsect. *Apoda*. It was not observed in *E. procurrens* and *E. backhousianum*, however, and was only occasionally present in *E. cubense*.

This structure has an area of parenchymatous cells. The epidermal cells abruptly lose their isodiametric shape becoming more irregular, and stomata are scattered throughout the epidermis (Fig. 3: e). The parenchyma cells adjacent to the epidermis are thinner-walled and have somewhat larger intercellular spaces, almost suggesting aerenchyma tissue. In most cases the aerophores are very difficult to observe because they are buried among the rhizome scales and are generally very narrow.

Elaphoglossum auripilum shows a well-developed aerophore which is fleshy and orange. This species is the only one growing in cloud forests. Lloyd (1970) suggested that the aerophores (pneumatophores) may function in aeration in association with a high metabolic rate; however, Bell (1955) indicated that they may not have adaptative significance because they are lacking in young fronds which are supposed to have a high metabolic rate.

Blade

Dimorphism

In *Elaphoglossum* there is a very sharp distinction between the trophophylls and the sporophylls. Wagner & Wagner (1977) suggested that this may be due to the role played by each type of frond. Nozu (1968) noted that leaf dimorphism is dependent on physiological and/or ecological effects and may be compared genetically. He also stressed that from the morphological characters of the leaf and rhizome, Elaphoglossum should be regarded as the most advanced and specialized genus of ferns. Walker (1966) based on his studies and field observations on ferns of Jamaica, stated that the species of Elaphoglossum differ widely in the frequency of production of sporophylls and in the number produced, apparently independent of season. On the other hand, Holttum (1978) suggested that the sporophylls are produced periodically in response to dry weather.

The trophophylls in this subsection are entire, upright or rarely pendent, lustrous green, and very scaly on the midvein and margin. The outline of the blade in most of the species varies from oblanceolate to slightly linear-lanceolate as in E. auripilum var. longipilosum. The apex varies from rounded-obtuse to subacute in E. procurrens, E. backhousianum and E. cubense, from acuminate to long-cuspidate in E. apodum, E. auripilum, and E. latum, or to long-caudate in E. amazonicum and E. raywaense. The base varies from cuneate or slightly rounded in E. backhousianum and E. auripilum to long-decurrent as in the rest of the species. The texture of the lamina is usually chartaceous to subcoriaceous (E. procurrens and E. cubense) or subcoriaceous (E. backhousianum, E. latum, and E. amazonicum).

The sporophylls vary from oblanceolate in E. amazonicum, E. cubense, E. latum, E. procurrens and E. raywaense to linear-lanceolate in E. apodum and E. backhousianum. In this subsection the sporophylls are shorter overall than the trophophylls although they do have longer stipes. In relation to the lamina the sporophylls are always narrower than the tropho-phylls. The trophophylls as well as the sporophylls grow oblique to vertical in relation to the rhizome.

Venation

All members of subsect. Apoda are characterized by an abaxially prominent midvein which is especially noteworthy in E. backhousianum, E. amazonicum, E. latum and E. raywaense. In these species the petiole seems to continue independent of lamina formation. Departing from the midvein are fine lateral veins which run toward the margin at an angle of 60°-70° or rarely 80° angle to midvein. The veins often dichotomize near their base and also at a broad angle 0.5 mm or less from the margin. The last bifurcation extends a short distance parallel to the margin, occassionally uniting with adjacent veins, to form a narrow, cartilaginous border on which scales are borne (Fig. 7: a-b). In some species, the point of attachment of the marginal scales coincides with the terminal tracheiodal endings of the secondary veins. It appears that the marginal, subulate scales are connected to the end of the vascular bundle and may function as a capillary tube for some type of exchange, perhaps as modified hydathodes. However, in *E. procurrens* the veins end freely 0.5-0.7 mm before the margin and the scales are attached to the margin without any relation to the tracheiodal bundle of the vein (Fig. 6: c).

The sporophylls lose the marginal scales in adult stages and the veins end freely 0.5-1 mm before a narrow sterile, cartilaginous margin, which is very conspicuous in *E. apodum*. The marginal vein connections are lacking in the sporophylls, as also reported by Holttum (1939) for species of *Lomariopsis*. Although reticulate venation is known in some species (e.g. *E. crinitum*, *E. crassifolium*, *E. aubertii*, *E. macropodium*, and *E. hybridum*), it does not occur in any members subsect. *Apoda*. Even in the sporophylls the veins remain simply forked.

Stomatal pattern

Stomata are hypostomatic (confined to the abaxial surface) and oriented with their long axes parallel to the lateral veins. They are less concentrated near the vein endings and do not occur

Fig. 6. Anatomy of the leaf

a. Cross-section of the midvein showing the distribution of the vascular bundles in _E. apodum_

b. Anatomical detail of the undifferentiated mesophyll of _E. apodum_

c. Cross-section of the blade margin showing glandular hairs in _E. apodum_

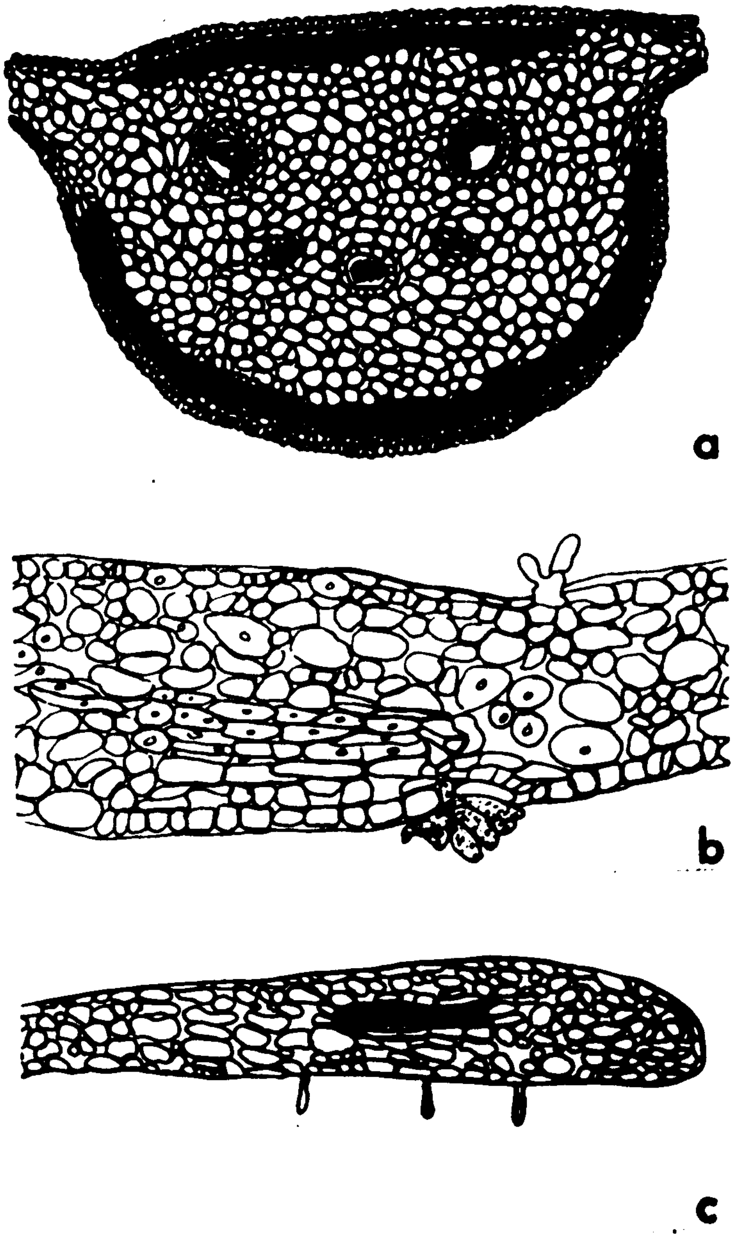


Figure 6

Fig. 7. Typical vein endings in the species of subsections Apoda and Setosa and morphological features of the glandular hairs and young gametophyte.

a. Vein ending in *E. cubense* showing the marginal subulate scales

b. Vein ending in *E. backhousianum* showing the scars of the marginal subulate scales

c. Vein ending in *E. plumieri* (sect. *Setosa*)

d. A branched glandular hair of *E. auripilum*

e. A simple glandular hair of *E. apodum*

f. Young gametophyte of *E. latum*

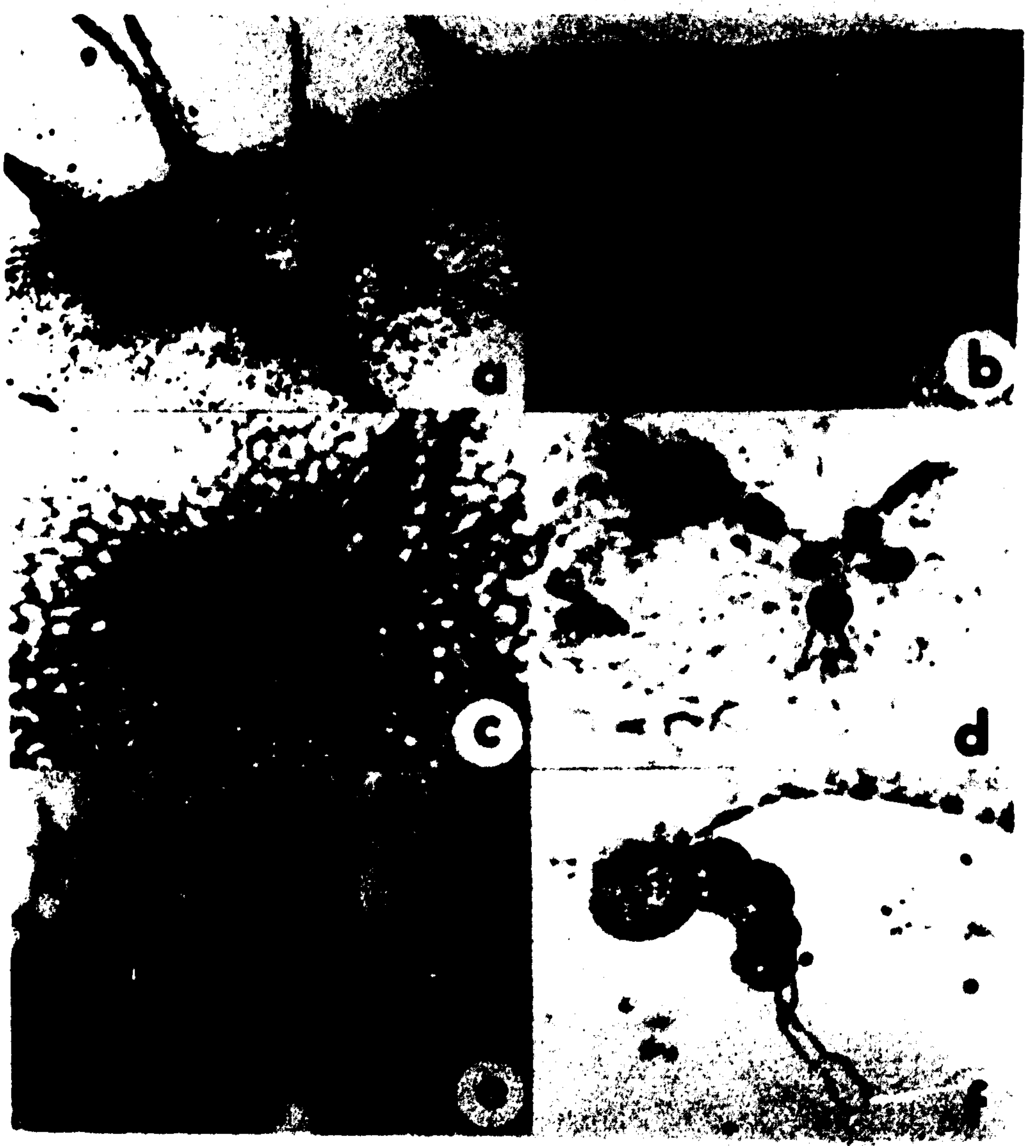


Figure 7

on the sporophylls (Figs: 8-11: a-d).

The structures of the stomata correspond to those described by Bell (1955) and Van Cotthem (1970a). Claessens & Van Cotthem (1973) described this type of stomata as eupolo- and copolo-mesoperigenous based on the subsidiary cell pattern.

Some measurements of stomatal frequency-- Stomatal Index (S.I.= $S / E + S \times 100$, where S= n_{o}. of stomata per unit area and E= n_{o}. of epidermal cells of the same area)-- Salisbury (1927) as well as stomatal size were made for each species treated here (Table V).

Salisbury (1927) emphasized that stomatal frequency is high when the epidermal cells are small and low when the epidermal cells are large. However, Luck (1966) criticized the use of the Stomatal Index, arguing that it is nothing more than a relative frequency because variation of S.I. depends upon the value of the frequency and unreliable because of the small size of the samples of leaf material upon which the S.I. is often based.

As shown in Table V the S.I. values and size of stomata for most the species of this subsection appear to be different and could be useful as a differential characters but only with a certain degree of caution because, as has been suggested (Wilkinson, 1979) the variation in stomatal length depends at least in part

Table V

Stomatal Index (S.I.) and size in the *Elaphoglossum apodum* complex *

Taxon	S.I.	Average stomatal size (microns)	Voucher
E. amazonicum	14.06	37.8 x 23.5	*Wurdack 1981* (Peru)
E. apodum	22.3	35.4 x 26.7	*Maxon 1827* (Jamaica)
E. auripilum var. *auripilum*	23.5	27.8 x 23.3	*Mickel 2657* (Costa Rica)
E. auripilum var. *longipil.*	15.7	34.8 x 28.0	*Lankester 829* (Costa Rica)
E. backhousianum	10.3	33.2 x 25.0	*Porter 4711* (Panama)
E. cubense	12.2	39.0 x 29.5	NYBG greenhouse acc. no. *394/70*
E. latum	20.8	38.8 x 29.7	*Smith 2688* (Colombia)
E. procurrens	20.7	34.4 x 26.0	*Shafer 8862* (Cuba)
E. raywaense	15.5	33.4 x 24.5	*Pinkley 482* (Ecuador)

* Measurements were made in the central region of the lamina, approximately midway between the midrib and the margin. The average was based on 20 counts per species.

upon differences in ploidy level and also on environment.

Elaphoglossum auripilum var. auripilum appears to have the smallest stomata (27.8 x 23.3 μm). This value may be related to habitat because it is the only species of this subsection growing in cloud forests at high altitude.

Because of the lack of cytological data for most of the species of this subsection it is very risky to make conclusions based on the size of the stomata, at least at this stage of knowledge. The only cytological report for this complex (Walker, 1966) is for E. apodum which is diploid ($n = 41$).

Although each species in this complex has its own average stomatal size, the differences are slight and probably not associated with ploidy level.

Epidermal cells

There is little variation in the pattern of the epidermal cells. The abaxial epidermal cells are generally less convoluted than those of the adaxial surface. The common cell pattern on the upper epidermis seems to be one of irregular, rectangular and wavy-walled cells (Figs. 8-11: a-d).

From the standpoint of comparison of species, epidermal pattern is of limited value because, as previously mentioned, the cells possibly are subject to differences in the environment. However, in this subsection in particular, the pattern is more or less consistent, perhaps due to the more or less stable condition of the tropical rainforest environment where most of the species occur.

Walls are generally thin except for the very thick walls of *E. backhousianum* and the rather thick ones of *E. amazonicum*. This reflects to some extent the subcoriaceous texture of fronds of the two species.

A cross-section of the blade shows scales and glandular hairs (Fig. 6: b-c). The epidermal cells are rectangular or nearly isodiametric, with a thin cuticle. The mesophyll consists of three to four undifferentiated layers of chlorenchyma cells (Figs. 4: a-b).

Lateral veins run through the mesophyll and have the same arrangement described by Bell (1955).

Indument

Christ (1899), Holttum (1947), Bell (1951b), Pichi Sermolli (1975), Mickel & Atehortúa (1980), and Roux (1982) stated that the scales are perhaps taxonomically the most valuable character

Fig. 8. Epidermal cell patterns in the *Elaphoglossum apodum* complex.

a. Upper epidermis of *E. apodum*

b. Lower epidermis of *E. apodum*

c. Upper epidermis of *E. amazonicum*

d. Lower epidermis of *E. amazonicum*

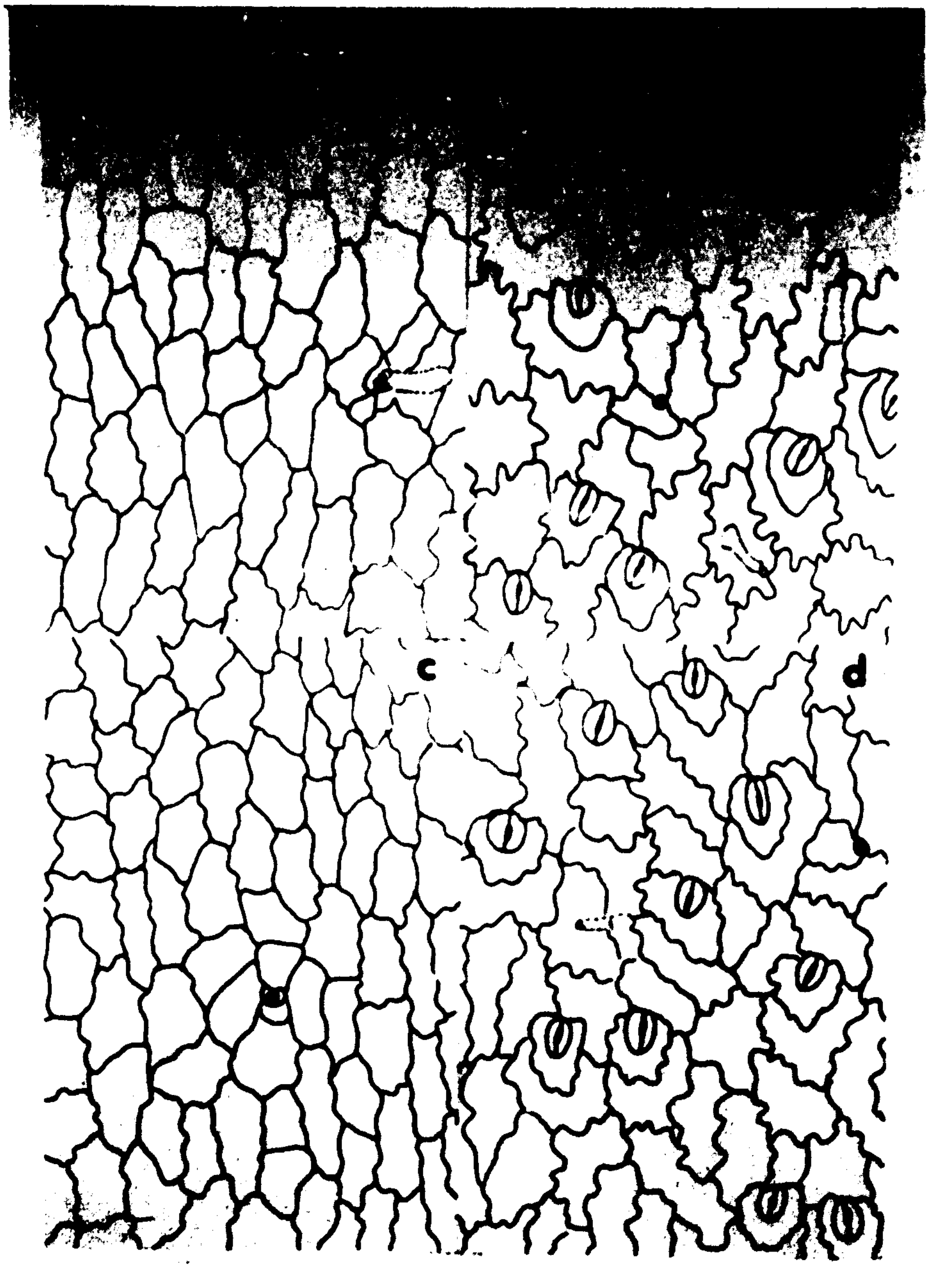


Figure 8

Fig. 9. Epidermal cell patterns in the _Elaphglossum apodum_ complex.

a. Upper epidermis of _Elaphoglossum procurrens_

b. Lower epidermis of _E. procurrens_

c. Upper epidermis of _E. auripilum_

d. Lower epidermis of _E. auripilum_

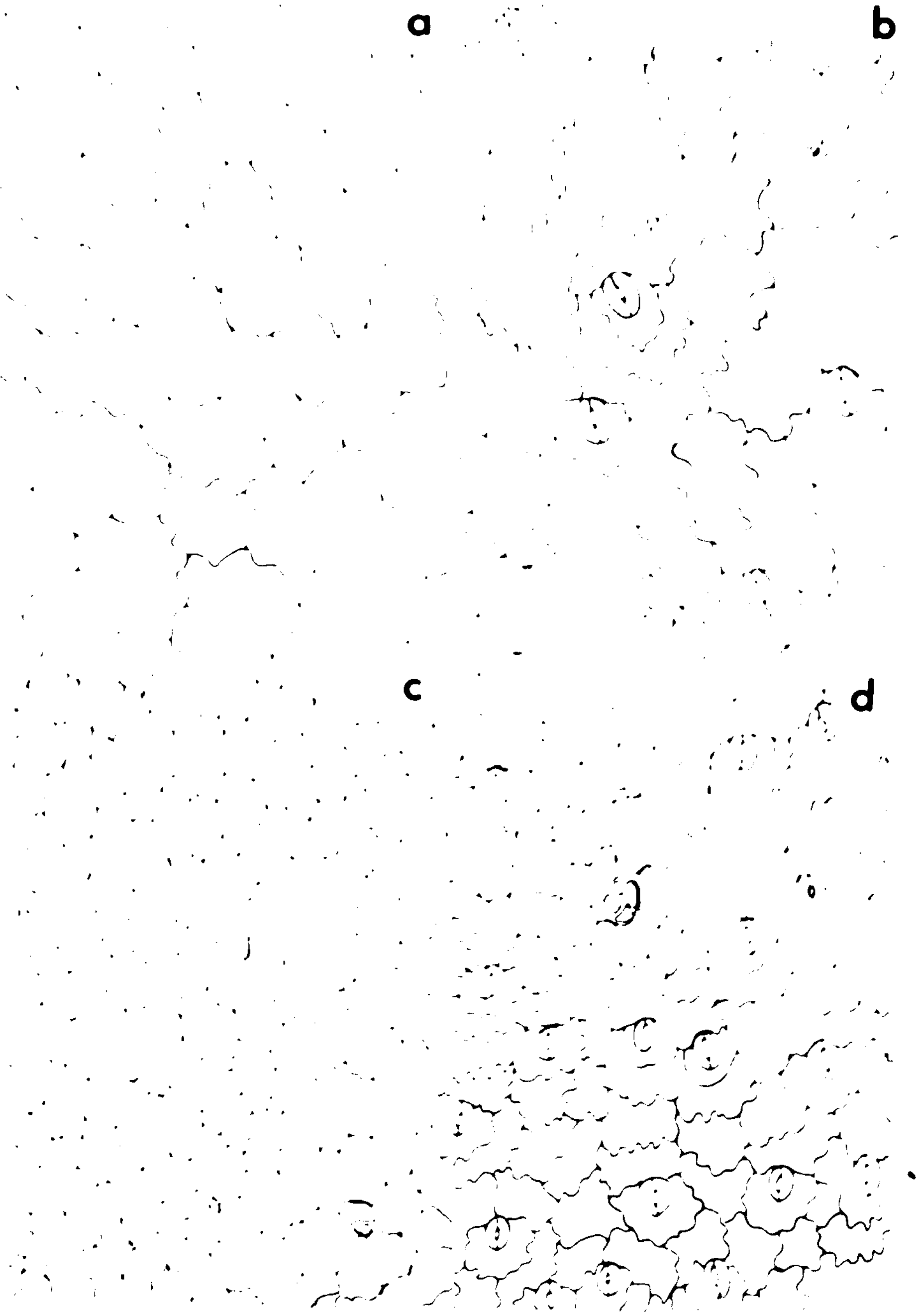


Figure 9

Fig. 10. Epidermal cell patterns in the <u>Elaphoglossum apodum</u> complex.

a. Upper epidermis of <u>E. raywaense</u>

b. Lower epidermis of <u>E. raywaense</u>

c. Upper epidermis of <u>E. cubense</u>

d. Lower epidermis of <u>E. cubense</u>

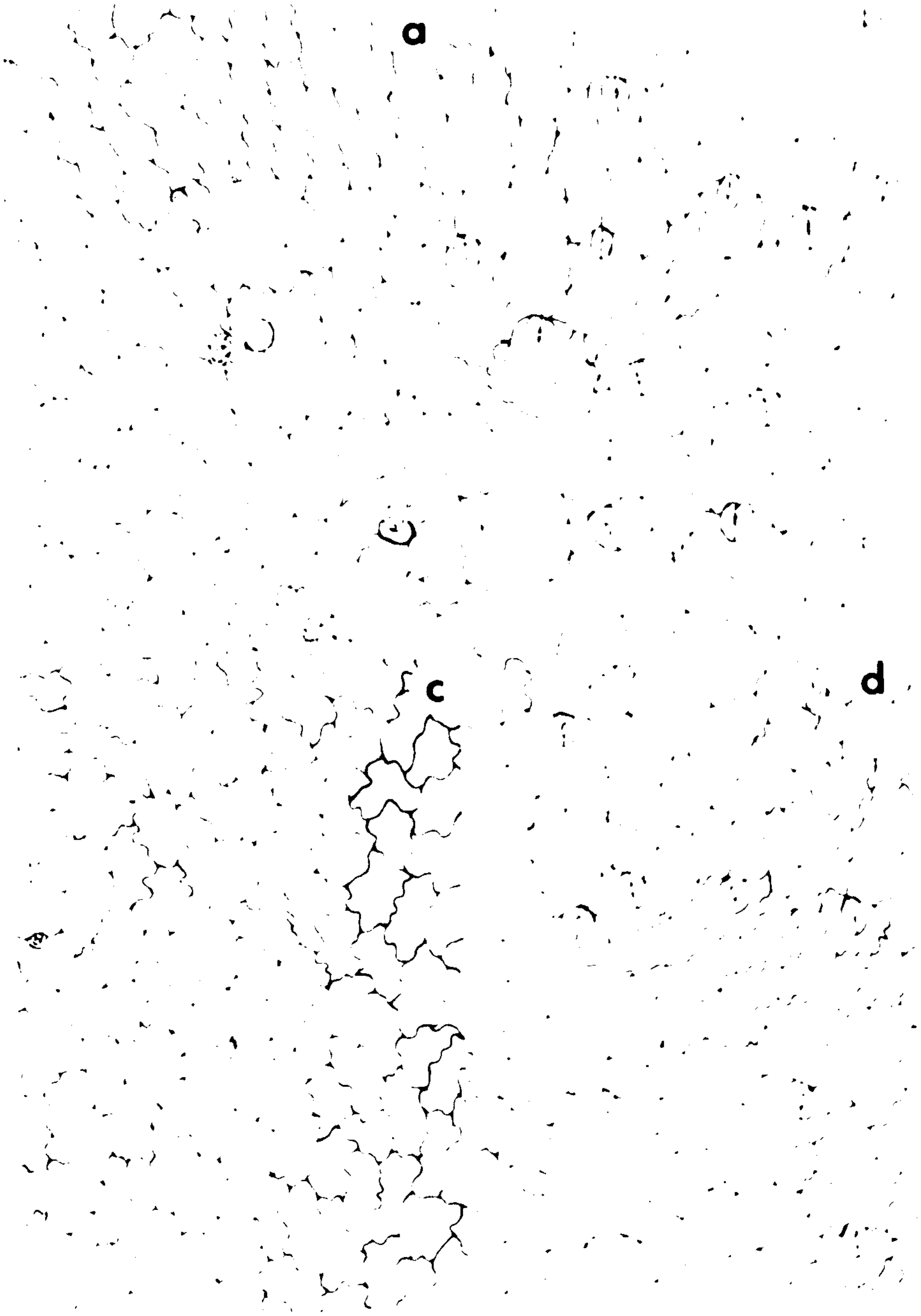


Figure 10

Fig. 11. Epidermal cell patterns in the <u>Elaphoglossum apodum</u> complex.

a. Upper epidermis of <u>E. backhousianum</u>

b. Lowe epidermis of <u>E. backhousianum</u>

c. Upper epidermis of <u>E. latum</u>

d. Lower epidermis of <u>E. latum</u>

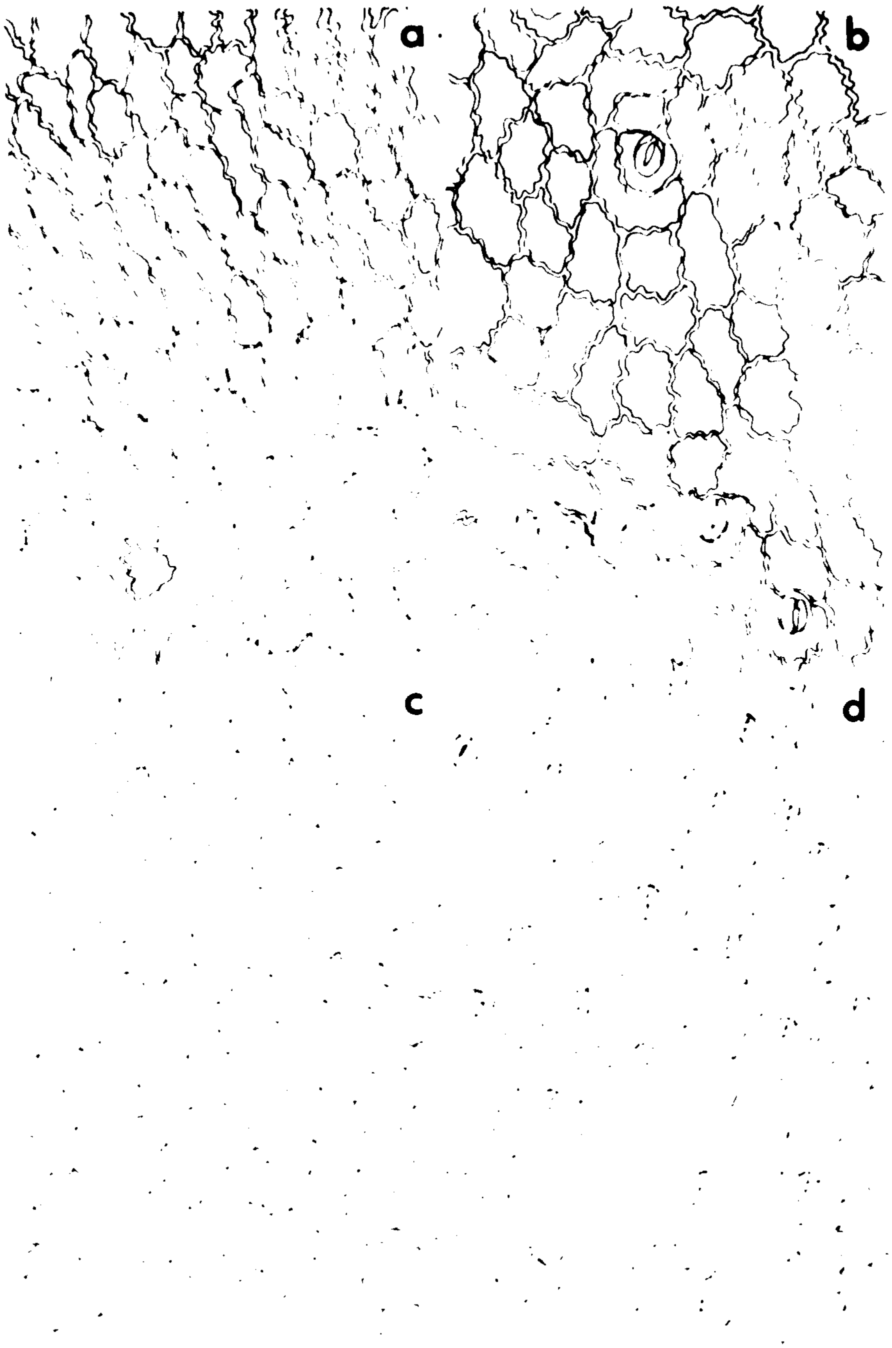


Figure 11

in the genus *Elaphoglossum*. Holttum (1966) placed special emphasis on these structures and considered them as the main character to divide the genus. The scales are densely spread over the rhizome, petiole, midvein, and margin, and are less abundant on the blade surfaces. In this complex the rhizome scales, and to a lesser extent the blade scales, have been the most useful characters to delimit the taxa.

Rhizome scales

Most species are characterized by a densely scaly rhizome. The generalized scale shape is triangular-lanceolate to linear lanceolate, with a truncate or cordate base and long-acuminate to caudate apex (Figs. 12-13: a-d). The size varies from 1.5-3.0 mm in *E. procurrens* to 0.8-4.0 mm in *E. latum*. The color ranges from yellow-orange in *E. auripilum* to yellow-brown in *E. raywaense*. *Elaphoglossum raywaense* has bicolored scales which gradually darken toward the tip, giving the appearance of being resinous (Fig. 12: d). The scale margins range from smooth in *E. auripilum* to dentate in *E. amazonicum*. The cells are rectangular and sligtly undulate in *E. auripilum* to conspicuously flexuous in *E. amazonicum* (Figs. 12: b-c). Table VI (Figs: 12-13: a-d) show the variation in rhizome scales among the species of this complex.

Fig. 12. Rhizome scales in the *Elaphoglossum apodum* complex.

a. *E. backhousianum*

b. *E. auripilum*

c. *E. amazonicum*

d. *E. raywaense*

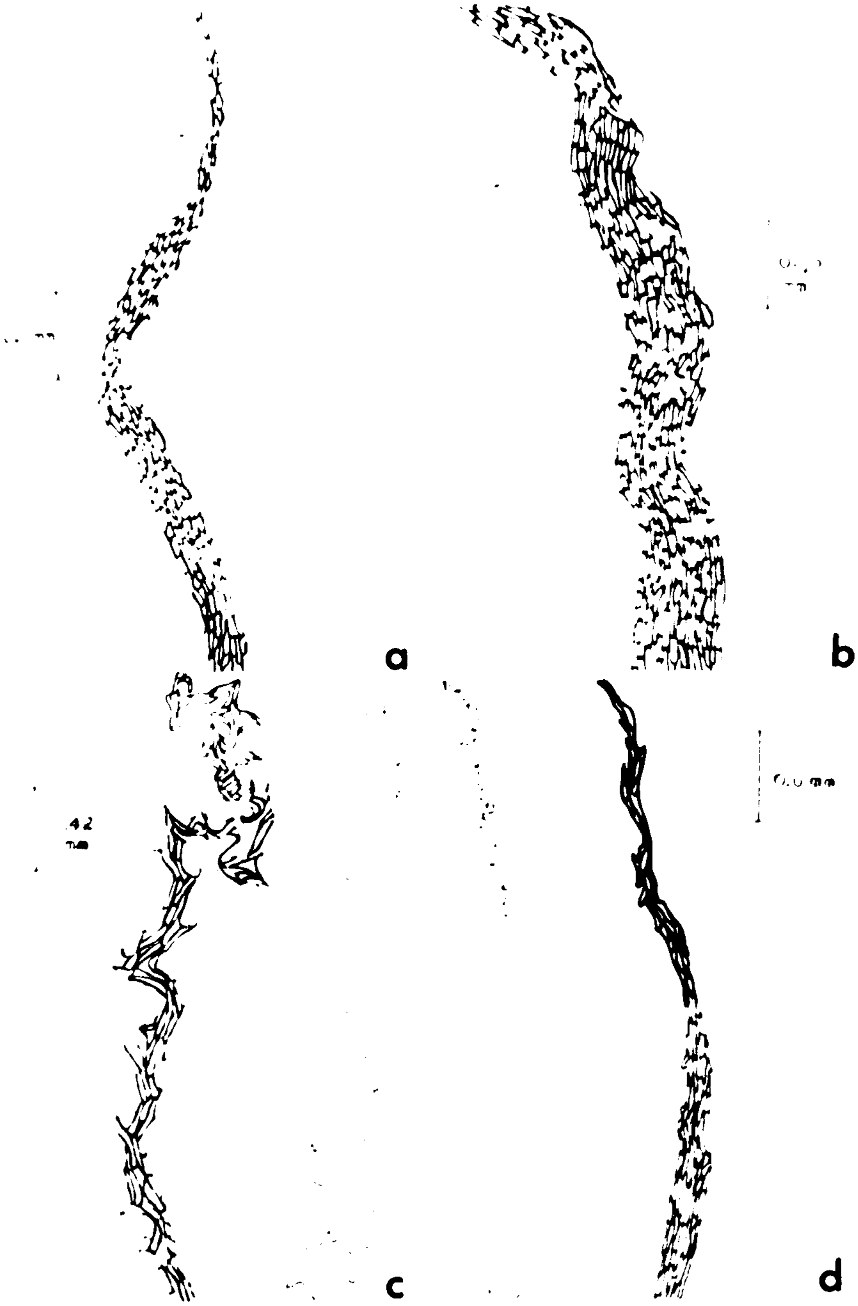


Figure 12

Fig. 13. Rhizome scales in the Elaphoglossum apodum complex.

a. E. apodum

b. E. latum

c. E. procurrens

d. E. cubense

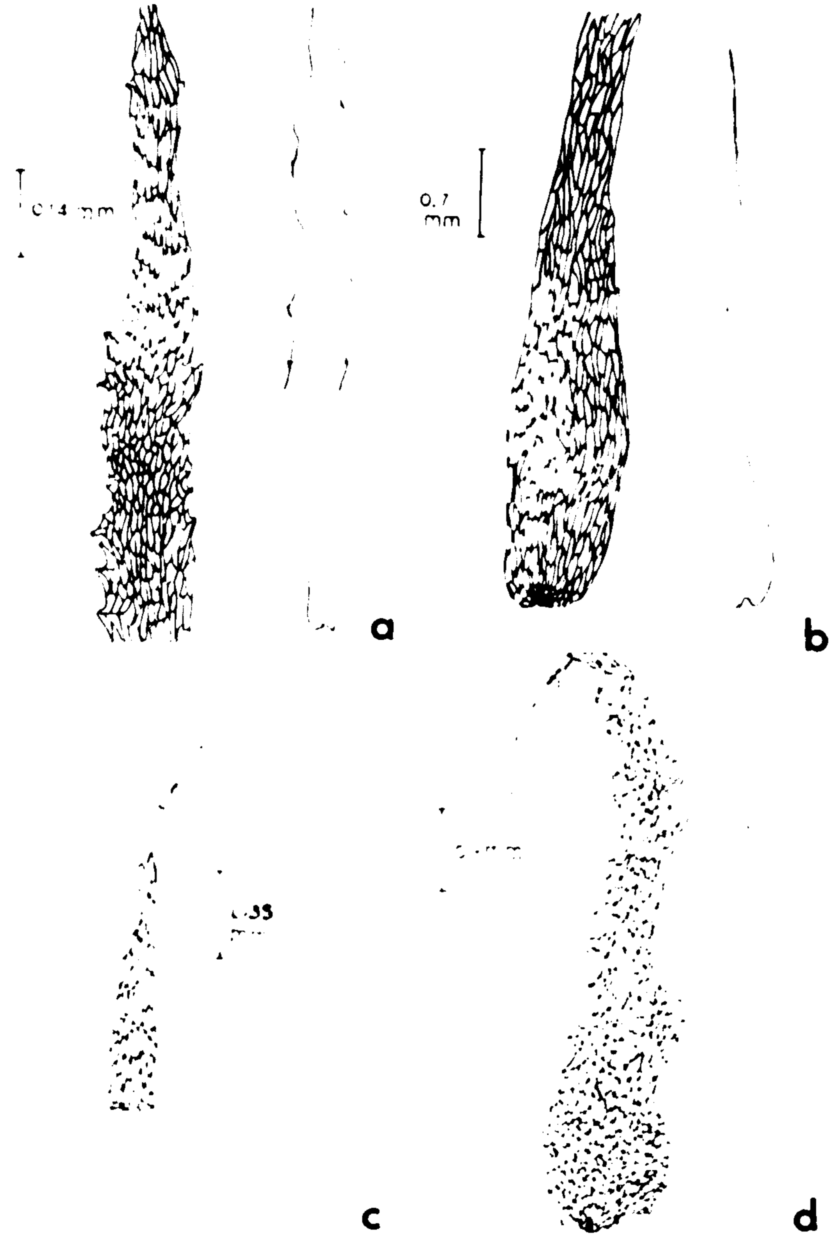


Figure 13

Table VI

Rhizome scale characters in the Elaphoglossum apodum complex

Taxon	habit	size(mm)	shape	margin	base	tip	cell shape	color
E.amazonicum	spread	0.5-15 0.1-10	linear lanceol	dentat	basif	cuspi	rect. flexuous	fulvous (concol.)
E. apodum	spread	0.5-15 0.3-0.8	triang lanceol	dentat	basif	acum	large rect.	golden yell (concol.)
E. auripilum	spread	10 - 25 0.1-0.5	linear lanceol	entire	basif	acum	long rect.thick end walls. und.	reddish-oran orange-brown (concol.)
E. backhousianum	spread	0.5-25 0.1-0.8	linear lancol	entire	basif	acum	rect. hexag. thich end walls	golden-yell golden-brown (concol.)
E. cubense	appres.	3.0-6.0 0.8-1.3	triang lanceol	irreg. tooth.	cordat	long acum.	rhomboidal-rect	golden-yell golden-brown (concol.)
E. latum	spread	0.8-40 0.8-1.2	linear lanceol	slightl dentat	basif	long cusp	rect. hexagon	orange-redd golden-yell (concol.)
E. procurrens	appres.	3.0-1.0	triang lanceol	entire	basif	long cusp	irregul rect	reddish-brow (concol.)
E. raywaense	spread	2.0-8.0 0.1	linear lancol	dentat	basif	long caud	rect. slender wavy	yellow-brown ferrugineous (bicolor.)

dentat= dentate; basif= basifixed; cuspi= cuspidate; cord=cordate; caud=caudate; rect=rectangular; thic=thick. acum=acuminate;

Scales of the Petiole and Blade

The scales on the petiole, midvein and blade margin are perpendicular to the surface to which they are aattached. They are usually persistent and differ in size and shape from those on the rhizome. All the species in this complex have subulate scales on the petiole and blade (Fig. 5: d).

Both surfaces of the trophophylls and upper surface only of the sporophylls are covered with subulate deciduous scales and glandular hairs.

The petiolar and marginal subulate scales of *E. backhousianum* are particularly distinct. The scales are broadly subulate, larger than in other species, dark-brown to maroon, heavily sclerified, and abruptly broader at the base which bears a laciniate margin; its apex is filiform and curved downward (Fig. 14: b-e).

In *Elaphoglossum latum* the basal petiolar scales often show and abruptly broader apex with irregular cells walls (Fig. 14: a).

Elaphoglossum auripilum var. *longipilosum* bears the most colorful type of petiolar and marginal scales in this complex.

Fig. 14. Scales and glandular hairs on petioles and blades in the Elaphoglossum apodum complex.

a. Petiole scale of E. latum

b. Midvein scale of E. backhousianum

c. Glandular hair of E. auripilum

d. The common type of glandular hair in subsect. Apoda

e. Marginal blade scale of E. backhousianum

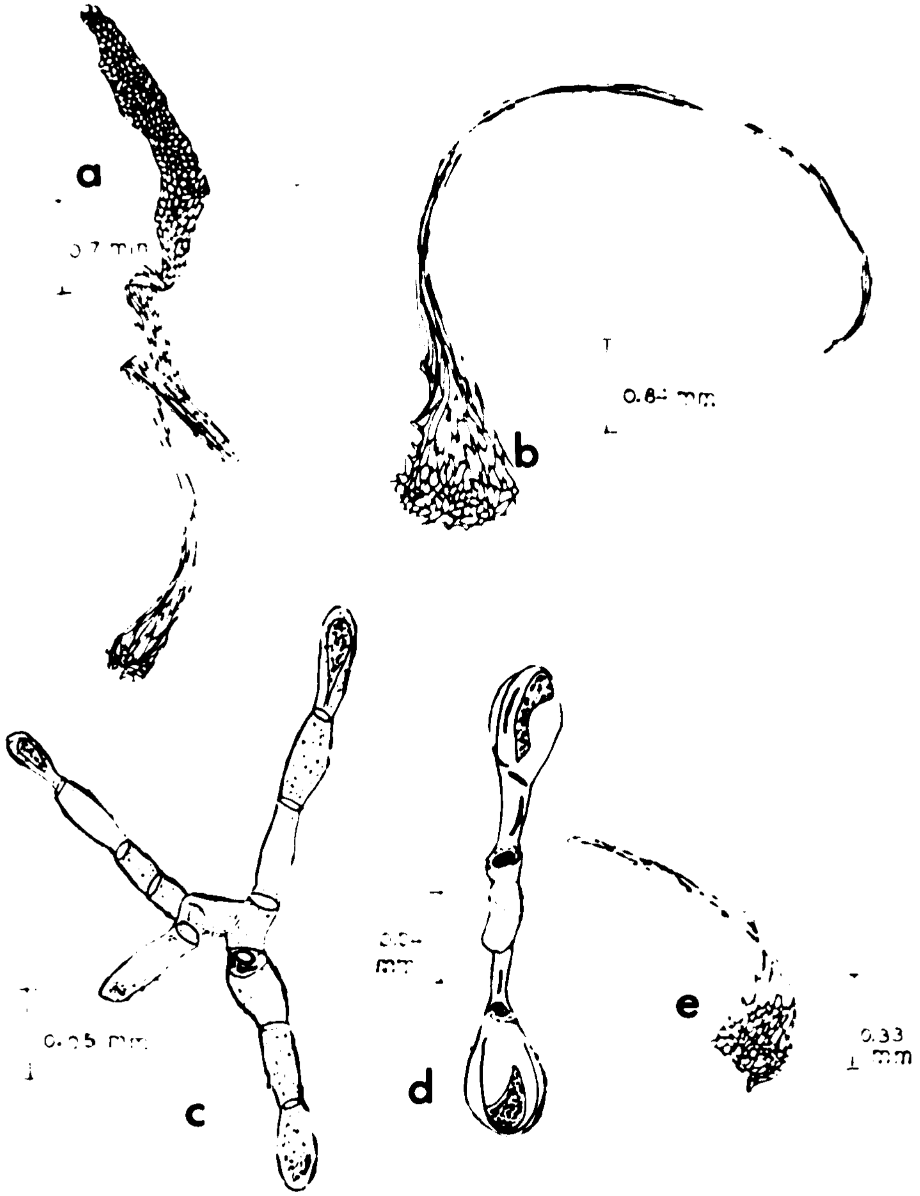


Figure 14

They are longer than in *E. auripilum* var. *auripilum* and are held rigidly perpendicular to the petiole and midvein, giving a peculiar appearance to this variety.

Almost all the species have scattered, subulate, laminar scales (Fig. 5: d) with the exception of *E. backhousianum*, which has a naked blade but bears scattered glandular hairs on both surfaces. Perhaps this condition could be correlated with its nearly coriaceous texture. The subulate scales in this species are concentrated on the midvein and margin.

Elaphoglossum procurrens bears the smallest subulate scales which are also very sparse on the laminar surface. *Elaphoglossum apodum*, *E. latum*, *E. auripilum*, and *E. raywaense* have the most abundant laminar scales in this group, particularly *E. auripilum* var. *longipilosum*.

In general, the petiole and blade scales of this complex have slightly toothed margins with their bases deeply cochleariform and auriculate. The base of the auricles is often covered with glandular hairs and is closely appressed to the surface of the stipe and blade. The attachment is at the center of the base of the sinus and sometimes may be shortly-pedicellate but usually the auricles are sessile. Scale structure has been illustrated by Christ (1899) and described in detail by Bell (1951) for *E.*

villosum (sect. Setosa), which has scales similar to those of subsect. Apoda (Fig. 5: d).

The degree of scaliness as well as the size and shape of the scales are variable within subsect. Apoda, but it is often difficult to judge the degree of scaliness because of the deciduous condition at least on the lamina (Fig. 1: e-f). The marginal and midvein scales persist longer and are therefore better for comparison.
However, in this group there is little variation among these, e.g., for they are uniform in size and shape, with the exception of those found in E. backhousianum, which are unique in this complex.

Glandular Hairs

Glandular hairs in the genus Elaphoglossum are restricted to sections Setosa and Polytrichia. In subsect. Apoda the glandular hairs are evenly distributed on the petiole and blade and highly concentrated around the abaxial part of the midvein and the base of the subulate scales. They usually consist of one elongated cell with a rounded apex that sometimes is broadly expanded to a capitate terminus. The simplest type of glandular hair consists of one long capitate cell, and the most complex consists of several rows of adpresed or shortly erect cells which branch in different directions. The common type consists of a furcate glandular hair (Fig. 14: c-d) of which the main axis is often oriented toward the midvein and runs parallel to the secondary vein. Elaphoglossum apodum, E. amazonicum, E. latum, E. cubense, E. procurrens and E. raywaense bear the simple as well as the furcate types, whereas E. auripilum bears the simple as well as the most complex types.

In E. backhousianum the glandular hairs are small, simple, and scattered throughout the laminar surfaces, but are also concentrated on the abaxial surface around the midvein, where they branch in several directions. In this species they are not present on the petiole, perhaps as a result of the dense mass of scales that covers it. Elaphoglossum auripilum has abundant glandular hairs which are shorter and erect giving a "viscous" consistency and seem to secrete some sort of resinous substance. They may play a physiological role as a secretion device or could be to gather atmospheric moisture as an epiphyte.

From a taxonomic point of view, the glandular hairs are relatively useful, at least at the species level. Their restriction to only certain sections may have some evolutionary implications in the diversification of this genus. A more careful study of these structures could give some clues about the interrelationships among the sections and their phylogenetic relationships.

Sporangia and Spores

The sporangia are borne on the abaxial surface of the sporophylls and densely cover it except for narrow sterile areas along the margin, on the midvein, and along both sides of the base of the midvein.

The sporangia are stalked, erect, slightly ovate, globose and 156-203 μm long x 146.9-171.6 μm wide. The annulus is vertical and consists of a row of 11-12 rectangular, thick-walled cells and a thin-walled stomium. The stomium consists of about seven elongate, smaller, and thin-walled cells, and extends downward adjacent to the stalk. The cells of the sporangia are irregular in size and shape, but no strong differences exist between species of this complex. The stalk consists of two ranks of cells.

Table VII shows the average sporangial size of the members of this complex. The sizes are only slightly different from one species to another and show not meaninful differences; so they are not considered here to be a good comparative character.

The spores of the Elaphoglossum apodum complex are bilateral, monolete, and slightly trapezoidal in lateral view, with a broader base and several collateral and rectangular areas which are apically connected by small, continuous ridges. They are elliptic to ovate in polar view and bear a conspicuous perispore. The color ranges from brown to yellow.

Table VIII shows the range of variation in spore length and the average size for each of the species based on 20 spores/sporangia per species. Although each species has its own average spore size, some are too close to be used as reliable taxonomic characters (e.g., *E. amazonicum*, $\underline{x}$= 28.3 µm and *E. backhousianum*, $\underline{x}$= 28.8 µm.

Tryon & Tryon (1982) have suggested that in the genus *Elaphoglossum* the smallest leaves bear the largest spores and vice versa. This is partially true, at least in this complex. *Elaphoglossum procurrens* which has the smallest leaves bears the largest spores (30 µm). However, *E. amazonicum* and *E. backhousianum* have the largest leaves but do not appear to bear the smallest spores (28.3 µm and 28.8 µm, respectively). *Elaphoglossum apodum*, *E. auripilum*, *E. cubense*, *E. latum* and *E. raywaense*, which have intermediate leaf size, do not show any relation with spore size.

In other fern genera spore size has been used as a clue to detect hybrids, the allopolyploids being conspicuous by their larger spores. In subsect. *Apoda*, however, spore size is relatively uniform, suggesting that they are no allopolyploids in the group. Furthermore, spore abortion was not seen, which suggests that hybridization is rare or non-existent in this group.

Table VII

Sporangial size in the *Elaphoglossum apodum* complex*

Taxon	Sporangium size (microns)	Vouchers
E. amazonicum	203.77 x 171.66	*Bües 1737* (Peru)
E. apodum	156.0 x 149.5	*Maxon 1827* (Jamaica)
E. auripilum var. *auripilum*	187.1 x 142.0	*Maxon & Harvey 8184* (C.R.)
E. auripilum var. *longipilosum*	172.9 x 150.6	*Croat 863* (Costa Rica)
E. backhousianum	164.5 x 155.1	*Folsom 3576* (Panama)
E. cubense	171.2 x 167.9	*Wright 1040* (Cuba)
E. latum	166.3 x 150.67	*Smith 2688* (Colombia)
E. procurrens	166.3 x 151.4	*Shafer 8862* (Cuba)
E. raywaense	156.8 x 146.9	*Schunke 10164* (Peru)

* Measurements were based on 20 counts per species.

Table VIII

Range and mean length of selected spores in the *Elaphoglossum apodum* complex.*

Taxon	Range of length (microns)	Mean length	Voucher
E. amazonicum	25.4-31.5	28.3	*Bües 1737* (Peru)
E. apodum	22.7-28.0	25.3	*Underwood 1589* (Jamaica)
E. auripilum var. *aur.*	21.0-31.5	27.3	*Maxon & Harvey 8184* (C.R.)
E. auripilum var. *long.*	22.7-29.5	27.0	*Croat 863* (Costa Rica)
E. backhousianum	24.5-33.3	28.8	*Folsom 3576* (Panama)
E. cubense	19.3-29.7	26.4	*Wright 1040* (Cuba)
E. latum	22.7-31.5	27.1	*Smith 2688* (Colombia)
E. procurrens	26.3-33.3	30.0	*Wright 793* (Cuba)
E. raywaense	22.7-31.5	27.6	*Schunke 10164* (Peru)

* Spores were measured across their greatest length not including the sculpturing; measurements were based on 20 samples per species.

Fig. 15. Spores in the Elaphoglossum apodum complex.

a. E. latum (3000x)

b. E. latum (6000x)

c. E. auripilum (3000x)

d. E. auripilum (6000x)

e. E. backhousianum (2800x)

f. E. backhousianum (6000x)

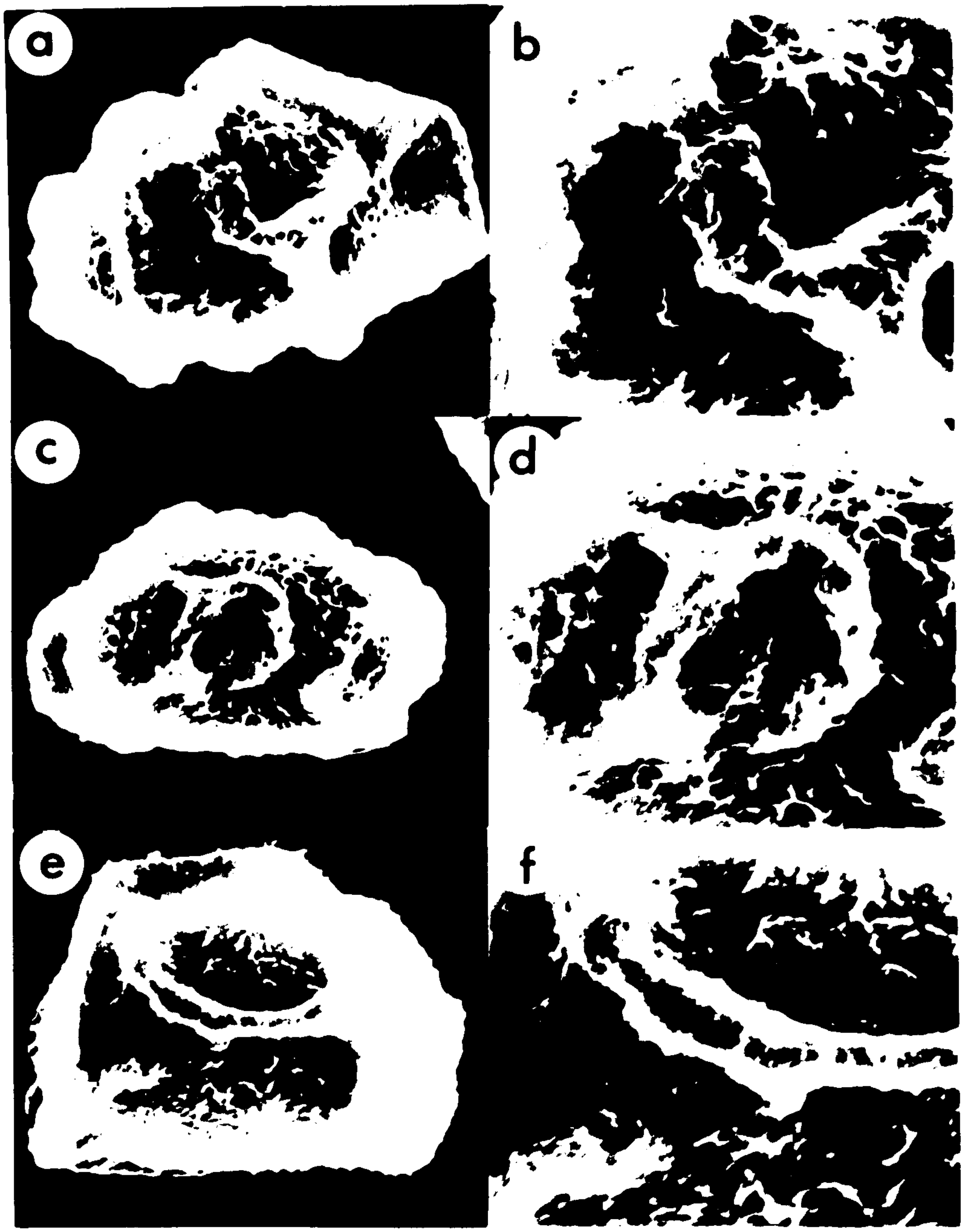


Figure 15

Fig. 16. Spores in the *Elaphoglossum apodum* complex.

a. *E. cubense* (2800x)

b. *E. procurrens* (3000x)

c. *E. raywaense* (2400x)

d. *E. amazonicum* (2600x)

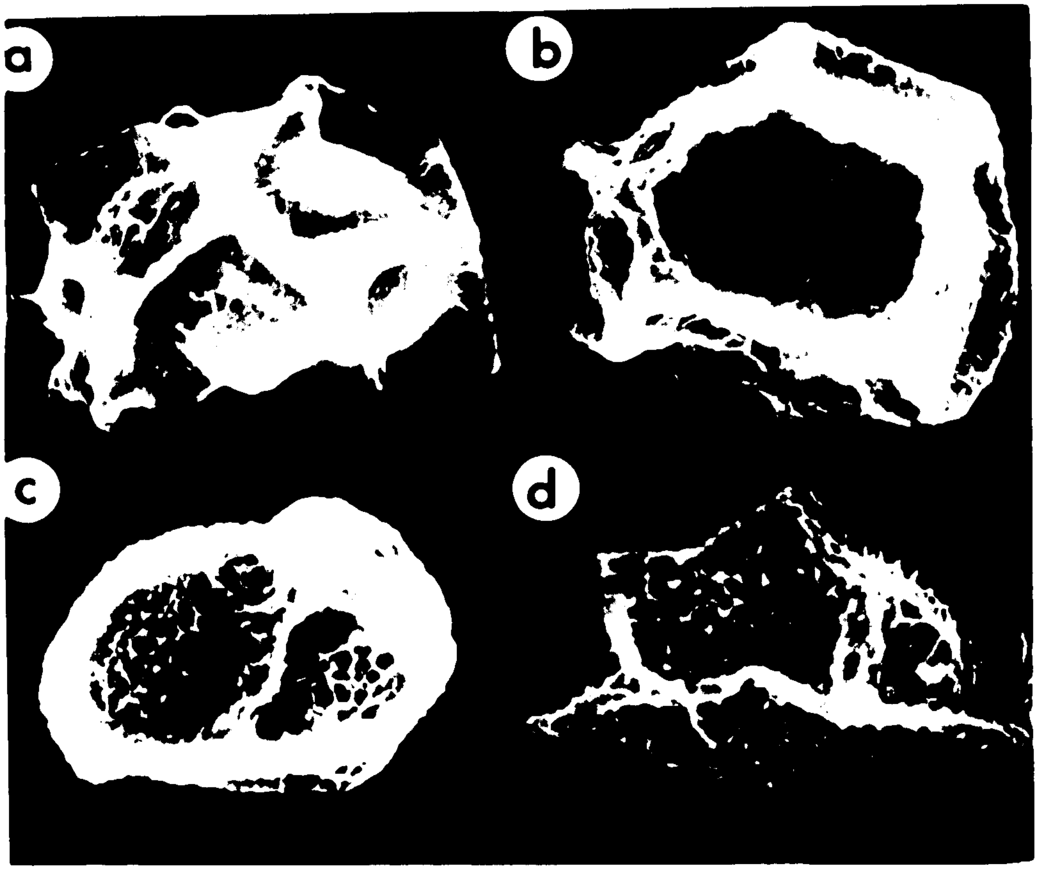


Figure 16

Tryon & Tryon (1982) also stated that the perispore of Elaphoglossum consists of three strata: superficial,central, and basal. The central stratum often has a columnar structure between the superficial and basal strata. In subsect. Apoda the perispore is perhaps less complex than in other sections of the genus and consists of a series of interconnected narrow, smooth or shortly-spined ridges which surround the central areas. These areas are often covered with fine but conspicuous perforations in E. procurrens (Fig. 16: b), E. latum (Fig. 15: a-b), E. auripilum (Fig. 15: c-d) and E. raywaense (Fig. 16: c), or sometimes are discretely perforated as in E. cubense (Fig. 16: a), or the protuberances which surround inner areas are covered by small, finely perforated ridges. In contrast, E. backhousianum has its own peculiar type of spore ornamentation with the ridges enclosing trapezoidal areas ornamented with small, irregular and basally connected fine ridges (Fig. 15: e).

In subsect. Apoda the spores offer a good criterion for distinguishing species, not only by themselves but also when combined with the rest of the characters, such as rhizome and marginal scales, anatomical features, and chemical spot patterns. Together they make delimitation of the taxa more reliable.

The spore sculpturing in this group shows a close affinity with the species of subsections Hybrida and Hymenodium, supporting presumed relationships based on other characters.

Gametophyte

The gametophyte of Elaphoglossum has been studied in some detail by Stokey & Atkinson (1957), although no species of subsect. Apoda were included. The present study has shown some slight variation from the descriptions made by Stokey & Atkinson (1957).

Spores of Elaphoglossum latum were obtained from living plants at the greenhouses of the New York Botanical Garden. Three different media were used as germination substrates: distilled water, inverted small pots filled with sphagnum moss and covered with a bell jar, and petri dishes filled with fresh sphagnum moss. The latter medium proved the best.

The spores were sown on sphagnum moss on September 1, 1982 into petri dishes at saturated humidity. The petri dishes were sealed with a Parafilm "M" tape and exposed to continuous light for four months. Germination was not observed during this period. In February the cultures were transferred to indirect, continuous daylight, and one week later the spores were slightly swollen which seems to be the first sign of germination. Two weeks later the first filament cell appeared. Four weeks later 3-4 more filament cells were formed and the basal rhizoid appeared (Fig. 7: f).

The cells of the filament are already rounded, brilliant green, and elongate considerably before lateral expansion occurs. At this stage of development they form a single filament of cells. The filament developed very slowly, and three months after germination the first longitudinal cell division occurrs initiating the two-dimensional growth phase.

Although the initial development was similar to that described by Stokey & Atkinson (1957) there were some differences in several respects. First of all, the germination period was extremely delayed (four months) in contrast to the 8-20 days reported by them. Another difference was that the filament of Elaphoglossum latum developed considerably before the first rhizoid appeared. This is in contrast to their observations in which the first rhizoid usually appeared on basal cells at about the same time as the germination filament emerged.

My observations are still in progress and it is expected that the following developmental stages will not differ from those reported by Stokey & Atkinson (1957), in which the filament continued growing until several rows of transverse walls developed forming a ribbon-shaped prothallium. The gametangia then developed along the center of the ribbon.

Chemotaxonomy

Although several reports on fern chemistry have been published (Berti & Bottari, 1968; Cooper-Driver, 1980; Swain & Cooper-Driver, 1973), no formal comparative phytochemical study has been done among the species of *Elaphoglossum*. A preliminary study of this group has been made by Giannasi (pers. comm.), who is working on a general survey of the genus. According to Giannasi, the genus *Elaphoglossum* is divided into four basic groups based on the presence of flavonols, flavones, xanthones, and anthochlors. He surveyed 34 species from different sections of the genus, finding strong chemical relations within sections and subsections. Section *Elaphoglossum* subsect. *Pachyglossa* for example, appears to be chemically uniform. Most of the species sampled within this subsection showed the presence of mangiferin, a tetrahydroxyxanthone-C-glycoside (Wallace *et al.*, 1982). However, during a survey of sect. *Polytrichia* subsect. *Hybrida* I found two xanthones in addition to mangiferin. One of these was characterized as isomangiferin, and the other from all known xanthones. The correlations found by Giannasi certainly have phylogenetic implications, but more work has to be done to elucidate the relationships among the sections.

The purpose of this study was to survey subsect. *Apoda* for leaf flavonoids and to determine any chemical correlations among this complex group of species. Equally important was to find whether or not the chemical spectra could be used to differentiate between chromatogram spots which had similar colors and Rf data. If so, spot data could then reliably be used to differentiate between taxa.

Dried leaf material of eight species involved in this complex was removed from herbarium specimens and fresh leaves from the living collections of the NYBG. Voucher citations for each group of species are given as follows:

Elaphoglossum amazonicum. BOLIVIA: *R. S. Williams 1027* (NY, US); PERU: *Bües 1737* (US).

Elaphoglossum apodum. HAITI: *Holdridge 2199* (NY, US); DOMINICAN REPUBLIC: *Ekman 13406* (US); JAMAICA: *Maxon 1740* (US), *Underwood 1589* (NY, US); NICARAGUA: *Schram 29* (US); PUERTO RICO: *Hioram 257* (US), *Chase 6213* (US).

Elaphoglossum auripilum. COSTA RICA: *Croat 863* (MO), *Jiménez 7900* (NY), *Lankester 829* (US), *Maxon 402* (NY, US), *39876*, *52258* (US), *Stork 1370* (MICH, UC); PANAMA: *Maxon 5035, 5036, 5239* (US); *Porter 4938* (NY).

Elaphoglossum backhousianum. COLOMBIA: *Lellinger 649* (COL, US); PANAMA: *Correa 196, 1886* (both US), *Porter 4828* (MO).

Elaphoglossum cubense. CUBA: *Morton 9707* (US), *Underwood 1358* (NY, US), *3259* (NY, US).

Elaphoglossum latum. COLOMBIA: *Lellinger 571* (COL, US), *H.H. Smith 2688* (NY); COSTA RICA: *Seidenschnur 108* (NY), *Lloyd 4162* (NY). GUATEMALA: *von Tuerckheim 8351* (US); PANAMA: *Correa* & *Dressler 186* (MO, US), *Porter 4938* (MO).

Elaphoglossum procurrens. CUBA: *Shafer 8862* (NY, US), *Wright 793* (GH, US).

Elaphoglossum rayawaense. BRAZIL: *Spruce 2186* (CGE, US); ECUADOR: *Pinkley* *482* (COL) *Sodiro s.n.* (US); FRENCH GUIANA: *Rombouts 871* (US), *Killip 26792* (NY,US), *28498* (US).

For comparative purposes it was decided to chromatograph representative samples of sect. *Polytrichia* subsections *Hymenodium* and *Hybrida* and sect. *Setosa* subsesct. *Pilosella*.

Section Polytrichia

subsection *Hymenodium*. *E. crinitum* (L.) Christ: CENTRAL AMERICA;
NYBG living collection, accession no. 554/79

subsection *Hybrida*. *E. tambillense* (Hook.) Moore: DOMINICAN
REPUBLIC; *Mickel 8264* (NY).

Section Setosa

subsection Pilosella. E. siliquoides (Jenm.) C. Chr.: DOMINICAN REPUBLIC; Mickel 8528 (NY)

Procedures

To isolate flavonoids from each species sterile fronds were cut into pieces and then ground up in an electric tissue grinder (homogenizer). This was a polytron PT 10-35 with two generators, 10 ST and 20 ST, both with saw-teeth for extracting plant tissue (Richardson, 1982). The speed control was set at number six. The extraction medium was 80% methyl alcohol. Because the samples were small, the extraction medium was usually carried out in centrifuge tubes (1.5 x 10 cm) using the smaller PT 10 ST generator. The extract was homogenized for 20 seconds and left for several minutes to allow gravity to clarify the solution. Small amounts of extract were carefully removed with a pasteur pipette for use on two-dimensional chromatograms.

Several applications of the extract were spotted (2.5 cm diam.) on a sheet of Whatman 3 MM chromatography paper (46 x 57 cm) and developed using two-dimensional descending chromatography in the following solvents:

Solvent I. TBA. tertiary-butanol: glacial acetic acid: water (3:1:1, v/v).

Solvent II. HOAc. glacial acetic acid: water (15: 85 v/v).

After chromatrography the sheets were dried and viewed in UV light (360 nm) both with and without ammonia vapor. Individual spots were circled with pencil, their colors were noted with and without exposure to ammonia fumes, and their Rf values were calculated. Rf values were determined for only the obvious and constantly recurring spots. The major spots are listed in Table IX.

Although the Rf values determined from the chromatograms of crude extracts varied somewhat, they were helpful, as were the color reactions, in determining which spots on different chromatograms may represent the same compound or at least the same type of flavonoid compound. Spots which were judged (on the basis of Rf values and color reactions) to represent the same compound were extracted from several chromatograms using a minimum of 10 chromatograms per sample.

The isolation, analysis, identification, and chromatographic data interpretation of individual compounds that were extracted in reasonable amounts were carried out following the techniques described by Crawford (1973). After the spectral data were obtained, several attempts to identify individual compounds were made. The data were compared directly with compounds identified from previous studies. (Giannasi, 1975; Harborne, 1967; Mabry *et al.*, 1970; Everett, 1977; Markham, 1982).

Results

Several attempts to extract and analyze the different compounds were made using standard techniques (Crawford, 1973; Harborne, 1967; Mabry *et al.*, 1970), and also using absorption maximum and Rf values listed by Everett (1977). Unfortunately, none of the isolated compounds in my study corresponded to known flavonoids. In spite of the fact that spot patterns are considered of limited value (Crawford & Dorn, 1974; Adams, 1974), or even almost worthless (Weimark, 1972), I decided to consider them as a possible approach to a chemical analysis of this complex group. Consequently, this analysis was based mostly on spot patterns, color reactions, and Rf values.

A total of 16 flavonoid compounds were detected in the chromatographic survey. The chromatograms of the eight species of *Elaphoglossum* subsect. *Apoda* examined fell into two basic spot patterns- the *E. apodum* type and *E. procurrens* type- (Table X).

The spot patterns were mostly uniform in six of the eight species- *E. amazonicum*, *E. apodum*, *E. auriplum*, *E. cubense*, *E. latum*, and *E. raywaense*. These species also are quite similar in terms of their external morphology and some anatomical characters, but the chemical features that distinguish one species from the others are very tenuous. Some differences occurred in the presence or absence of certain spots and not all individuals of a species displayed exactly the same flavonoid profile.

Intraspecific variation seems to be common but is seldom extensive. This could not be relate with geographical distribution. The species profile given in Fig. 17 includes the spots most commonly encountered.

Compared to the aforementioned species, E. procurrens and E. backhousianum show very different spot patterns (Table X). Although these two species are quite different from each other morphologically, they seem to have nearly identical chromatographic spot patterns.

Spot number 12 seems to characterize the six species first mentioned, whereas spots 5 and 7 are unique to the second group (Table X).

Figure 17 shows a composite chromatogram of the flavonoids of subsect. Apoda. The numbers correspond to those in Tables IX and X. Figures 18-20 correspond to the chromatographic profiles of representative species of sect. Polytrichia, subsections Hymenodium and Hybrida and sect. Setosa subsect. Pilosella.

Table IX

Paper chromatographic properties of the

Elaphoglossum apodum complex

Spot no.	color		Rf values (x100)	
	UV	UV-NH_3	TBA	HOAc
1	pale-yellow	light-yellow	9	8
2	purple	yellow	25	15
3	purple	yellow	34	24
4	orange	orange	90	16
5	purple	orange-yellow	12	32
6	purple	yellow	14	38
7	purple	yellow	18	36
8	purple	yellow	32	67
9	blue	blue	34	75
10	blue	blue	32	82
11	blue	blue-green	40	85
12	purple	yellow	66	57
13	purple	yellow	82	52
14	blue	blue	82	64
15	blue	blue-green	88	68
16	purple	yellow	85	73

Table X

Taxonomic distribution of leaf flavonoids in the *Elaphoglossum apodum* complex

Taxon	Spot															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
E. amazonicum	+	+						+	+		±	+		+	+	
E. apodum				±				+			+	+	+	+	+	
E. auripilum		±		±				+	+	±	±	+	+	+	+	±
E. cubense								+	+	±	+	+	+			
E. raywaense	±	±		±				+	±	±	±	+		±	±	
E. latum								+	±	±	±	+	±	+	±	
E. backhousianum						+	+									+
E. procurrens			+		+	+	+									

Symbols: + = present: ± = sometimes present

Table XI

UV spectral data of compounds isolated from the *Elaphoglossum apodum* complex

Taxon	Spot no.	MeOH	NaOMe	$AlCl_3$	$AlCl_3/HCl_3$	NaOAc	$NaOAc/H_3BO_3$
E. amazonicum	12	264 355	234 sh 270 345 405	270 418	270 350 385	270 359	261 370
E. cubense	12	252 354	268 402	270 393	271 352 398	270 325	257 368
E. procurrens	5	242 266 294 347	240 347 408	266 307 sh 350 372		262 315 sh 348	262 315 348 sh
	6	245 265 307 350	245 265 sh 300 345 400 sh	266 305 347	245 266 305 347	245 264 305 342	245 264 306 345 434 sh
	7	246 266 311sh 350	245 265 305 351 411 sh	245 264 302 sh 350 387 sh	245 266 305 sh 350 385 sh	245 265 310 345 410 sh	245 265 311 350

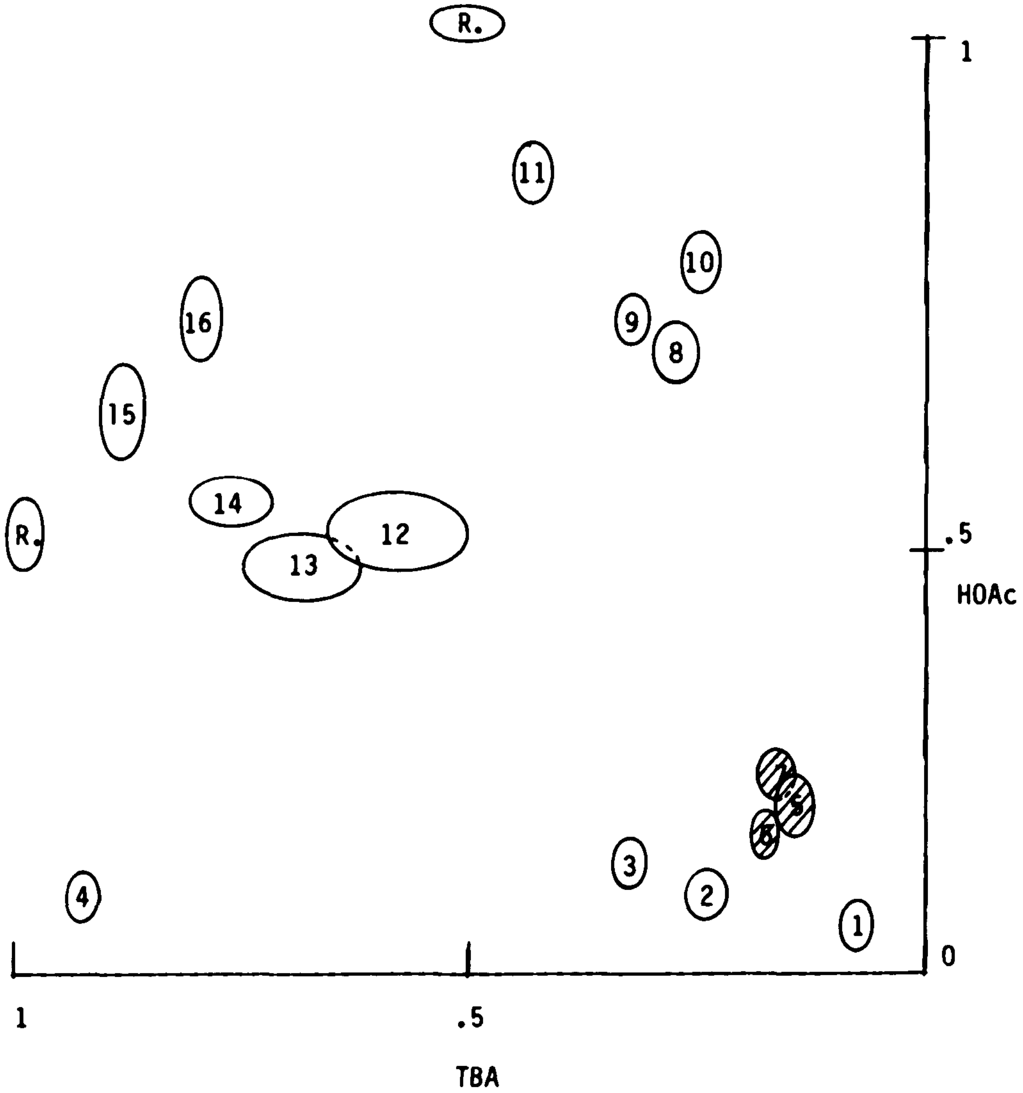


Fig. 17. Composite chromatogram of *Elaphoglossum* subsection *Apoda* flavonoids, showing mobility in two chromatographic solvents. Numbering corresponds to Tables IX-X. Unshaded spots correspond to species of group I and shaded spots correspond to species of group II.

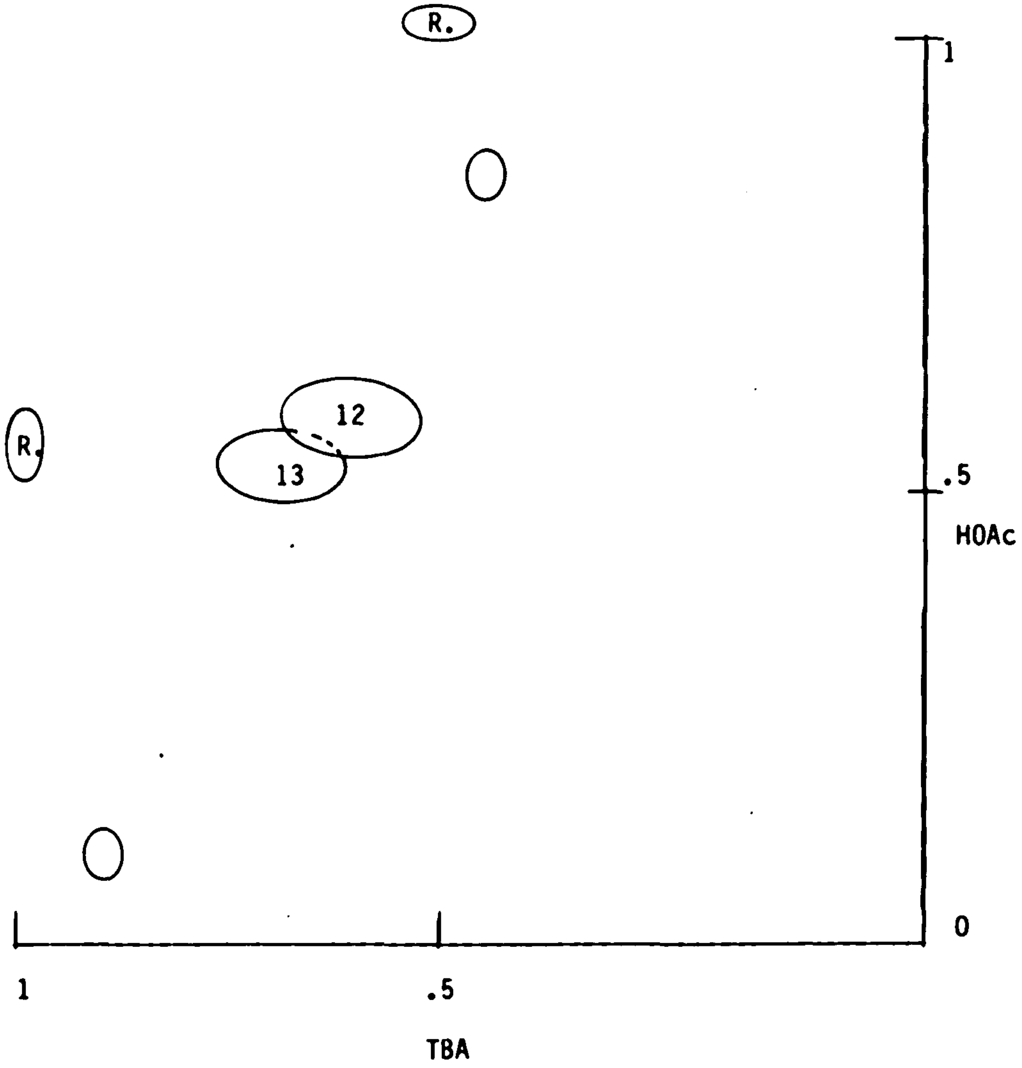


Fig. 18. Chromatographic profile of _E_. _crinitum_.

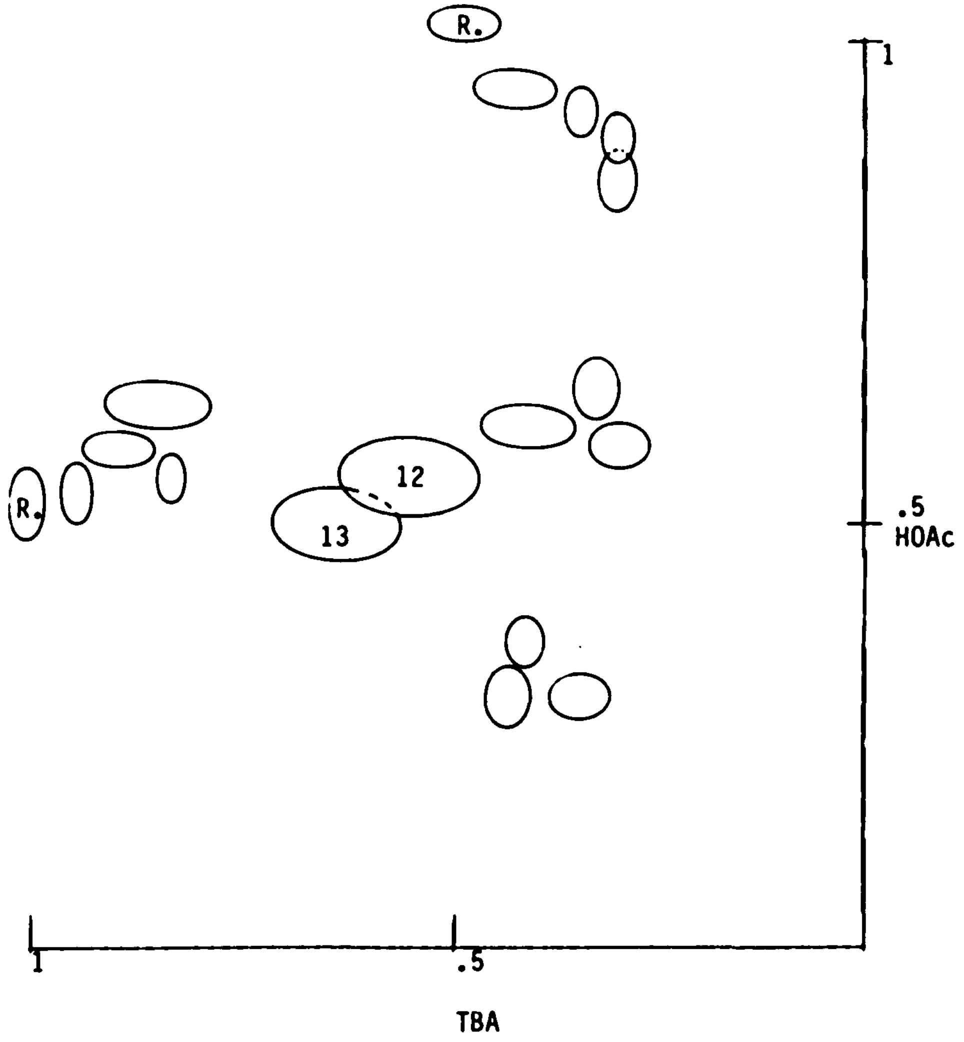


Fig. 19. Chromatographic flavonoid profile of E. tambillense.

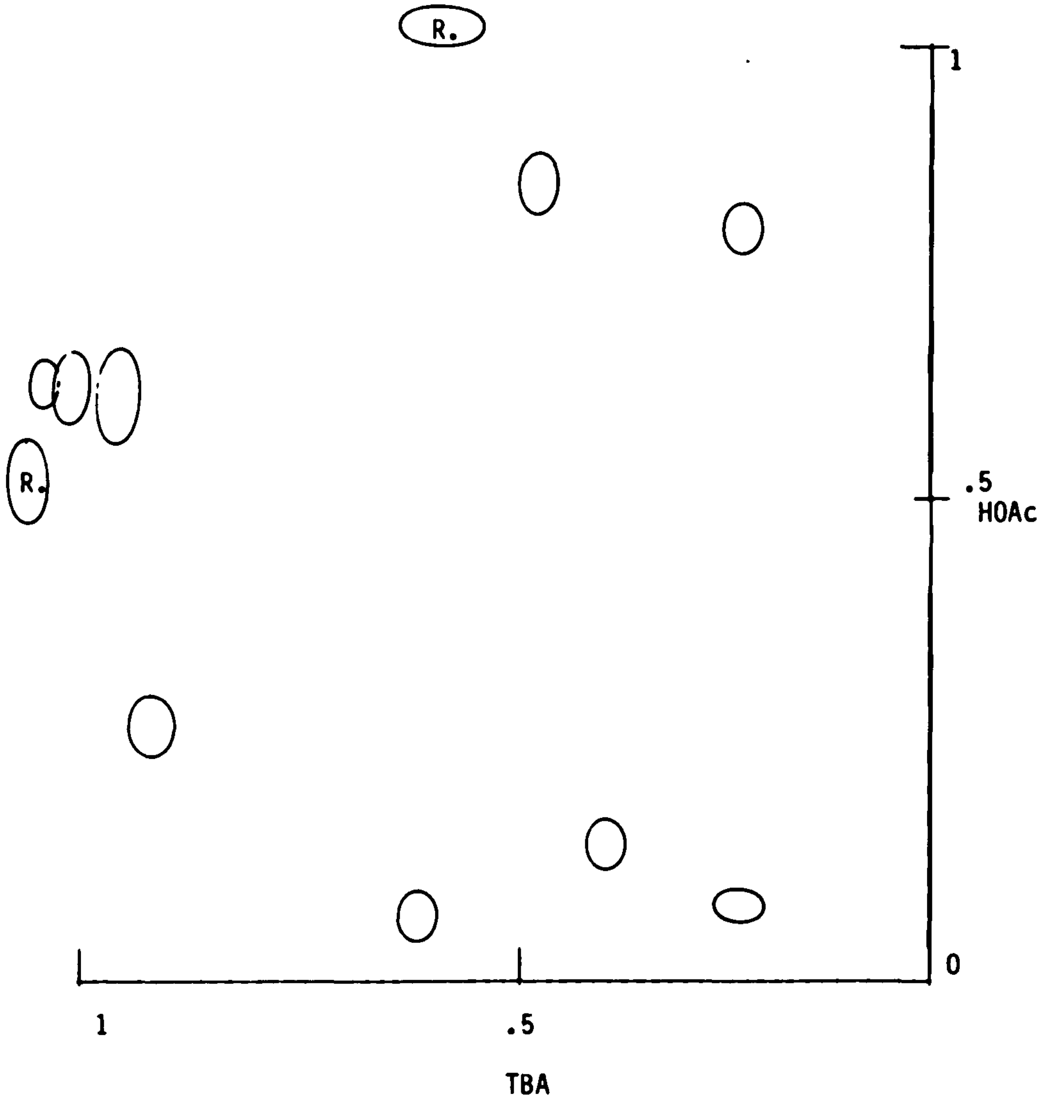


Fig. 20. Chromatographic profile of E. siliquoides.

Discussion

Although none of the compounds were fully identified, it appears that chromatographic data can add some taxonomic information to the well-established morphological and anatomical data. As shown in Table X, species in subsect. *Apoda* can be divided into two groups on the basis of the spot patterns. Group I includes six of the eight species--*E. amazonicum*, *E. apodum*, *E. auripilum*, *E. cubense*, *E. latum* and *E. raywaense*--and Group II includes the remaining species--*E. backhousianum* and *E. procurrens*. Although each of the species in the first group has its own chromatographic profile, the group itself seems to be held together by spot no. 12. This is supported by morphological data. It is important to point out that this spot was also present in some sampled species of subsect. *Hymenodium* and *Hybrida* (Figs. 18-19). These are thought to be the subsects. closest to subsect. *Apoda* (Mickel & Atehortúa, 1980). These three subsections form sect. *Polytrichia*, and the chemical data give strong support to the published classification of the genus (Mickel & Atehortúa, 1980). However, the chromatographic data of *E. siliquoides* (Fig. 20) showed a quite distinct spot pattern from the above subsections. Mickel & Atehortúa (1980) proposed this species as belonging to subsect. *Apoda*, but anatomical and chemical data now suggest it belongs instead to sect. Setosa subsect. Pilosella.

Table XI shows the UV spectral analysis for compounds from E. cubense in Group I and E. procurrens in Group II. Spot no. 12 was extracted and purified from E. amazonicum and E. cubense. Spot nos. 5,6,7 were extracted and purified from E. procurrens. Spectral analysis of spot no. 12 revealed minor differences between the two samples, but the reason for this is unknown. Elaphoglossum backhousianum and E. procurrens in the second group show a very different chromatographic pattern from the previous group (Table XI, Fig. 17). These two species are rather different from each other in many morphological features, so strong chemical similarity was unexpected. The two species are linked solely on the mutual occurrence of spot nos. 5 and 7. Until these spots are characterized from both species and proven to be the same in each case, it would be unwise to assume a close relationship based upon the chromatographic data. Another question raised from the chemical data is the connection of these two species with the rest of the species in the subsection, at least in terms of their flavonoid composition. There appears to be no chemical character to link the whole subsection together. From the morphological and anatomical point of view, these two species fit into the general picture of this subsection, but chemically they suggest a divergent line or lines.

In conclusion, it appears that the preliminary chromatographic data can add some taxonomic information at the species level as well as the subsectional level. Based on morphological and anatomical data, it is not unlikely that the six species of the first group share a common ancestor. This is reflected to some extent in the spot pattern that is common to them.

The two remaining species, E. backhousianum and E. procurrens, although each is unique in its morphology, have similar chromatographic spot patterns. These phytochemical spot patterns appear to yield no further information about these species, at least at this level of comparison. Identification of the compounds that produce the spots may lead to a better understanding of the relationships among the groups since the chemistry of these two species indicates that they are rather divergent from the first group.

One limitation in this study was the use of herbarium specimens which were often old and some of which may possibly have been pretreated with formaldehyde, which could have affected the results (Runemark, 1968; Cooper-Driver & Balick, 1978; Coradin & Giannasi, 1980). This may account for the intraspecific variation in spot pattern, which, though common, was seldom extensive.

Cytology

To the present, 11 papers reporting chromosome number in Elaphoglossum have been published (Manton & Sledge, 1954; Bir, 1960; Brownlie, 1965; Anderson & Crosby, 1966; Walker, 1966; Roy & al., 1968; 1973; Mickel, Wagner & Chen, 1966; Manton & Vida, 1968; Sorsa, 1966; and Smith & Mickel, 1977), including a total of 33 species. All are based on $n = 41$ with 20 diploid, 11 tetraploid, 1 hexaploid, and 1 sterile triploid (Table XII).

Manton & Sledge (1954) noted that chromosome counting in Elaphoglossum is a rather difficult task because few fertile leaves are usually available and the identity of the species is often doubtful due to the chaotic taxonomy of the genus.

The greatest number of chromosome counts has been made by Walker (1966, 1973) who reported data numbers for 13 Elaphoglossum species of Jamaica. He stated that in spite of the fact that a number of species are not only abundant but frequently grow in close proximity to one another or even completely intermixed, there are surprisingly low number of hybrids. However, one plant was proved to be triploid. The plant shows intermediate characters between its presumed parents and has abortive spores. Although the hybrids seem to be rare, this

Table XII

Cytology of *Elaphoglossum*

Taxon	Ploidal level	Chromosome no.		Source
		n	2n	
E. aemulum (Kaulf.) Brack.	Diploid	41	-	Anderson & Crosby, 1966
E. alatum Gaudich	Diploid	41	-	Anderson & Crosby, 1966
E. angulatum (Blume) Moore	Diploid		82	Manton & Sledge, 1954
E. apodum (Kaulf.) Schott	Diploid *	41	-	Walker, 1966
E. ceylanicum Krajina ex Sledge	Tetraploid	82	164	Manton & Sledge, 1954
E. chartaceum (Baker) C. Chr.	Tetraploid		164	Walker, 1966
E. aff. conforme (Sw.) J. Sm.	Diploid		82	Mickel et al., 1966
E. crassifolium (Gaudich) A.& C.	Diploid		82	Anderson & Crosby, 1966
E. crinitum (L.) Christ	Diploid		82	Sorsa, 1966
E. cuspidatum (Willd.) Moore	Diploid		82	Sorsa, 1966
E. denudatum (Jenm.) Maxon	Diploid		82	Walker, 1966
E. firmum (Mett.) Urban	Diploid		82	Sorsa, 1966
E. hybridum (Bory) Moore	Diploid		82	Manton & Vida, 1968
E. latifolium (Sw.) J. Sm.	Diploid		82	Walker, 1966
E. laurifolium (Thours.) Moore	Hexaploid ?		246? ca. 250	Manton & Vida, 1968
E. laurifolium sensu Bir	Tetraploid		164	Bir, 1960
E. martinicense (Desv.) Moore	Diploid	41	-	Smith & Mickel, 1977
E. maxoni Underw. ex Morton	Diploid		82	Walker, 1966
E. micans (Mett. ex Kuhn) P. S.	Tetraploid		164	Anderson & Crosby, 1966
E. muscosum (Sw.) Moore	Diploid		82	Walker, 1966
E. pellucidum Gaud.	Diploid		82	Anderson & Crosby, 1966
E. petiolatum (Sw.) Urban	Tetraploid		164	Walker,1966
E. rigidum (Aubl.) Alston	Diploid		82	Sorsa, 1966
E. sphatulatum (Bory) Moore	Tetraploid		164	Manton & Sledge, 1954
E. setigerum (Wall.ex Bak.) Moore	Tetraploid		164	Roy et al., 1971
E. stigmatolepis (Fée) Moore	Tetraploid		164	Bir, 1965
E. succisifolium (Thours.) Moore	Tetraploid		164	Manton & Sledge, 1968
E. tectum (H.& B. ex Willd.)Moore	Tetraploid		164	Walker, 1966
E. vieillardii (Mett.) Moore	Tetraploid		164	Brownlie, 1965
E. villosum (Sw.) J. Sm.	Diploid		82	Walker, 1966
E. wawarae (Luerss.) C. Chr.	Diploid		82	Anderson & Crosby, 1966
E. chartaceum x E. latifolium	Triploid	irregul.meis.		Walker, 1973

* Species of *Elaphoglossum apodum* complex

hybrid appears to be very common in herbara specimens, which suggests the possibility of extensive vegetative reproduction or that it is independently formed on a number of occasions.

In subsect. Apoda the chromosome number is known only for Elaphoglossum apodum which has n= 41 (Walker, 1966).

It is postulated that the ploidal levels could be extrapolated from the spore size and stomatal length (Mickel, 1962; Blasdell, 1963). According to spore and stomatal size (Figs. 8-11: b-d; 15-16: a-e; a-d; Tables V-VIII), there is no direct evidence of polyploids in this complex. It is quite possible that all members of subsect. Apoda are diploids.

Based on current morphological and chemical evidence, there are no suspected hybrids in this subsection.

Distribution and Ecology

A paucity of literature deals with the ecology of Elaphoglossum (Christ, 1899; Walker, 1966; Lloyd, 1970; Tryon & Conant, 1975; Holttum, 1978; and Roux, 1982). Consequently, most of the remarks herein are based on a composite of herbarium data, floristic works, and personal observations.

Generally species of subsect. Apoda occur at lower elevations than most species of the genus. The members of this complex are restricted to the neotropical regions between 16° N and 17° S latitude. The most widely distributed species are E. apodum (West Indies and Central America), E. latum (Central America, northern South America, and Hispaniola), and E. raywaense (Venezuela, Guianas, Brazil, and Ecuador). The other five species are more localized: E. procurrens is restricted to Haiti and eastern Cuba, E. cubense to Cuba and Jamaica, E. backhousianum to central Panama and western Colombia, E. auripilum to Costa Rica and western Panama and E. amazonicum to northern Bolivia, eastern Peru, and southwestern Brazil.

The habitat for most of the species appears similar. All, but E. auripilum are epiphytes-hygrophytes on tree trunks in wet lowland forests near streams or river banks, where the humidity is high, and at elevations of 20-1500 m. The exceptional *E.auripilum*, grows in wet secondary forests and cloud forest at elevations of 1000-2400 m (Fig. 21). Most of the species have thin fronds and occur in sheltered places on tree trunks not far above the ground level, as has been observed by Holttum (1978) in of *Elaphoglossum* of Malaysia. Tryon & Conant (1975) working on some epiphytic *Elaphoglossum* species of Brazil (Amazonia), recorded observations on micro-habitat preferences. Seventy six per cent of the species of *Elaphoglossum* studied by them grow 0-1 m from the stream bank or edge which indicates the moisture requirements for those species. Another observation was the apparent stratification of these plants on the host tree in relation to ground level. The species have a tendency to grow 0-5 m above ground level with the highest concentration of them between 40-160 cm above the ground. Although Tryon & Conant (1975) suggested that those species do not grow according to a humidity gradient, labels indicate that they do grow in places where the humidity is high. J. Luteyn and B. Øllgaard (pers. comm.) found that in Añangu, Ecuador *E. raywaense* grows in areas where the humidity is 95-99% at a temperature of 25°C. They also observed that this species grows 2-5 m above the ground on palm and other tree trunks. It seems that this species grows along a humidity

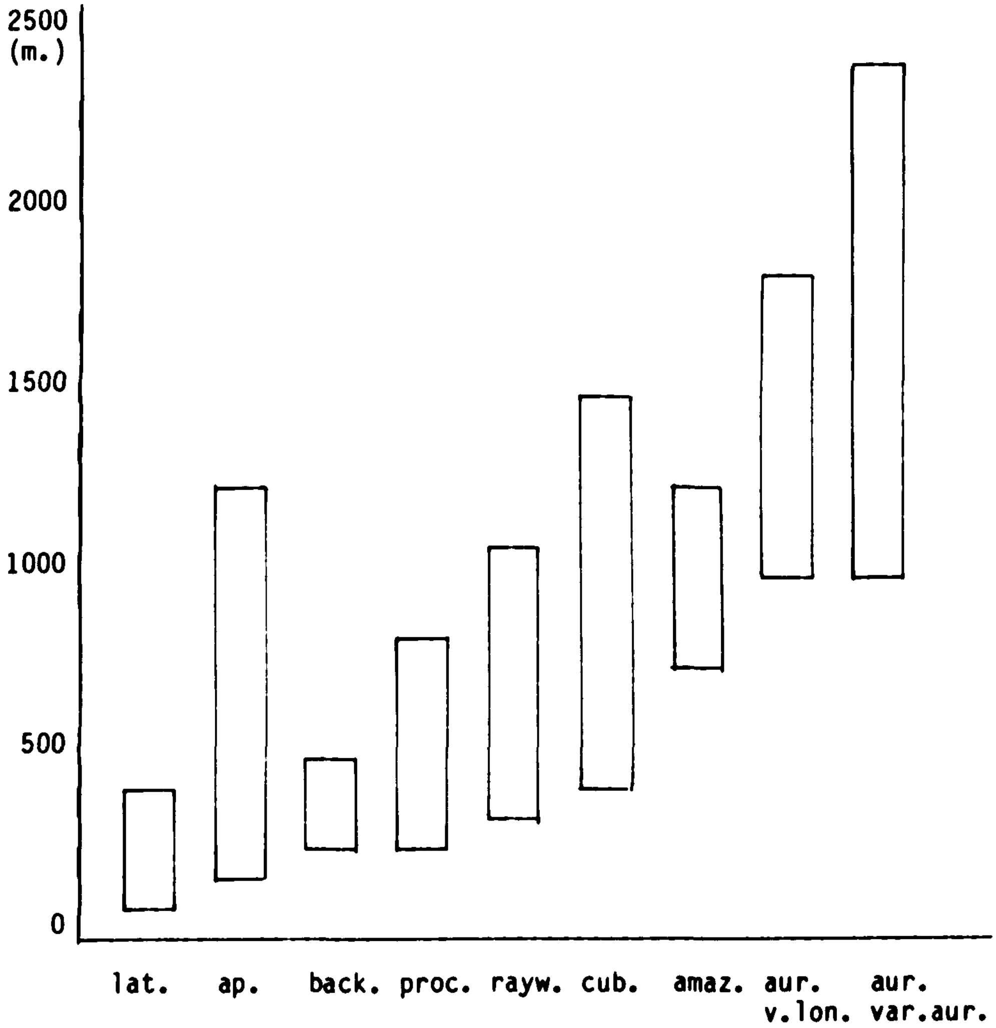


Fig. 21. Distribution of the species of subsect. Apoda according to their altitude in meters above the sea level.

gradient, but it may be due to the thin texture of its lamina and its large size, whereas the species studied by Tryon & Conant were of thicker texture (e.g., *Elaphoglossum glabellum*). Luteyn (pers. comm.) also observed that this species has a pronounced preference for a proximity to streams and swamp perhaps responding to greater light in such places.

Lloyd (1970) surveyed some morphological features in the genus *Elaphoglossum* in relation to the habitat. He studied petiolar joints and swelling (phyllopodia), pneumatophores (aerophores), frequency of scales, sporangial characters (paraphyses), frond length and width, rhizome scales, and hydathodes. These characteristics were relatet with the basic habitat of the species. Although he did not provide names for all his collection numbers, I have been able to identify one member of subsect. *Apoda*, *E. auripilum* var. *longipilosum* (*Lloyd 4227*). This particular taxon grows in the cloud forest of San Vito de Java (Puntarenas Province, Costa Rica). Following his tabulated observations, I found some discrepancies in relation to the type of scales found on the abaxial surface of the blade. In *E. auripilum* all the scales are of the bristle type, instead of the laminate and lobed or cordate at the base. One of the features that he overlooked, also the glandular hairs which are dense and very conspicuous. In fact, many of the collection labels made reference to them in terms of "viscous" and "sticky." Perhaps their abundance is in some way related to the high humidity and low temperature of the cloud forest. It is also possible that they may function as a protective device against dampness and cool wind currents at this altitude or may be gathering atmospheric moisture as an epiphyte.

Sporophyll production is another feature that seems to correspond to environmental conditions. Holttum (1978), says that the sporophylls are produced periodically, probably in response to dry weather, according to his own experiences and observations. He had a plant of E. amblyphyllum in cultivation which produced only one sporophyll in 20 years and argued that this may have occurred because it was watered on rainless days.

I had a similar experience with one of our living collections of E.latum at the greenhouse of the NYBG in which it was constantly watered. After I moved it to another greenhouse where the humidity was much lower the plant started to produce sporophylls. At one time I counted seven of them. However, these observations appear to contradict those made by Walker (1966), who stated that in Jamaica the species differ widely in the frequency and number of sporophylls produced, apparently independently of the season. Since he did not provide any meteorological data, it is difficult to relate levels of humidity with the data of herbarium collections.

Certainly sporophyll production in subsect. Apoda is very rare and therefore poorly represented by specimens. For example, in a collection of 20 specimens of E. procurrens, only two specimens were fertile and each of them with only one sporophyll.

Another important fact in the life history these species is the ability of their spores to germinate, which I found to be extremely low and slow. In the germination experiments with E. latum (a living collection), the time for germination was almost six months and furthermore only a few of the thousand spores germinated on fresh sphagnum moss, which seems to be the best medium for that purpose. I found that the quantity of light might have some influention in germination. Since these species are epiphytes on lower parts of tree trunks, the light filtering through the canopy is relatively weak and therefore the spores should be preadapted to such conditions. Only after a short period of reduced light, did germination take place. Whether this was actually due to the reduced light or whether the spores are normally slow to germinate is not known. The fact, generally true for the genus that these species do not often reproduce vegetatively (except through the branches of the rhizome), must disminish their reproductive capabilities. Perhaps individually and collectively these factors have helped to determine in their rates of evolution as well as dispersal and migration.

Judging from the present distribution of the members of subsect. Apoda, it seems probable that the center of radiation and diversification is the lowland forest of the neotropical region, perhaps northern South America.

Unfortunately, there is no fossil record available for the genus. However, Christ (1899) suggested that the center of origin of the genus is the Andean region of Tropical America where the major diversification and radiation might have taken place. On the other hand, Bell (1955) suggested that the center of origin was the paleotropical region where the species which he thought to be more primitive are widely represented. He also argued that speciation in the genus has probably been continuous (at least since the Tertiary) in a relatively stable and continuous tropical environment since the establisment of the angiospermous forest. This furnished the necessary habitats for epiphytic plants, and it is probable that the species within the genus evolved "solely in it," allowing that much of the original variation is still present in the extant forms.

For both theories there are some points to be considered.

Geological data show that the high Andean habitats have been available for colonization only since the end of the Tertiary and several geological events have taken place since then. The relatively stable and continuous tropical environment has always been assumed rather than proven, and the events of the Pleistocene during the Quaternary may have played an important role in the speciation pattern of this group. It is now known that climate and vegetation changed drastically during the Pleistocene in tropical regions of America (van der Hammen, 1974; Simpson, 1975). During the glacial periods when the vegetation zones were lowered, most plant species expanded their ranges of distribution to warmer areas (lowland forest) of the continental and island regions with a relatively moderate degree of warmth. At lower elevations in the northern Andes and along the Eastern Cordillera, direct migration was possible at that time because of increased contiguity of upper montane forest habitats (Simpson, 1975). Fragmentation of species ranges in the neotropical lowlands and mountains, and subsequent differentiation of isolated populations (divergence) in Elaphoglossum could be postulated as one of the main causes for its high diversity in the Andean tropical region. The species were forced to seek "refuge" in the warmer "lowland forest," causing geographical isolation and subsequent divergence.

Present distributions show that the genus is predominantly mesothermic in tropical mountain or island climate with a relatively moderate degree of warmth. The mass of species appears only at an altitute of 1500 m and higher (Christ, 1899).

The refuge theories (Haffer, 1969; Vanzolini, 1970; Prance 1973, 1982) seem to have support from the distribution patterns of some species of this subsections. For example E. backhousianum in the Choco area of Colombia, E. raywaense in the Guiana area and Amazonian basin, and E. amazonicum also in the Amazonian basin. It is important to stress that these species are very similar in their morphological features, and it may be due to their geographical contiguity. This does not hold for the species of the West Indies that appear distinct morphologially from one another. However, the high degree of endemism as a result of isolation mechanisms may account for their small degree of divergence, and also reproductive limitation factors may be directly implicated in the narrow range of distribution and speciation of this group.

Under the high humidity conditions where the species of this subsection grow, a rich epiphyllous flora is developed and ferns in general are one of the best hosts for epiphyllous organisms.

As Holttum (1978) noted, old fronds of Elaphoglossum bear a considerable growth of epiphyllous bryophytes and lichens. Dr. R. Harris at the NYBG identified the species of lichens growing on members of this subsection and recorded 24 species of lichens, two of them new (Harris, pers. comm.) His results are tabulated in Table XIII. Apparently, there is not any detectable relation between the species of Elaphoglossum and the species of lichen growing on them. However, it might be interesting to study the relationships between these ferns and lichens in more detail.

Table XIII

Foliicolous lichens growing on Elaphoglossum apodum complex

Lichens	Elaphoglossum spp							
	1	2	3	4	5	6	7	8
1. Aspidothelium fugiens (Mull. Arg.) Sant.			x					
2. Aulaxina minuta Sant			x					x
3. Aulaxina quadrangula (Stir.) Sant.			x	x				
4. Bacidia sp					x	x		
5. Bacidia apiahica (Mull. Arg.) Zahlbr.						x		
6. Bacidia rhaphidophylli (Rehm) Zahlbr.			x			x		
7. Byssoloma leucoblepharum (Nyl.) Vain?								
8. Byssoloma subdiscordans (Nyl.) James		x						
9. Byssoloma polychromum (Mull. Arg.) Zahlbr.						x		
10. Catillaria semicarpi Vain						x		
11. Coccocarpia domingensis Vain			x					
12. Crytothecia candida (Kremp.) Sant								x
13. Dimerella epiphylla (Mull. Arg.) Malme								x
14. Dimerella dilucida (Kremp.) Sant.				x				
15. Gyalectidium filicinum Mull. Arg.			x					x
16. Mazosia sp.				x				
17. Porina epiphylla (Fée) Fée				x		x		x
18. Porina leptosperma Mull. Arg.			x					
19. Porina rufula (Krem.) Vain		x						x
20. Tricharia sp.								x
21. Tricharia "leucothrix Fée"				x				x
22. Tricharia "melanothrix Fée"		x	x	x		x		x
23. Tricharia urceolata (Mull. Arg.) Sant.			x			x		
24. Trichothelium epiphyllum Mull. Arg.						x		

(1) E. amazonicum (2) E. apodum (3) E. auripilum (4) E. backhousianum (5) E. cubense (6) E. latum (7) E. procurrens (8) E. raywaense

Species Relationships

An attempt to evaluate species relationships has been made using Wagner's "Ground Plan Divergence Method" (1962, 1969, 1980) explained by Mickel (1962) and used by many authors including Hardin (1957), Iltis (1959), Stern (1961), Hauke (1963), Brown (1964), Evans (1969), and Hoshizaki (1972).

Comparison of the characters of the subsect. *Apoda* were compared with those of other closely related subsects. *Hymenodium* and *Hybrida* of section *Polytrichia* and with *Elaphoglossum* as a whole was made.

In some cases my opinion was contrary to what some others have considered to be primitive or advanced. One example is the rhizome habit in which I believe along with Holttum (1964) that the creeping-dorsiventral solenostelic rhizome is probably derived from an ancestral stock having a radially organized rhizome. In this case the long-creeping dorsiventral rhizome of *E. procurrens* is considered an advanced character rather than a primitive one as Bell (1955, 1956) suggested.

In his phylogenetic series Bell found that most of the species he studied have a dorsiventral, two-ranked condition with bud traces posterior to each leaf trace, and therefore it was considered primitive. However, in this subsection and allied subsections the common condition is the compact short-creeping and almost radial rhizome type.

To determine which of two alternative states of a character is primitive I have used mainly the "age-old concept of generalized ground plan character states and its corollary that the primitive attributes tend to coincide more often with other primitive characters than the primitive with divergent, and also that the most generalized character seems to coincide with those of the prototype" (Wagner, 1980).

Sixteen characters were chosen to show various structural conditions or character states that were considered the most obvious, constant and easily understood.

Advancement Index was constructed in which each character was given a value: (0) for those which were considered primitive (0.5) for those that were considered intermediate, and (1) for those that were considered extremely advanced conditions.

In Figure 33 the theoretical starting point represents the hypothetical ancestor with an Advancement Index of (0). Elaphoglossum backhousianum with an Advacement Index of 9.5 is considered the most advanced species in the group.

An explanation of the characters used in the Index follows:

A. RHIZOME HABIT: The compact or short-creeping rhizome is the rule for the genus including subsect. Apoda and allied subsections *Hymenodium* and *Hybrida*. The long-creeping rhizome of *E. procurrens* is the advanced character in the group.

B. PHYLLOTAXIS. According to Bell (1955, 1956) the distichous condition is the most common character in the genus and therefore he considered it primitive. On the contrary, I agree with Holttum (1964) in considering it to be advanced and the polystichous type the primitive state.

C. RHIZOME SCALE APPEARANCE: The primitive condition is like that found in *E. auripilum*, *E. procurrens*, and *E. backhousianum* in which the cell walls are straight. The advanced condition is illustrated by *E. amazonicum* and *E. raywaense* in which the cell walls are wavy or very flexuous.

D. RHIZOME SCALE MARGIN: Again the primitive condition is like that found in *E. auripilum*, *E. procurrens* and *E. backhousianum* in which the scales have an entire margin. The advanced condition is found in the rest of the species within the subsection which have scales with dentate or irregularly toothed margin.

E. RHIZOME SCALE COLOR: This character is very difficult to evaluate since it is variable from one section to another and even within a section. The orange-yellow rhizome scales occur in isolated species groups, such as some members of sect. *Elaphoglossum* subsect. *Pachyglossa*. However, all the species of subsect. *Apoda* have orange-yellow to slightly brownyellow rhizome scales and this character is also partially shared by some of the outgroup species, but the dark tipped rhizome scales of *E. raywanense* seem to represent advanced character state.

F. STIPE LENGTH: Although most species of subsect. *Apoda* have nearly sessile fronds which is considered a reduction, the usual condition in the genus as a whole and in the outgroup is to have long-petiolate fronds and this is considered the primitive condition.

G. STIPE HAIRS: Among the subulate scaly species of *Elaphoglossum* short glandular hairs on the stipe are generally present. Their absence is considered advanced. They are lacking in *E. backhousianum*.

H. FROND SIZE: A height of less than 12 cm is considered reduced and therefore the advanced condition. Generally the fronds in *Elaphoglossum* are 15-95 cm long.

I. BLADE BASE: Although the long-decurrent blade base is represented in most of the sections of the genus, it is restricted to a few species. In subsect. *Apoda* most of the species have a long-decurrent blade base which is considered an advanced character. The cuneate to rounded blade base found in *E. auripilum* and *E. backhousianum* is considered the primitive character state.

J. BLADE APEX. The common type of blade apex in the genus as a whole is acuminate and in this subsection is considered primitive. The long-cuspidate to long-caudate apex found in *E. amazonicum*, *E.latum* and *E. raywaense* is an advanced feature.

K. BLADE SURFACE SCALES: Most species of subsections *Apoda*, *Hybrida*, and *Hymenodium* have subulate scales on the blade surface as well as the margin and midvein and this is the general condition. In the subsect. *Hybrida* the surface scales are present but sparse and early deciduous. *Elaphoglossum backhousianum* is unusual in sect. *Polytrichia* in having the laminar surface completely devoid of subulate scales, which are strictly limited to the margin and midvein.

L. BLADE MARGIN SCALES: Most species of all three subsections of sect. *Polytrichia* (*Apoda*, *Hybrida*, and *Hymenodium*) as well as of sect. *Setosa* have subulate scales which are gradually narrowed at the base. The exception is found in *E. backhousianum* in which the subulate scales have an abruptly broad base and laciniate margin, representing an extremely advanced condition.

M. BLADE HAIRS: *Elaphoglossum auripilum* is considered specialized in having a dense mass of short, glandular hairs covering the blade surface. In most species these glandular hairs are more sparse on the blade surface.

N. EPIDERMAL CELL WALLS: Most species in subsect. *Apoda*, *Hybrida* and *Hymenodium* have the primitive condition in which the epidermal cell walls are very thin. *Elaphoglossum backhousianum* has specialized, very thick epidermal cell walls.

O. CHEMICAL SPOT PATTERNS: Most species of subsect. *Apoda* and allied subsections share a similar spot pattern. *Elaphoglossum procurrens* and *E. backhousianum* seem to diverge in this respect and therefore are considered advanced.

P. SPORE ORNAMENTATION. Having fine perforations on the spore surface is the common character state in the subsect. *Apoda* as well as in the allied subsections; their absence is considered advanced. An intermediate condition is found in *E. backhousianum* and the most specialized type is found in *E. amazonicum* in which the perine is covered with fine spicules.

Specialization in subsection *Apoda*

A. Rhizome compact (0) to long-creeping (1)

B. Leaves polystichous (0) to distichous (1)

C. Rhizome scales straight (0) to very flexuous (1)

D. Rhizome scales with margin entire (0) to dentate (1)

E. Rhizome scales orange-yellow (0) to dark-tipped (1)

F. Fronds distinctly petiolate (5-18 cm long) (0) to nearly sessile (2.3-4.0 cm long) (1)

G. Stipe hairs present (0) to lacking (1)

H. Fronds large (15-95 cm long) (0) to greatly reduced (1-12 cm long) (1)

I. Blade base cuneate or rounded (0) to long-decurrent (1)

J. Blade apex acuminate (0) to cuspidate or long-caudate (1)

K. Blade surface scales present (0) to lacking (1)

L. Blade margin subulate scales gradually narrowed at the base (0) to abruptly broad at the base (1)

M. Blade hairs scattered (0) to very dense (1)

N. Epidermal cell walls thin (0) to thick (1)

O. Chemical spot pattern widely distributed (0) to restricted (1)

P. Spore surface smooth to perforated (0) to spiculate (1)

Table XIV

Character states in subsect. *Apoda*

Taxon	Character states*																Divergence formula	Divergence level
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P		
E. amazonicum			1	1		1			1	1						1	CDFIJP	6
E. apodum			½	1		1			1								CDFI	3.5
E. auripilum													1				M	1
E. backhousianum		1				1	1		1		1	1		1	1	½	BFGIKLNOP	8.5
E. cubense		½	½	1		1			1								BCDFI	4.0
E. latum			½	1		1			1	1							CDFIJ	4.5
E. procurrens	1	1				1		1	1						1		ABFHIO	6
E. raywaense			1	1	1	1			1	1							CDEFIJ	6

* Underlined letter means an intermediate character.

Fig. 22. Specializations in the Elaphoglossum apodum complex.

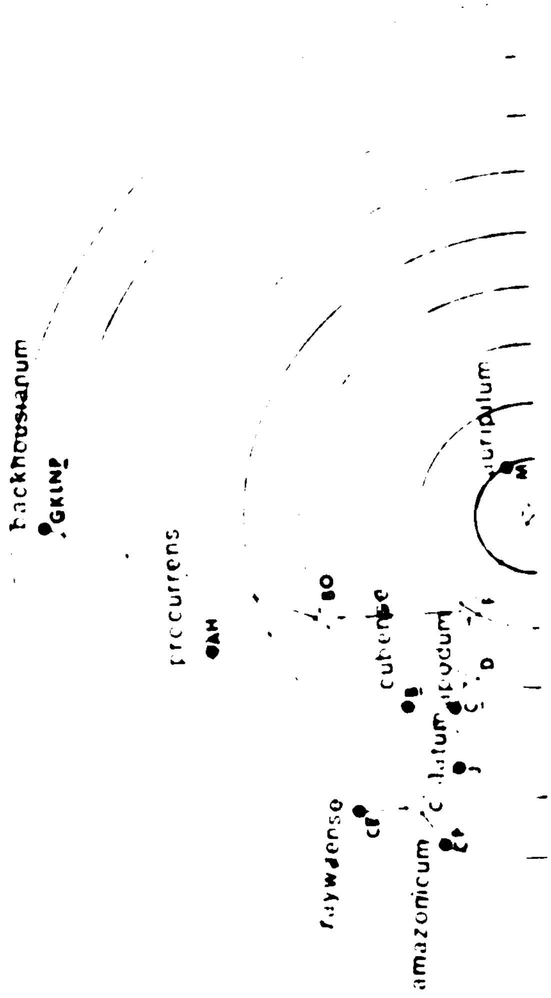

backhousianum
GKLNP
precurrens
AH
BO
raywdense
CE
cubense
B
amazonicum
C
latum
ipodum
CF
J
C
D
F
uripulum
M

Figure 22

Subsection Apoda seems to have three lines of evolution. These lines do not seem far from each other in origin and the common ancestor probably appeared very similar to E. auripilum. This hypothetical ancestor probably had a short-creeping rhizome; orange-yellow to brown-yellow rhizome scales; stipe relatively short and covered by subulate scales and short glandular hairs; subulate scales covering the midvein, blade surface, and margin; oblanceolate blade with acuminate apex and slightly decurrent base; spores probably smooth to perforated.

In the largest of these lines, represented by E. apodum E. cubense, E. latum, E. amazonicum, and E. raywaense, there is a tendency to have flexuous rhizome scales, a long-cuspidate blade apex, a long-decurrent blade base, and larger fronds.

In the second line, represented by E. backhousianum and E. procurrens, there is a tendency to have a more specialized flavonoid type, a rounded to slightly acuminate blade apex, distichous leaves, and the extremes of frond size.

In the third line, represented by E. auripilum, there is a tendency toward increased in density and complexity of the glandular hairs on the blade surface. This species seems to be the link with subsections Hybrida and Hymenodium.

Systematic Treatment

Revision of the Genus Elaphoglossum subsect. Apoda

Elaphoglossum Schott ex J. Smith

Generally epiphytes in wet montane forest, the majority terrestrial at high elevations; rhizome short- to long-creeping, rarely erect, slender to stout (1-15 mm in diam.); rhizome scales orange to black, basally attached or peltate, entire to toothed; fronds 2-200 cm long, erect, spreading, or pendent, simple (pedate in one South American species); stipe glabrous or scaly, sometimes also with minute glandular hairs; stipe long or very short, base often darker (phyllopodium) with abscission at its upper demarcation rather than at the rhizome; blade linear to ovate or oblanceolate, apex acuminate or caudate to obtuse, base rounded to long-attenuate; midvein grooved adaxially, usually with scales of the stipe abaxially; veins generally free, rarely netted or with a marginal commissural vein, simple or 2-forked, ending near the margin; those stopping well short of the margin usually end in conspicuous hydathodes; blade scales sometimes different from those of the rhizome or stipe, abundant to lacking, often so greatly reduced as to resemble as stellate hairs; fertile fronds longer or shorter tha the sterile fronds but generally with narrower blades and proportionally longer stipes; fertile blade completely covered beneath with sporangia (acrostichoid sori); sporangia long-stalked, the annulus erect, interrupted by the stalk; paraphyses in some species but generally lacking; spores bilateral, monolete, most with high crests or low ridges, but some echinate or tuberculate without ridges or crests (Mickel, 1981a).

Section *Polytrichia* Christ

Rhizome short- to long-creeping and occasionally erect; rhizome scales linear to linear-lanceolate; phyllopodia short and usually covered with dense mass of scales sometimes lacking or very inconspicuous; stipe present or almost lacking covered with dense mass of subulate scales and capitate glandular hairs; blade linear-lanceolate, elliptic-lanceolate, ovate-lanceolate to oblanceolate, the margin and midvein covered with conspicuous subulate scales; hydathodes present only in juvenile stages and lacking in adult fronds; spores with low ridges and often small spiculate ridges and fine perforations.

Key to subsections of *Polytrichia*

1. Blade broadly elliptic and fleshy; veins netted, obscure. .... subsect. *Hymenodium*
1. Blade linear-elliptic, ovate-lanceolate to oblanceolate, subcoriaceous or papyraceous; veins free, usually evident.
    2. Stipe 2-35 cm long; blade scales maroon, dark-brown to black, located mostly on midvein and margin.......... .... subsect. *Hybrida*
    2. Stipe very short (2.5 cm) or nearly lacking; blade scales orange-yellow, yellow-brown to reddish-brown, distributed uniformily over the blade surfaces, midvein and margin. .... subsect. *Apoda*

Subsect. *Apoda* Mickel & Atehortúa

Rhizome short- to long-creeping; rhizome scales 0.5-40 mm x 0.1-1.0 mm, linear-lanceolate to triangular-lanceolate, basifixed to cordate at the base, acuminate to long-cuspidate at the apex, concolorous to bicolorous, orange-yellow, reddish-orange, to yellow-brown; phyllopodium conspicous, dark brown; aerophores bilateral to the phyllopodium like long strips; fronds crowded at the tip of the rhizome, erect or ascending, 2-112 cm long; stipe short (up 2.5 cm) to nearly lacking, densely scaly and mixed with minute capitate, glandular hairs (lacking only in one species); blade 2-110 x 0.6-10 cm, linear-lanceolate to oblanceolate, base cuneate to long-decurrent, apex rounded, acute to long-caudate, papyraceous to subcoriaceous; veins free once or twice forked, running at 45°-70° angle to midvein; hydathodes lacking; midvein prominent on the abaxial side; blade scales especially persistent on midvein and margin; both surfaces of the trophophylls and the upper surface of the sporophylls covered with subulate deciduous scales and capitate glandular hairs; fertile frond shorter than the sterile, similar in size and shape to the sterile; scales lacking among the sporangia; spores 19.3-33.3 μm in length, with narrow, short, smooth to spiculate ridges surrounding a central area covered by fine perforations.

Epiphyte of tropical rain and cloud forests at 20-2400 m elevation.

TYPE SPECIES: Elaphoglossum apodum (Kaulf.) Schott ex J. Smith

OTHER SPECIES INCLUDED: Elaphoglossum amazonicum Atehortúa, E. auripilum Christ, E. backhousianum Moore, E. cubense (Mett. ex Kuhn) C. Chr., E. latum (Mickel) Atehortúa, E. procurrens (Mett. ex D. C. Eat.) Moore, and E. raywaense (Jenm.) Alston.

Key to the species of
subsect. Apoda

1. Rhizome long-creeping and slender, to 4 mm in diameter including the scaly cover. Eastern Cuba and Haiti... .... E. procurrens

1. Rhizome short-creeping and stout, 5-45 mm in diameter including the scaly cover.

    2. Marginal blade scales basally semi-urceolate or abruptly and conspicuously expanded at the base, with a laciniate margin, dark brown to black; stipe short, 3.5-4.5 cm long; blade base rounded-truncate. Western Colombia and central Panama.................... E. backhousianum

    2. Marginal blade scales slightly flared at the base with shallowly toothed or subentire margin, yellow-orange to brown; stipe short to long, 1.2-14.5 cm. long; blade base long-attenuate-cuneate to slightly rounded.

        3. Sterile blade base gradually long-attenuate, varying to wide attenuate-cuneate to nearly rounded; stipe usually excerted from basal scale cover, 1.2-14.5 cm long.

4. Blade spatulate to oblanceolate, apex obtuse or acute to slightly acuminate, base gradually attenuate; scales of midvein and stipe scattered, light reddish-brown. Cuba and Jamaica........... .... E. cubense

4. Blade oblong-lanceolate, apex acuminate, base attenuate-cuneate to somewhat rounded; scales of the midvein and stipe abundant, reddish-orange to yellow-orange. Costa Rica and western Panama..... .... E. auripilum

3. Sterile blade base long-decurrent; stipe short and often buried in the basal scale cover, 0.5-10 cm long.

5. Rhizome scales conspicuously flexuous; sterile blade 45-95 x 7.7-9.5 cm; apex acuminate to abruptly cuspidate; spores ridges narrow, short spiny and surrounding an area with fine spines. Northern Bolivia, eastern Peru and south-western Brazil...................... E. amazonicum

5. Rhizome scales slightly sinuous; sterile blade 12-56 x 1.7-6.0 cm; apex acuminate to long-caudate spore ridges narrow, smooth, surrounding a perforated area.

    6. Apical rhizome scales 3-8 x 0.2 mm linear-lanceolate, with very irregularly toothed margin, yellow-brown to ferrugineous, distinctly darker toward the tip (bicolorous); blade 18-56 x 2.2-6.0 cm; apex long-caudate. Venezuela, Guianas, Brazil, Ecuador......... .... E. raywaense

    6. Apical rhizome scales 5-28 x 1.0-1.5 mm, linear to narrowly triangular, undulate with irregular teeth or rarely entire, orange to brown (concolorous); blade 25-48 x 4.5-5.7 cm; apex acuminate to long cuspidate. West Indies and Nicaragua.

        7. Sterile frond linear-oblanceolate, 10-33.5 x 2.5-3.6 cm, base cuneate, apex acuminate; rhizome scales 0.5-1.4 cm long, linear-lanceolate to narrowly triangular, yellow to light brown with conspicuous dentate margin;

basal petiolar scales acuminate at the apex. Mainly in West Indies...... E. apodum

7\. Sterile frond broadly oblanceolate, 25-48 x 4.5-5.7 cm, base cuneate to rounded, apex long-acuminate to cuspidate;rhizome scales 0.8-2.8 cm long, linear-lanceolate, orange to reddish-brown, with slightly dentate margin; basal petiolar scales with an abruptly broad apex. Central America, Hispaniola and northern South America. .... E. latum

1. Elaphoglossum amazonicum Atehortúa, sp. nov.

Fig. 23. Fig. 24.

Ab affinibus rhizomate crasso, rhizomatis paleis flexuosis, laminis sterilibus latioribus apice cuspidatis, sporisque spinulosis differt.

Plants tufted; rhizome short-creeping to erect, fibrous, 2.0-3.2 cm in diameter including the scaly cover; scales 15 x 0.5 mm, linear-lanceolate, fulvous, concolorous, crispate to very flexuous toward the tip, lustrous; phyllopodium conspicuous, 1.5 cm long, dark brown; aerophores bilateral to the phyllopodium like a long strip and visible even in dry specimens but totally covered with dense mass of scales; fronds crowded at the tip of the rhizome, erect or ascending, 45-95 x 7.5-10.0 cm; stipe of the sterile frond 2-10 cm long, conspicuously winged, fibrous, stout, terete but abaxially deeply canaliculate, 0.4 mm in diameter, densely scaly; scales subulate, 0.8 mm long, fulvous to brown-ferrugineous toward the midvein, also with minute short, resinous, capitate glandular hairs on the stipe and midvein; blade oblanceolate, at base long-decurrent, apex acuminate to abruptly long-cuspidate, membrano-chartaceous to subcoriaceous; veins free, once or twice forked, 1-2 mm apart, running at 45° angle to midvein; hydathodes lacking; midvein prominent on the abaxial side and densely scaly; blade lacking scales (at least in dry specimens) except on the midvein and margin, but lamina densely covered with appressed, yellow, branched, glandular hairs, which are usually oriented toward the margin; margin hyaline, densely covered with 2-3 rows of fine, orange to yellow, subulate scales similar in size and shape to those that cover the midvein, and mixed with erect, capitate, glandular hairs; fertile frond shorter than the sterile but with a longer stipe (3.0-8.5 cm long), blade 25-50 x 2.3-4.0 cm, narrowly lanceolate, apex acuminate, base gradually narrowed and becoming winged proximally, with inconspicuous sterile margin and also basally sterile along the midvein; scales lacking among the sporangia; spores 25.4-31.5 µm in length with narrow, short, spiculate ridges.

Epiphyte of tropical rain forests at 792-1200 m elevation.

TYPE: PERU. Dpto. San Martín. Zepelacio, near Moyobamba, 1100-1200 m, Oct-Nov. 1933, G. Klug 3330 (HOLOTYPE: US; ISOTYPES: BM, MO, NY).

DISTRIBUTION. Central and western South America.

OTHER SPECIMENS EXAMINED: BOLIVIA. San José, R.S. Williams 1027 (NY, US); BRAZIL. Mato Grosso. Municipio Alto Araguaia, Rib. Claro, Hatschbach 36206 (NY, UC); PERU. Dpto. Junín. Province de Jauja: Satipo, Monte Alto margen del río, Riodoutt 11562 (US); prope Tarapoto, in monte Campana, Peruvia orientalis, Spruce 4639 (BM); Cochagoc, Bües 1737 (US).

This species is very closely related to E. raywaense and E. latum but differs in flexuous rhizome scales, large size, the cuspidate apex of the blade, the stout and fibrous stipe, and finely spined spores.

Underwood annotated specimens of this plant (R.S. Williams 1027) as a new species of Elaphoglossum, using the epithet williamsii but did not publish the name. There is already an Elaphoglossum williamsii Vareschi in sect. Elaphoglossum subsect. Pachyglossa.

Fig. 23. Habit of *E. amazonicum*.

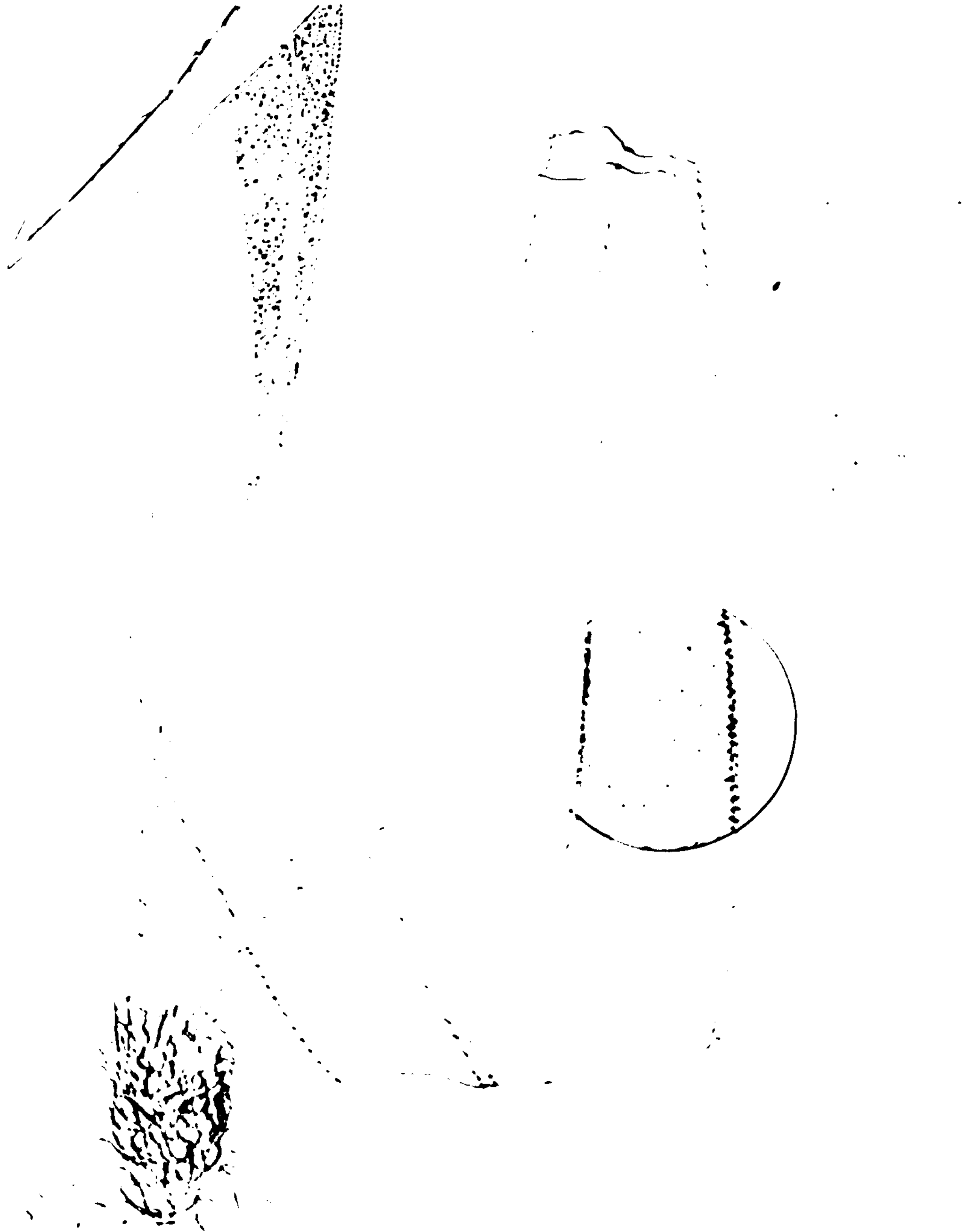


Figure 23

Elaphoglossum amazonicum

Fig. 24. Geographical distribution of _E. amazonicum_ and _E. raywaense_. Map. No. 1.

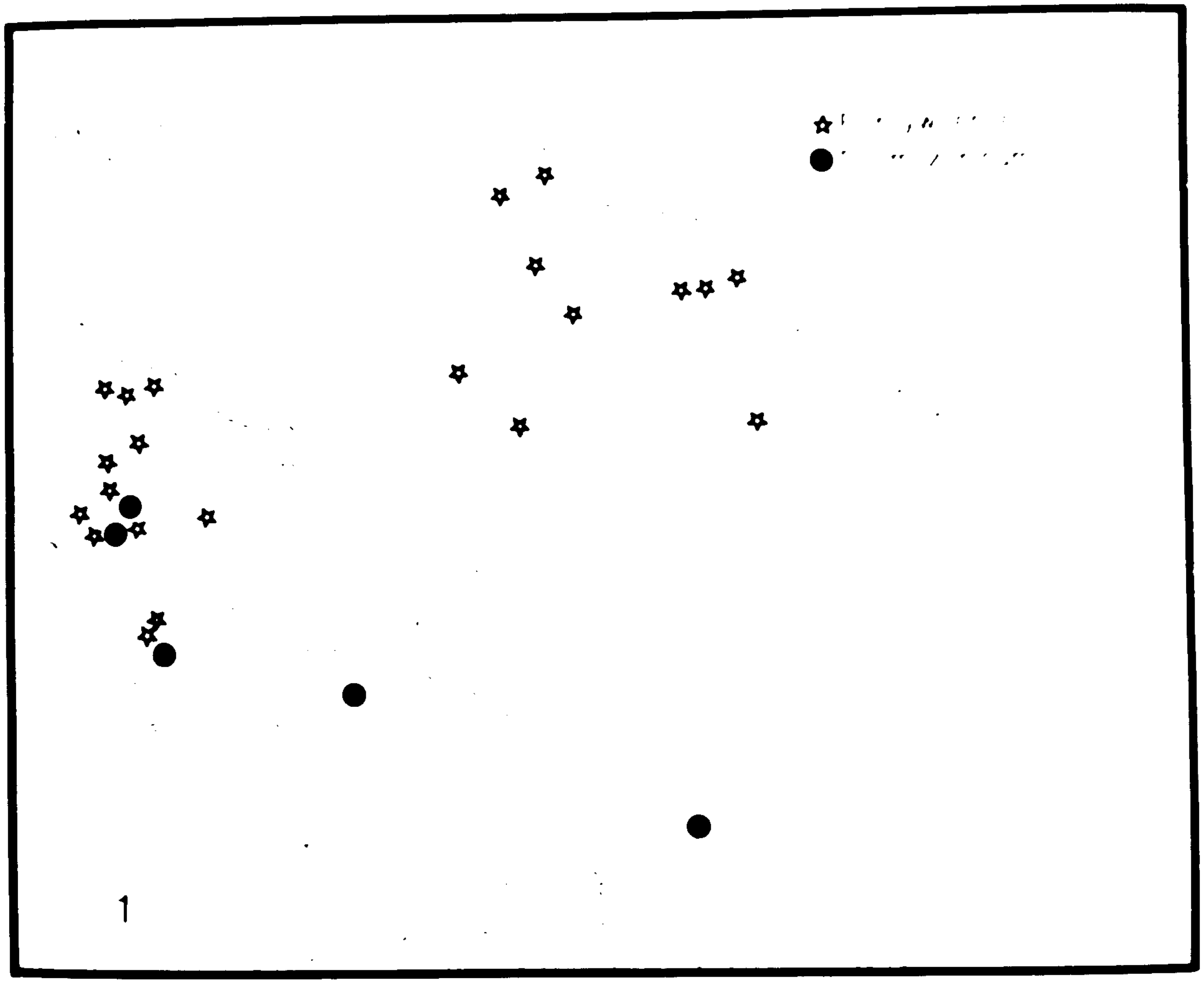


Figure 24

2. *Elaphoglossum apodum* (Kaulf.) Schott ex Smith, J. Bot. (Hooker) 4:148. 1841. Fig. 25. Fig. 26.

Basionym: *Acrostichum apodum* Kaulf., Enum. Fil. 59. 1824.
Syn: *Olfersia apoda* Presl, Tent. Pterid. 233. 1836.
Acrostichum platyneuron Fée, Mém. Fam. Foug. 2: 43. t.4, f.1. 1845.
Elaphoglossum platyneuron (Fée) Moore, Ind. Fil. 1857.

Plants tufted; rhizome short-creeping, ca. 1.5-2.5 cm in diameter including dense scale cover; scales golden-yellow to slightly reddish-brown, 0.5-2.8 x 0.3-1.5 mm at the base, linear or narrowly triangular, tapering from the base to an acuminate apex, basifixed, the margin with irregularly spaced teeth; phyllopodium weakly defined, to 1 cm long; fronds clumped, erect or ascending, to 33.5 x 3.6 cm; stipe nearly lacking to 2 cm long, commonly very narrowly winged, covered with tiny glandular hairs and spreading, reddish-brown, subulate scales 0.7-6 mm long; blade linear-oblanceolate to broadly oblanceolate, base cuneate, gradually tapering to the stipe; apex acuminate to cuspidate, papyraceous to slightly coriaceous or subcoriaceous; veins free, undivided or once forked, ca. 1 mm apart, running

60°-70° angle to midvein; hydathodes lacking; blade scales subulate, orange-yellow to brown, especially concentrated on the midvein and margin, scales very sparse on both surfaces, blade also with minute, capitate, glandular hairs which are mainly concentrated in the abaxial part on and near the midvein fertile fronds much smaller than the sterile; stipe to 2.3 x cm long; blade to 14 x 1.3 cm, linear or rarely linear-lanceolate to oblanceolate, acute at the apex, long-attenuate at the base; sterile margin about 2 mm wide and also sterile portion in the lower part of the midvein; scales lacking among the sporangia; spores 22.7-28.0 µm in length with smooth or rugose ridges surrounding a central area covered by fine perforations.

On tree trunks or epipetric on wet rocks in tropical rain forest at 20-1300 m elevation.

TYPE: Insula Monserrat, Vahl. s.n. (Ryan Herb.) (HOLOTYPE: C).

DISTRIBUTION: West Indies, Nicaragua.

OTHER SPECIMENS EXAMINED: BRITISH WEST INDIES. Grenada: Parish St. Andrew, east spur of Mt. St. Catherine, Proctor 17232 (US), Sherring 357 (BM, NY, US); Sherring 130 (BM). St. Kitts: N.E. slope of Mt. Misery, Box 278 (BM, US). St.Lucia: Roseau Milette Reige, "Moi un Fois" district West of Morne Gimie, Proctor 17759 (US). St. Vicent. Smith & Godman 380 (B, BM); Forest of Wallilabo

Valley *Smith & Smith 1137* (BM). Antilles: Montagnu Pela, *Husnot 1868*, (P). Guadaloupe: Viena habitatits-Bois de l'hab. La Grivelière, *Père Duss 4321* (NY), *Guilding s.n* (BM, NY). Martinique: *Garnier 290* (BM); *Père Duss 1621* (B); la Cale basse du Camp Colson, *Père Duss 4577* (F, MO, NY, US). Dominica: *Nicholls 193* (B). DOMINICAN REPUBLIC. Prov. Monte Cristi: Central, La Cumbre, Los Guananitos, *Ekman 11562* (B, NY, US); Laguna de Cenobi, *Ekman 12857* (NY); in Montis de Isabel de la Torre, *Eggers 2745* (B); Samaná Peninsula, vicinity of Laguna, chiefly on the Pilón de Azúcar, *Abbott 276* (US). Province de Santiago: Dist. of San José de las Matas, arroyo Juan Fino Jicomé, *Valeur 657* (BM, F, US). HAITI. Road from Camp No. 1 to La Barrière Couchant, *Nash & Taylor 1067* (NY); Rivière Glace, *Holdridge 2199* (NY, US). Massif du Nord, St. Louis du Nord ridge between Morne Chavary and Haut Pilon, *Ekman 4729* (B, BM, F, MO, NY, US); Morne Brigand, *Ekman 2987* (B). CUBA. Cuba orientali, prope Villam Monte Verde dictam, *Wright 967* (B, BM, MO, P); Sierra Nipe, in the manacales at Río Piloto, *Ekman 2102* (B, NY); South of Lumber, Crest of Sierra Nipe, *Morton & Acuña, 3194* (NY, UC, US); *Shafer 3714* (NY, US); Sierra Maestra on the divison between Río Yara and Río Palmocha, *Ekman 14416* (B); Sta. Ana, *Maxon 4173* (NY, US); Summit of Gran Piedra, *Maxon 4071* (US).

Yateras: Monte Verde, Maxon 4335 (BM, NY, US); Pinal de Sta. Ana, Eggers 4997 (B). Prov. Santiago: El Yunke, Mt. Baracoa, Undewrwood & Earle 924 (NY, US); near Baracoa, Pollard & Palmer 152 (F, MO, NY, P, US); Loma de Gato and vicinity Sierra Maestra, Bro. Hioram & Bro. Clément 6353 (US); Fre. Leo et al. 10524 (NY); El Cobre, Fre. Clément 944 (BM, NY). Guantánamo: La Prenda, Bro. Hioram & Maurel 4710 (P, US). JAMAICA. Portland Parish: Base Camp, Morley & Whiteford 548 (BM), 921 (US); Valley of Trafalgar river, Maxon & Killip 818 (F, NY, US); East of John Crow Mts, Proctor 25660 (F); spur of John Crow Mts. opposite Hill Bank, Maxon 9379 (NY, US). St. Elizabeth: Cook Bottom, north of Ipswich, Maxon & Killip 1453 (B, F, NY, US); vicinity of Hollymount, Mount Diabolo, Maxon 1914, 2248 (both US). St.Thomas: Cuna Cuna trail above Mattis River, Maxon & Killip 171 (F), Maxon 1740 (US), Fredholm 3218 (US); upper southern slopes of Gossamar Peak, Maxon 10545 (US); immediate vicinity of Corn Puss Gap, Anderson & Steaiberg 3139 (US); Wilson & Murray 553 (US); above House Hill, Maxon 8834 (NY, US), 9138 (US); trail between House Hill and Cuna Cuna gap, Maxon 8930 (NY, US); Underwood 2698 (NY). St. Andrew: Mount Janes, Maxon 8520 (NY, US); Mansfield near Bath, Maxon 2395 (NY, US), Maxon 1827 (US); Second Breakfast Spring, near Tweedside, Maxon 882 (P, US), Underwood 1589 (NY, US), *2027, 2067* (both NY); *Harris 7432* (B, BM, NY, US). St. Mary Parish: south of Longroad, *Proctor 5457* (MO); Cockpit county: north of Quick Step, above Aberdeen, *Proctor 4125* (US). Kingston and vicinity, 1884-1885 , *Balch s.n.* (NY); 1866, *Puerdel s.n.* (BM); 1874-1879 *Jenman s.n.* (NY, UC); 1855, *Whaston s.n.* (B). Gordon Town, *Hart s.n.* (US); 1896, *Hart 117* (B); *Walker HS 38* (BM). PUERTO RICO. Prov. Maricao: *Sintenis 523* (B); *Chase 6313* (US); *Hess 355* (B, NY); *Britton 2668* (NY); Sierra Luquillo and Monte Jiménez, *Sintenis 1338* (B, BM, PR, P); *Wilson 253* (NY, US), *321* (B, NY); *Hess 216* (US); S.W. side of Loma Francesa to falls of Río Prieto, *Shafer 3222* (NY). Prope Arecibo: *Sintenis 6443b* (B); Prope Adjuntas: Monte Galsa, *Sintenis 4277* (B); Monte Torresilla, *Bro. Hioram 257* (US).

CENTRAL AMERICA. NICARAGUA. Sangsangta Dist., *Schramm 29* (US).

SOUTH AMERICA. COLOMBIA. Dpto. Guajira: Serranía de la Macuira, Palua, *Bernal & Sudgen 62* (COL).

In general appareance this is similar to *E. raywaense*, *E. cubense*, and *E. auripilum*. It differs from them in its very distinctive rhizome scales, which are slightly wavy and irregularly dentate, and in its short stipe, which is almost lacking and buried among the rhizome scales. It could be easily confused with *E. raywaense*, which is its closest relative, but its rhizome scales and spore ornamentation are very distintive.

Fig. 25. Habit of _E. apodum_.

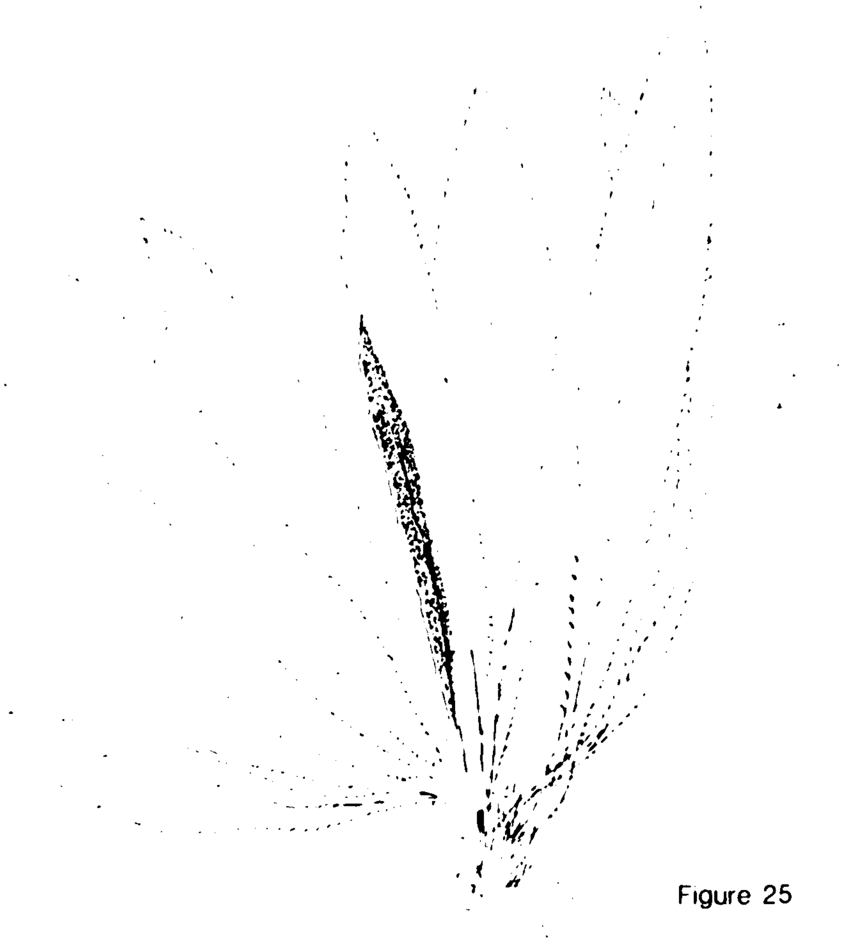


Figure 25

Elaphoglossum apodum

Fig. 26. Geographical distribution of <u>E. apodum</u> and <u>E. latum</u>.

Map. No. 2.

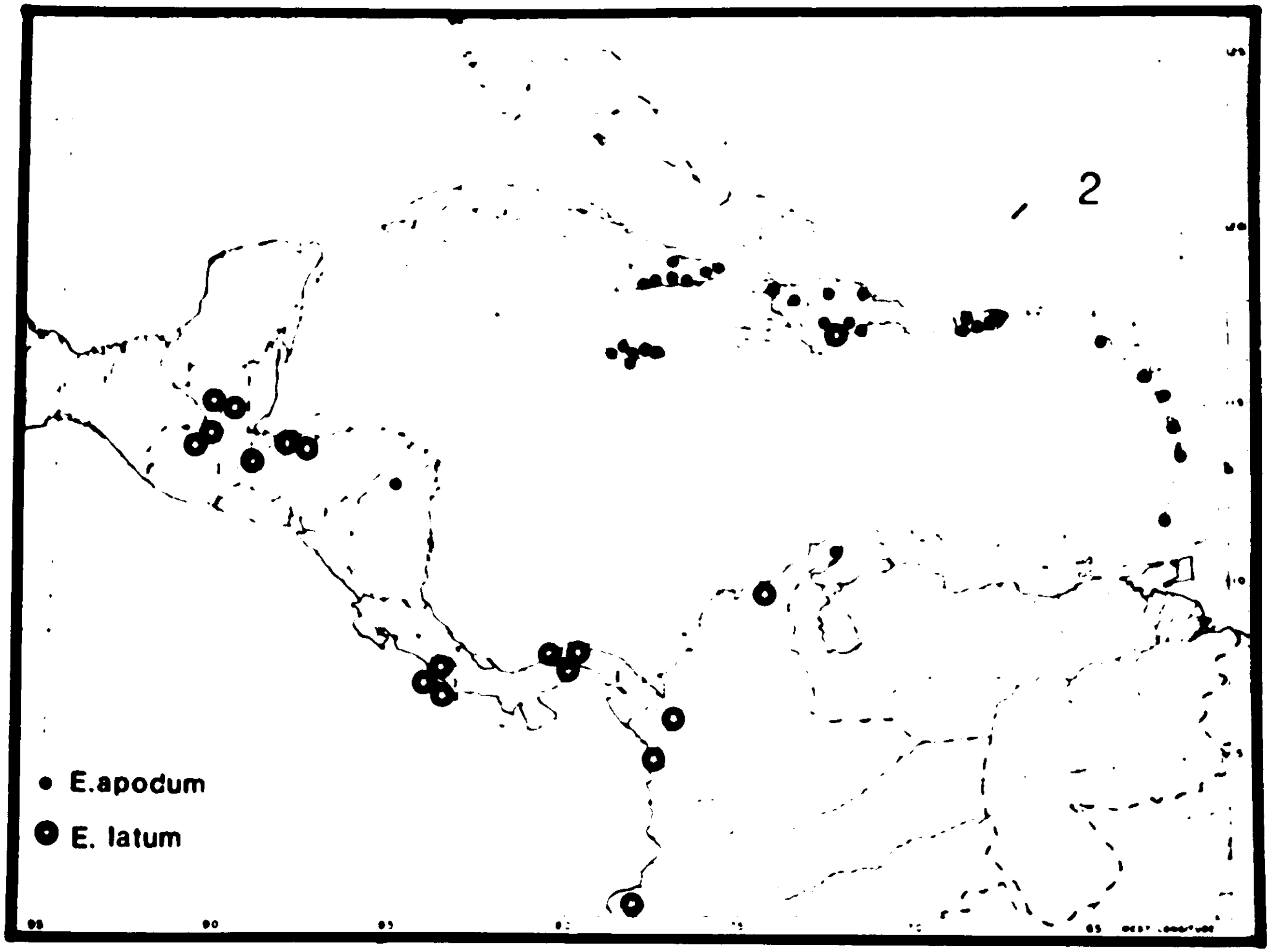


Figure 26

3. Elaphoglossum auripilum Christ, Bull. Herb. Boissier II. 5: 8. 1905. Fig. 27. Fig. 28.

Plants tufted; rhizome oblique, short-creeping, 1.5-4.5 cm in diameter including the scale cover; scales linear-lanceolate, reddish-orange to orange-brown, to 1.3 cm long; phyllopodium 1 cm long covered by dense mass of scales; aerophores visible and bilateral on the phyllopodium; fronds clumped, 6.5-112 x 1.5-7 cm; stipe 1.5-15 cm long, stramineous, terete; stipe scales reddish-orange to reddish-brown, subulate, densely to widely spreading on the stipe and midvein, to 0.5-0.7 cm long, also with dense, erect, branched capitate glandular hairs on the stipe and midvein; blade oblanceolate to linear-lanceolate, base rounded, attenuate-cuneate, apex long-acuminate; veins free, once or twice furcate, ca. 1 mm apart, at 45°-60° angle to the midvein; hydathodes lacking; midvein with subulate orange scales which are basally broad and mixed with many capitate glandular hairs; blade scales golden-yellow, fine, 1 mm long, spreading on both surfaces but more densely concentrated on the abaxial surface, also with conspicuous, simple or branched, capitate glandular hairs; margin with dense orange to yellow subulate scales; fertile frond shorter than the sterile, narrower, lanceolate to linear-lanceolate with a noticeable sterile margin, 7-15 cm long, 1.2-2.6 cm broad;

stipe longer than the sterile, 5-18 cm long; scales lacking on abaxial surface; spores 21.0-31.5 µm in length with broad and smooth ridges and conspicuous fine perforations on the central surface.

On tree trunks in montane rain forest or evergreen cloud forest, common in eastern and central Costa Rica at 1000-2400 m elevation.

Key to the varieties of _E. auripilum_

1. Sterile frond oblanceolate, 6.5-70 x 1.5-7 cm; stipe sparsely scaly; scales 0.5 cm long, orange-brown... 3a. _E. auripilum_ var. _auripilum_

1. Sterile frond linear-lanceolate to lanceolate, 25-112 x 2-6 cm; stipe densely scaly; scales 0.7 cm long, orange to reddish-orange................ 3b. _E. auripilum_ var. _longipilosum_

3a. _Elaphoglossum auripilum_ Christ var. _auripilum_

Rhizome clothed with lanceolate, entire, reddish-orange, lustrous scales up to 2.5 cm long; frond clumped, 6.5-70 x 1.5-7 cm; stipe 15 cm long, stramineous, with reddish-orange to reddish-brown subulate scales up to 0.5 mm long; blade oblanceolate, base attenuate to slightly rounded, apex acuminate; veins evident, running at 60° angle to midvein; fertile fronds considerably shorter than the sterile, but longer-stiped and somewhat narrower, lanceolate with a noticeable but narrow, sterile, cartilaginous margin; scales lacking on abaxial surface and scattered on the adaxial side; spores 21.0-31.5 µm in length with broad, smooth ridges and conspicuous fine perforations on the central surface.

Epiphyte of cloud forests at 1000-2400 m elevation.

TYPE: Costa Rica. In 1903, *Wercklé s.n.* (HOLOTYPE: P!; ISOTYPE: P!).

DISTRIBUTION. Costa Rica and western Panama.

OTHER SPECIMENS EXAMINED: COSTA RICA. Prov. Cartago: Sta. Clara de Cartago, *Maxon & Harvey 8184* (US); Carpinteria, *Brade 276* (NY); S of Cartago, highest Carpinteria, *Stork 1370* (MICH, UC); *Standley 35571* (US); El Muñeco, on the Río Navarro, *Standley 51767* (US); vicinity of Orosí, *Standley 39876* (US). Prov. Heredia: Vara Blanca, between Poás and Barba volcanos, *Maxon & Harvey 8348* (US); from Vara Blanca (between Poás and Barba volcanos) to La Concordia, *Harvey 8443* (US); vicinity of Coliblanco, *Maxon 275* (NY) between Poás and Barba volcanos, *Scamman 7161* (GH); Finca La Selva, pendiente north del Volcán Barba, *Jiménez 7900* (NY); Cerro de las Caricias, north of San

Isidro, *Standley & Valerio 52258* (US); Prov. Puntarenas: Monte Verde, *Seidenschnur 13* (NY). San José: vicinity of La Palma, on road to La Hondura, *Maxon & Harvey 8184* (US); *Maxon 402* (NY, US); *Scamman 7700* (US); La Palma, *Standley 38187* (US); *Valerio A92* (US); ca 1.5 km west of El Alto de la Palma, toward Cerro Zurquí, *Kimnach 59.042.1* (US); ca. 10 km N of San Rafael de Heredia on Volcán Barba, *Mickel 2657* (NY). PANAMA. Prov. Chririquí: 10 miles above El Boquete, *Killip 5298* (US); along Río Caldera, 1 to 2 miles above El Boquete, *Killip 5014, 5030* (both US); 10 miles above El Boquete, *Killip 5262, 5277* (both US); upper Caldera, western above El Boquete, *Killip 5369* (US); between Alto de las Palmas and top of Cerro de la Horqueta, *Maxon 5512, 5522* (both US); El Boquete, *Maxon 5035, 5036, 5239* (all US).

This variety is well distinguished by the short but very conspicuous orange scales that cover the rhizome as well as the petiole and blade. An important field character is the viscosity of its abundant glandular hairs.

3b. *Elaphoglossum auripilum* Christ var. *longipilosum* Atehortúa, var. nov.

A. var. *auripilum* fronde sterile lineari-lanceolato 25-112 x 2-6 cm (nec oblanceolato 6.5-70 x 1.5-7 cm), stipite dense (nec dissite) squamoso, squamisque 7 mm longis aurantiacis vel rubro-aurantiacis (nec 5 mm longis bruneo-aurantiacis) diversum.

Rhizome short-creeping clothed with lanceolate, entire, reddish-orange, lustrous scales up 1 mm long; fronds clumped 2.5-112 x 2-6 cm; stipe 3-15 cm long, clothed with reddish-orange subulate scales up to 0.5 mm long which run throughout the midvein; blade linear-lanceolate; apex acuminate, base rounded to slightly attenuate; veins evident, running at 60° angle to midvein; fertile fronds considerably shorter than the sterile, longer-stiped, somewhat narrower, lanceolate to linear-lanceolate with a noticeable but narrow sterile cartilaginous margin; scales lacking on abaxial surface and scattered on the adaxial side; spores 22.7-29.5 µm in length with broad, smooth ridges and conspicuous, fine perforations on the central surface.

Epiphyte of cloud forests at 1000-1800 m elevation.

TYPE: COSTA RICA. Prov. Puntarenas: Bob Wilson's finca near San Vito, 1000-1400 m elevation, 22 Aug 1965, Croat 863 (HOLOTYPE: MO; ISOTYPE: MO).

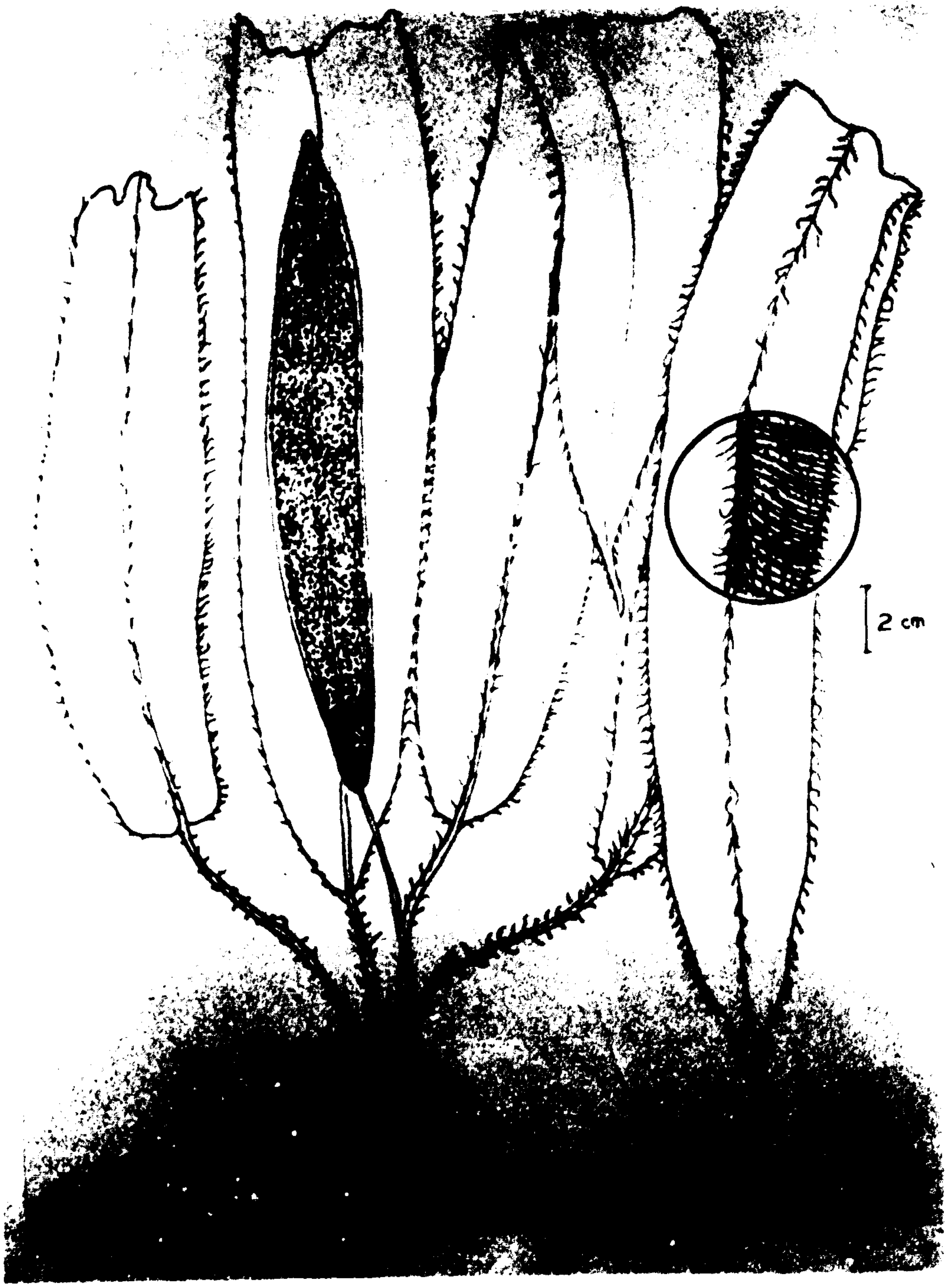
DISTRIBUTION. Costa Rica.

Other specimens examined: COSTA RICA. Prov. Cartago:

Pejibaye, *Lankester 829* (US); Orosí, Finca del Dr. Valverde, *Brade 16813* (P). Puntarenas: San Vito: 5 km S of San Vito de Java, vicinity of OTS station at Finca Wilson, *Lloyd 4226, 4227, 4242* (all NY); *Seidenschnur 132, 135, 150, 161, 185, 200* (all NY); *Raven 21966* (F, MO); *Mickel 3098* (NY).

This variety can be distinguished from *E. auripilum* var. *auripilum* by its larger size, longer lustrous, reddish-orange, subulate scales which densely cover the stipe and midvein, and conspicuous, large, branched, capitate glandular hairs. This is a morphological variety rather than a geographical or ecological variety.

Fig. 27. Habit of _E. auripilum_.



2 cm

Fig. 28. Geographical distribution of E. auripilum var. auripilum, E. auripilum var. longipilosum, E. cubense, and E. backhousianum. Maps. 3-4.

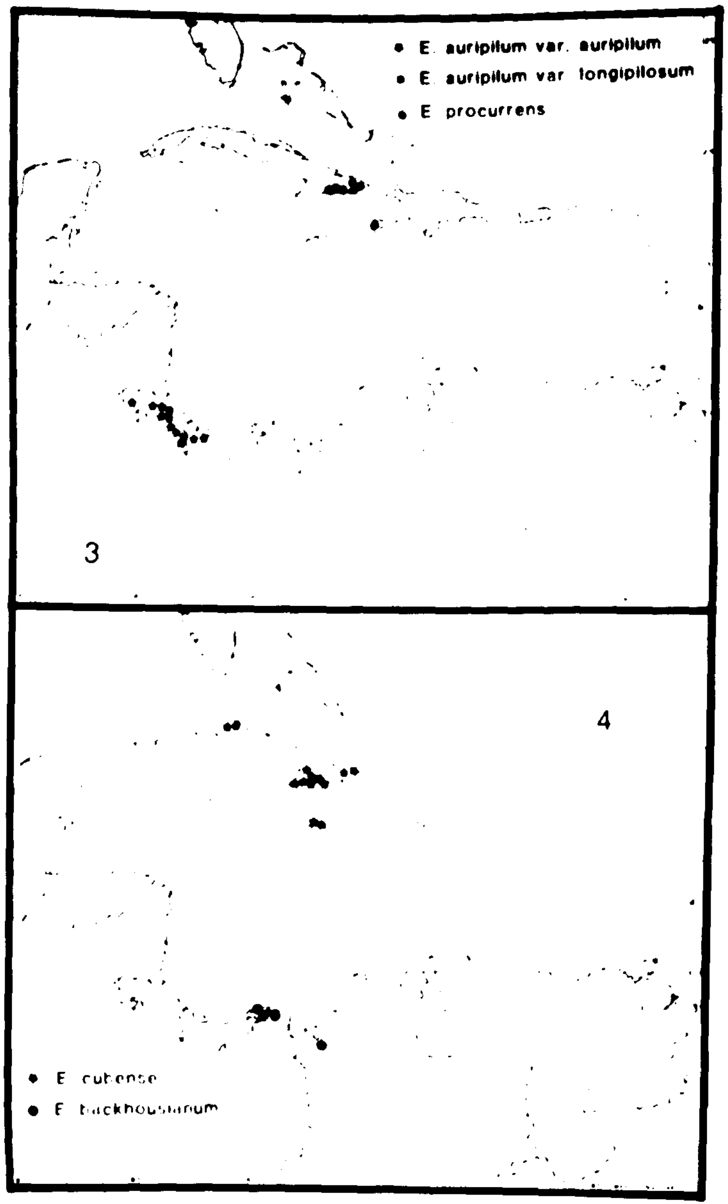
● E. auripilum var. auripilum
● E. auripilum var. longipilosum
● E. procurrens
3
4
● E. cubense
● E. backhousianum

Figure 28

4. Elaphoglossum backhousianum Moore, Gard. Chron. n.s. 17: 672, f. 103-105. 1882. Fig. 28. Fig. 29.

Plants tufted; rhizome stout, decumbent, short-creeping, densely scaly, 1-4.5 cm in diameter including the scale cover; rhizome scales golden-yellow, lustrous, linear-lanceolate, to 3 cm long, entire; phyllopodium very short (0.5-0.8 cm long) and unconspicuous, covered by dense mass of scales; aerophores bilateral to the phyllopodium like long stripes; fronds clumped, 34-70 x 5.5-10.0 cm; stipe short, woody, stout, brown and densely scaly, to 4 mm diameter, 3.5-4.5 cm long; scales of the stipe yellow-brown to dark brown toward the midvein, thin, subulate lanceolate with abruptly and conspicuously expanded base and laciniate margin, to 5 mm long and highly concentrated on the abaxial base; blade smooth, subcoriaceous to coriaceous, oblong-lanceolate, apex acute, base rounded, the costa prominent, which is rounded on the abaxial side and densely scaly; subulate scales abruptly broad at the base with a laciniate margin, reddish-brown to dark brown, mixed with minute, brown branched glandular hairs; margin decorated with black to dark brown subulate scales similar in size and shape to those of the midvein; veins free, once or twice forked, 1.5 mm apart, running at 70°-80° angle to midvein; hydathodes lacking; blade scales lacking except on the midvein and margin; fertile frond much smaller than the sterile, narrowly linear-oblanceolate, attenuate both at the apex and decurrent base, adaxially thickly sprinkled with deciduous dark subulate scales; stipe twice as long as that of the sterile frond, to 5 cm long, scales of the stipe and costa very dark brown; scales lacking among the sporangia; spores 24.5-33.3 um with smooth narrow ridges which surround irregular areoles.

On tree trunks in wet tropical forest at 150-1500 m elevation.

TYPE: MEXICO (?). Introduced with orchids by Backhouse and Son (HOLOTYPE: K!).

DISTRIBUTION. Panama and western Colombia.

OTHER SPECIMENS EXAMINED: SOUTH AMERICA. COLOMBIA, Dpto. Chocó: slopes and ridges of Loma del Cuchillo, 15 km SW of Chigorodó, Lellinger & de la Sota 6490 (COL, US); CENTRAL AMERICA. PANAMA. San Blas: El Llano-Cartī road, 13 km from El Llano at the junction with the Pan-American hwy., Skog & Folsom 4163 (MO). Prov. Colón: Sta. Rita ridge at end of road from trans isthmian hwy., ca. 10 miles from hwy., Porter et al. 4791, 4828 (both MO); Sytsma 1356 (MO). Prov. Panamá: El Llano to Cartī road, 13.7 km N of Panamerican highway, Folsom 3576 (MO); Cerro Jefe, 10 miles S. of Goofy lake in Cerro Azul, Correa 187 (MO); Correa & Dressler 192 (MO, US); Camino del Llano-Cartī, entre los

14-25 km de la carretera a Chepo, Correa et al. 1886 (US); 14 km above Pan-American hwy., on road from El Llano to Cartí-Tupile, Kennedy 2497 (NY).

This species can be distinguished by the large size and coriaceous texture of the fronds and epecially by the costal and marginal scales which are basally semi-urceolate or abruptly and conspicuously expanded at the base, with a very distinctive laciniate margin.

Although the type specimen is said to come from Mexico, most likely it originated in Panama, or perhaps it was introduced to Mexico and then taken to Kew Garden by Messrs. J. Backhouse & Son. All the collections examined are from Panama and Colombia and match the original description, illustrations made by Moore, and the type collection at British Museum.

Fig. 29. Habit of *E. backhousianum*.

Figure 29

Elaphoglossum backhousianum

5. Elaphoglossum cubense (Mett. ex Kuhn) C. Chr., Ind. Fil. 305. 1905. Fig. 28. Fig. 30.

Basionym: Acrostichum cubense Mett. ex Kuhn, Linnaea 36: 46. 1869.

Plants tufted; rhizome short-creeping, 0.5-1.5 cm in diameter, including the scale cover; scales light brown or golden-brown to yellow, 2-6 x 0.4-0.8 mm at the base, broadly linear to broadly triangular, apex acuminate, base peltate or basifixed, slightly wavy, margin with spaced teeth; phyllopodium weakly defined, to 0.5 cm long; fronds clumped, erect or ascending, 4.8-16.7 x 1.6-4.7 cm; stipe 1.2-6 cm long, sometimes very narrowly winged, covered by tiny glandular hairs and fine, spreading, subulate scales; scales light to reddish-brown, 1.3-5.2 mm long; blade spatulate to oblanceolate, apex acute, obtuse to slightly acuminate, at base gradually attenuate, papyraceous, covered with tiny capitate glandular hairs and subulate scales on either surface, scales often abraded from the surfaces and persistent only on the margin and midvein; veins free, once or twice forked, ca. 1 mm apart; hydathodes present only in juvenile stages; fertile fronds smaller than the sterile; stipe of the fertile frond longer than that of the sterile, 1.3-6.5 cm long; fertile blade 1.6-6.7 x 0.6-1.7 cm, oblanceolate or sometimes linear-lanceolate, apex acute, base long-attenuate; scales lacking among the sporangia; spores 19.2-29.7 µm in length, with fine, very smooth ridges and discrete fine perforations on the surface.

On tree trunks or on rocks and mossy earth banks in wet forest at the upper to middle elevation of 350-1500 m.

TYPE: CUBA. In Cuba orientalis, Wright 1040 (HOLOTYPE: B!; ISOTYPES: BM!, GH!, US!)

DISTRIBUTION. Cuba and Jamaica.

OTHER SPECIMENS EXAMINED: WEST INDIES. CUBA. Prov. Santiago de Cuba: Roche du Chemin du Sommel, Clément 711 (P); Loma de San Juan, El Cobre, Clément 731 (US); El Cobre, Sierra Maestra, Clément 948 (BM, P, US); Loma de Gato, Sierra Maestra, Clément 1247 (BM, US); Loma de Gato and vicinity El Cobre, range of Sierra Maestra, León et al. 9841 (NY,US); Loma de San Juan, Hioram 7016 (US); Oriente: along Río Peladero below aserradero San Antonio de las Cumbres, crest of Sierra Maestra, Morton 9507 (US); Sierra Maestra, region Bayamesa, Morton 9577 (US); Sierra Maestra, finca La Reunion south of Hongolo-Longo, Ekman 7024 (NY, US); Pico Turquino, Acuña 9965 (US). Prov. Sta. Clara: Buenos Aires, Trinidad hills, Jack 8058 (NY); Pinal de Sta. Ana, Eggers 4997 (B). JAMAICA. Vinegar Hill, Watt 3 (P); Pleasant Hill road, Watt 11 (P); Maxon 1526 (US); Maxon 2782 (NY, US); From Morce's

Gap to Vinegar Hill, Maxon & Killip 313 (B, BM, F); Maxon & Killip 1313 (F, NY, US); Underwood 1358 (NY, US); 1526 (US); 2599 (NY); 3259 (NY, US); Hart 168, 2261 (both US); Johnson s.n. (US); Harris 7444 (B, BM, F, NY). Portland Parish: Blue Mountains, near Vinegar Hill, Perkins 1042 (B); without locality, Jenman s.n. (NY), Sherring s.n (US).

This species is similar in appearance to *E. apodum* and *E. auripilum* but differs from them in the peculiar type of rhizome scales, which are broader and have a different type of cells, in the short but distinctive rhizome, and the almost obtuse blade apex.

Fig. 30. Habit of *E. cubense*.

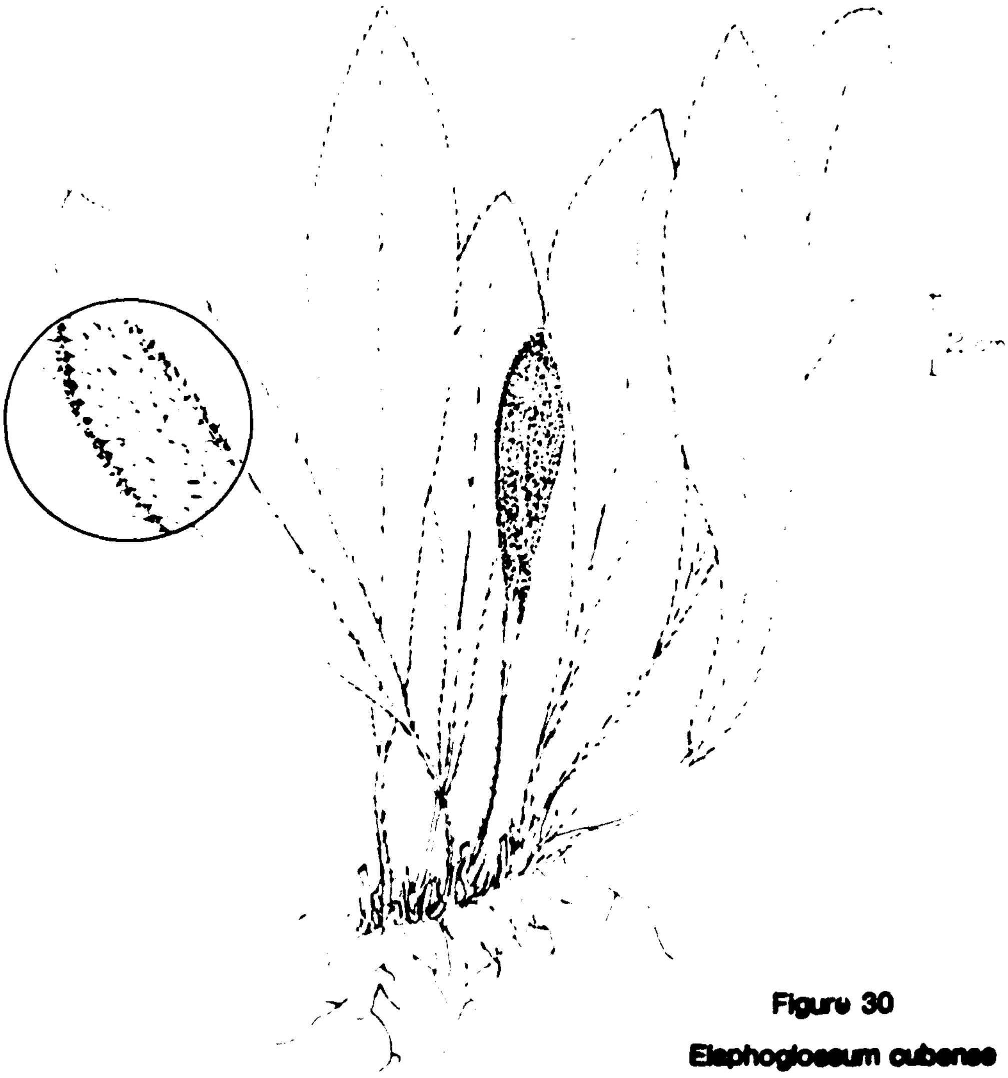


Figure 30

Elaphoglossum cubense

6. Elaphoglossum latum (Mickel) Atehortúa, status nov.

Fig. 26. Fig. 31.

Basionym: Elaphoglossum apodum (Kaulf.) Schott ex Smith var. latum Mickel, Amer. Fern J. 69: 100. 1979.

Plants tufted; rhizome short creeping, up to 6 mm diameter including the scale cover; rhizome scales orange-reddish brown, entire, 2.5 cm long; phyllopodium short (0.5-1.0 cm); fronds clumped, 25-48 x 4.5-5.7 cm; stipe nearly lacking, to 1 cm long, stout, clothed with orange, spreading subulate scales, and minute glandular hairs; blade oblanceolate, papyraceous to coriaceous, base cuneate, narrowing very gradually to somewhat abruptly, apex long-acuminate to cuspidate; veins free, once or twice forked, ca. 1 mm apart, running at 60°-70° angle to midvein; hydathodes lacking, blade scales subulate, orange, especially concentrated on the midvein and margin, some on abaxial blade surface, very sparse on adaxial surface; blade also with minute, erect glandular hairs; fertile fronds much smaller than the sterile ones, with long linear orange scales on the abaxial midvein, none among the sporangia; spores 22.7-31.5 μm in length, with low broad ridges that surround an areole covered by fine perforations.

On tree trunks or wet rocks, in wet tropical rain forests at 20-270 m elevation.

TYPE: GUATEMALA. Dpto. Alta Verapaz: along route no. 5 between Semococh and La Laguna on road to Chajmayic, epiphyte on trunks, 500 m elevation, 10 May 1942, Steyermark 46368 (HOLOTYPE: F!; ISOTYPE: US!).

DISTRIBUTION: mainly in Central America and northern South America.

OTHER SPECIMENS EXAMINED: WEST INDIES. Dominican Republic. Prov. Azua: Cordillera Central, San Juan, Loma de Vieja, Ekman 13406 (BM, NY, US). HAITI. Massif des Bahos, Pte. Riv. de l'arbibomte, road to Perodu, Ekman 3489 (B, US). CENTRAL AMERICA. COSTA RICA. Prov. Puntarenas: Osa Penninsula, east of OTS station, Lloyd 4148 (NY); 15 km of OTS station, on road to Pacific Ocean, Lloyd 4159 (NY); 17 km south of OTS station, on road to Pacific ocean, Lloyd 4162 (NY); Tropical Science Center field station, SW of Rincõn de Osa, Seidenschnuer 108, 109 (both NY); GUATEMALA. Dpto. Alta Verapaz: vicinity of Cubilquitz, 1.5-2 miles south of Cubilquitz, Steyermark 44475 (F, US); bei Cubilquitz, von Tuerckheim II 1465 (P); Cubilquitz, von Tuerckheim 8351 (US). Dpto. Izabal: along rīo Frio and tributaries, Steyermark 41554 (F, US). Dpto. de Petēn: Chanchacan, Lundell 16456 (US).

HONDURAS: Dpto. Atlántida: vicinity of San Alejo, at the base of hills south of San Alejo near río San Alejo, Standley 7679 (F); Lacentilla valley, near Tela, Standley 52981 (F, US); Chickering 109a (US). PANAMA. Prov. Coclé: El Valle de Antón forest, Alston 8704 (BM). Prov. of Colón, forest around Porto Bello, Maxon 5820 (US); Sta. Rita ridge, end of road of Transisthmian Highway, ca. 10 miles from hwy., Porter et al. 4793 (MO). Prov. Panamá: Cerro Jefe, 10 miles S of Goofy lake, Cerro Azul, Correa & Dressler 186 MO, US); Canal Zone, near Río Medio, from top of tree, Miller 1722 (US); summit of Cerro Campana, Porter et al. 4937, 4938 (both MO).

SOUTH AMERICA. COLOMBIA. Dpto. Chocó: upper río Truandó, 2 km Sw of the confluence of the río Nercua near the MADUREX camp, Lellinger & de la Sota 571 (COL, US); 8 km from Puerto Mutis (Bahía Solano), along the road to El Valle, Lellinger & de la Sota 106 (COL); Truandó falls, Schott 85 (F, NY). Dpto. Magdalena: Sta. Marta, H. H. Smith 2688 (BM, NY). ECUADOR: Prov. Esmeraldas, 8/1904, Sodiro s.n. (B, P, US); San Antonio, Cachaby, 8/1904, Sodiro 13 (B, P, US); Prov. El Oro: 11 km west of Pinas on new road to Sta. Rosa, Dodson et al. 9143 (MO). Prov. Pichincha, froest at the confluence of rios Toachí and Pilatón, Bell 244, 272 (both BM); Sodiro 5 (BM); Sodiro s.n. (P); Centinella, Cantón

Sto. Domingo, km 12 E of Patricia Pilar, *Dodson et al. 7246* (US); path following ridge line at El Centinela at crest of Montañas from road to Patricia Pilar to 24 de Mayo at km 12, Patricia road is at km 45 on road to Sto. Domingo to Quevedo, *Dodson & Gentry 10346* (MO); Sto. Domingo de los Colorados, 37 km S of Sto. Domingo, *Pennington 46 SD* (NY).

This species is very similar to *Elaphoglossum apodum* and *E. raywaense* but differs from them in the distinctive petiolar scales which are abruptly broad at the apex, in the large fronds with cuspidate apex, and the more colorful rhizome scales.

Fig. 31. Habit of E. latum.

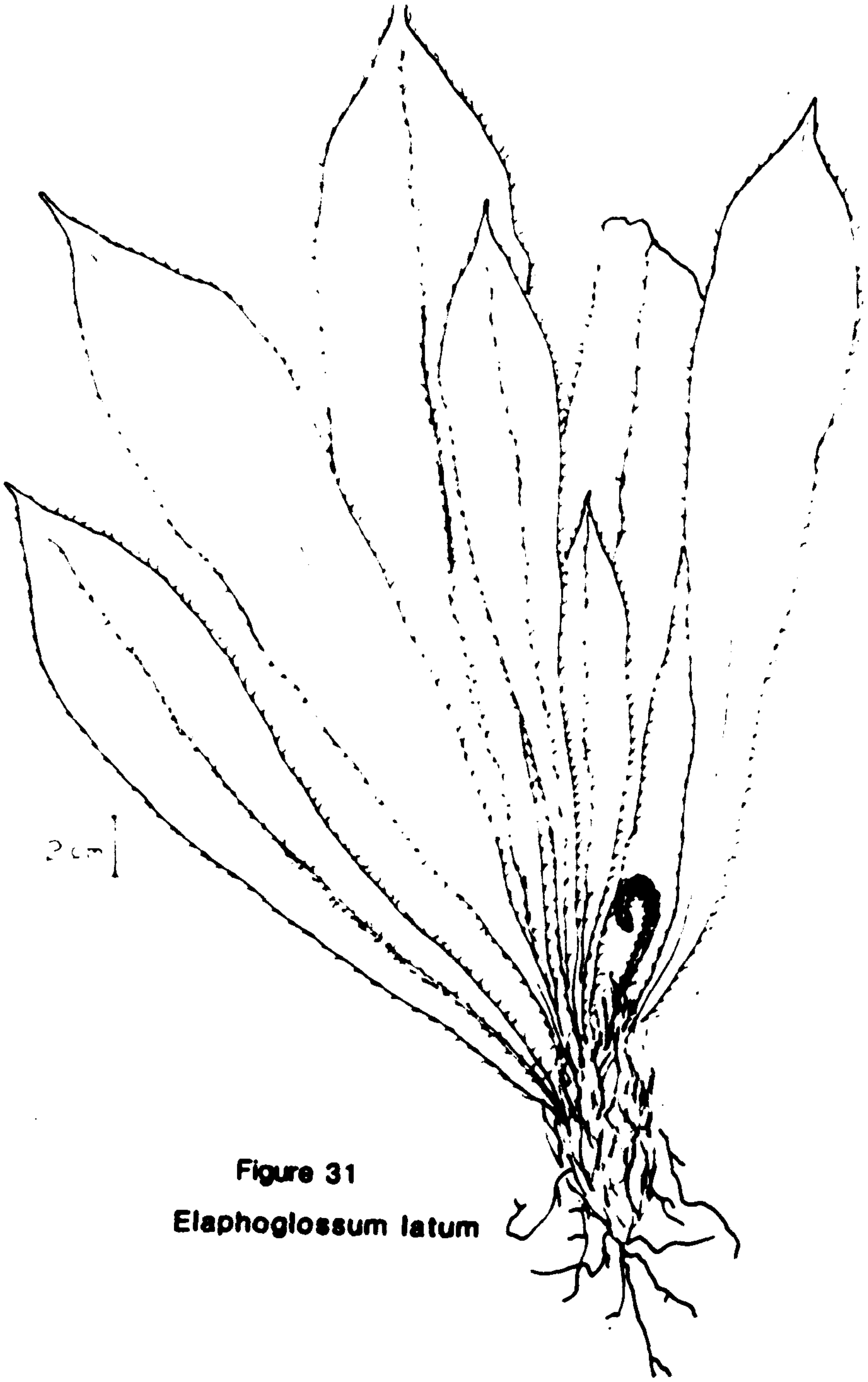


Figure 31
Elaphoglossum latum

7. *Elaphoglossum procurrens* (Mett. ex D. C. Eat.) Moore, Ind. Fil. 365. 1862. Fig. 28. Fig. 32.

Basionym: *Acrostichum procurrens* Mett ex D. C. Eat., Mem. Amer. Acad. Arts. n.s. 8: 194. 1860.

Plants small; rhizome long-creeping, filiform, scaly, 0.5-1.5 mm in diameter, which bears fronds from 0.6-1.5 cm apart in an alternate pattern, somewhat glutinous; scales lustrous, reddish-brown to yellow, lanceolate, entire, appressed to slightly spreading, 3 mm long; phyllopodium short (0.2-5.0 mm) black to dark brown, sometimes inconspicuous or lacking, usually covered by scales; fronds solitary, 1-12 x 0.6-1.8 cm; stipe briefly alate, scaly, distant, mostly 0.5-2 cm or more apart; stipe scales yellow-brown to yellow, subulate, densely to widely spreading, to 0.5 mm long, mixed with scattered, minute, erect glandular hairs, which run along the midvein; blade spatulate to obovate-lanceolate, or elliptic when young, apex obtuse, base broadly cuneate to long-decurrent; veins sometimes evident, free, commonly once furcate, ca. 1 mm apart, running at 60° angle to midvein and ending a little before the margin; hydathodes lacking; midvein with subulate yellow to yellow-brown scales mixed with capitate glandular hairs; margin sometimes crenate and decorated with yellow-orange subulate scales similar in size and shape to those of the midvein; fertile frond shorter than the sterile; blade entire, obovate-lanceolate to elliptic, 2.5 x 1.0 cm, with a noticeable sterile margin; scales lacking among the sporangia; spores 26.3-33.3 µm in length, with narrow ridges surrounding a central area covered by fine and conspicuous perforations.

On tree trunks in wet lower montane and tropical rain forest at 150-800 m elevation.

TYPE: CUBA. Oriente: prope villam Monte Verde dictam, Cuba Orientalis, Jan-July 1856-1859, Wright 793 (HOLOTYPE: YU!; ISOTYPES: B!, BM!, GH!, MO!, P!, US!).

DISTRIBUTION. Eastern Cuba and Haiti.

OTHER SPECIMENS EXAMINED: WEST INDIES. CUBA. Pinal de San Juan, Eggers 5168 (B, P). Guantánamo: La Prenda, Eggers 5328 (B, (NY); Hioram & Maurel 2428 (P, US). Oriente: Pinales de Monte Verde to falls of Río Palenque, Shafer 8862 (NY, US); Yateras, Monte Verde, Maxon 4334 (BM, GH, NY, US). HAITI. Massif de la Hotte: western group, Jérémie between source Cahonane and la Source Chaude, Ekman 10259 (BM, F, GH, US). St. Louis du Sud, slope of Bommer Carré, Ekman 9212 (BM).

This species is unique among the species of this complex in the slender, long-creeping rhizome and broadly appressed rhizome scales. However in gross morphological appareance it somewhat resembles <u>E. cubense</u>.

Fig. 32. Habit of E. procurrens.

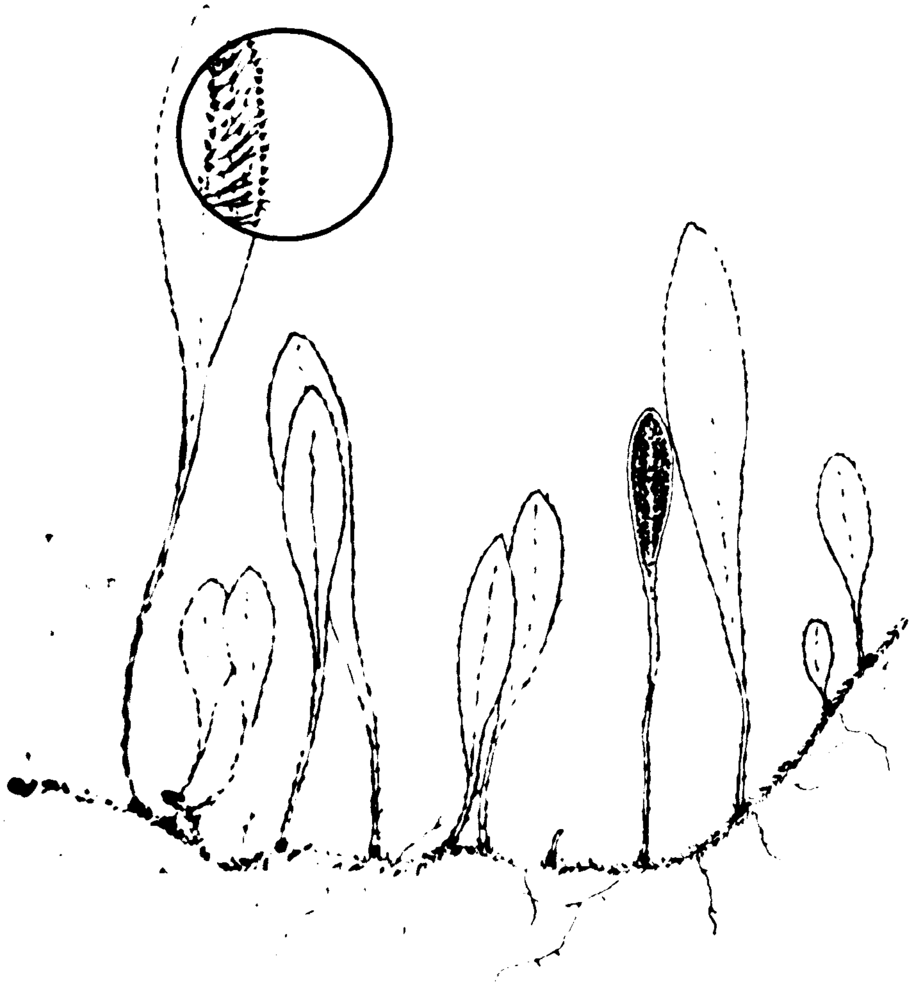


Figure 32

Elaphoglossum procurrens

8. *Elaphoglossum raywaense* (Jenm.) Alston, Bol. Soc. Brot. 2. s. 32. 1958. Fig. 24. Fig. 33.

Basionym: *Acrostichum raywaense* Jenm., Ferns & Fern allies Brit. West Ind. & Guiana 341. 1909.

Syn: *Acrostichum apodum* var. *Sprucei* Baker, in Mart., Fl. Bras. 1 (2): 578. 1870.

Acrostichum apodum sensu Fée, Crypt. Vasc. Brés. 1: 6 1869.

Plants tufted; rhizome short-creeping, stout, 0.5-1.5 cm in diameter including the scale cover; scales linear-lanceolate, wavy, yellow-brown to ferrugineous, lustrous and sometimes resinous toward the tip, 0.5-0.8 x 0.2 mm; phyllopodium present, 0.8 cm long, dark brown; fronds clumped, 18-56 x 2.2-6 cm; stipe almost lacking, giving the appearance of sessile fronds, 0.5-1.0 cm long, covered by dense mass of subulate scales, ferrugineous to stramineous, terete; scales 0.6 cm long, subulate, golden-orange, densely spreading on the stipe and at the base of the midvein, to 0.4-0.6 cm long, also with short, minute, resinous, brown, capitate glandular hairs on the stipe and both flanks of the midvein; blade oblanceolate, membrano-characteous, base long-decurrent, apex acuminate to long-caudate; veins free, once forked, ca. 0.8

mm apart, running at 45° angle to midvein; hydathodes lacking; midvein scales abundant, fine subulate scales, orange to orange-brown, mixed with many short, minute, resinous, capitate glandular hairs; blade scales brown-orange to yellow-orange, fine, 0.5-1.5 mm long, spreading mostly on the upper surface; lamina also densely covered with short, appressed, resinous capitate glandular hairs which are usually oriented toward the margin; margin thick, densely covered by 2 or more rows of fine subulate scales, similar in size and color to those that cover the costa; fertile frond shorter than the sterile, narrower, lanceolate to linear-lanceolate, with a narrow hyaline margin and also basally sterile along the midvein; apex acuminate, base gradually narrow, becoming alate, 27 x 24 cm; stipe about equal to that of the sterile frond; scales lacking among the sporangia; spores 22.7-31.5 μm in length, with rugose ridges which surround central areoles covered by conspicous fine perforations.

On tree trunks in tropical rain forests near streams at 400-1200 m elevation.

TYPE: GUIANA. Region of Mt. Raywa: on upper parts of Isorooroo River, Jenman s.n. (HOLOTYPE: NY!; ISOTYPE: NY!).

DISTRIBUTION. Venezuela, Guianas, Brazil, and Ecuador.

OTHER SPECIMENS EXAMINED: SOUTH AMERICA. BRAZIL. Pará: Tanaii, ad rio Acara, juxta Pará, *Spruce 16* (B, BM, CGE, P); prope San Gabriel da Cachoeira do Rio Negro, Brasilieae borealis, *Spruce 2186* (BM, CGE, P, US); Amazonas: Territorio of Roraima, Serra dos Surucucus, *Prance et al. 10113* (NY). GUYANA: *Jenman 2158* (BG); Basin of Shodikar Creek (Essequibo tributary), *A. C. Smith 3011* (NY); New River, *Guppy G.377* (BM); Sebai creek, Kaitum river, *Fanshawe F.2430* (BM). ECUADOR. Prov. Napo: Parque Nacional Yasuní, Añangu, *Luteyn et al. 8549, 9014, 9112* (all NY); Northwestern Amazon basin, Dureno on Río Aguarico, *Pinkley 482* (COL); San Pablo de los Secoyas, Río Aguarico, *Brandbyge et al. 32531, 32577* (both AAU); Río Cuyabeno, *Brandbyge et al. 33826* (AAU); Prov. Pastaza: Río Bobonaza, near outlet into Río Pastaza, between Destacamento Cabo Pozo and La Roca, *Øllgaard et al. 34926* (AAU); Río Bobonaza, *Øllgaard et al 35254, 35312* (both AAU). FRENCH GUIANA. Oyapock: Oyapock, *Leprieur 58* (P), 244 (US); 1834, *Leprieur 316* (BM, US); 1842, *Mélinon s.n.* (B). PERU. Dpto. Amazonas: Prov. de Bagua, rain forest along quebrada Tambillo, (below km 280 of Marañón above Cascadas, *Wurdack 1989* (NY); valley of Río Marañón above Cascadas de Mayasi near Campamento STte. Montenegro, km 280-284 of Marañón road, *Wurdack 1858* (US). Dpto. Huánuco: Pampayacu, *Kanehira 151* (US); trail along Río

Monzón near Huallaga at Tingo María, Croat 21255 (MO); Tingo María, Allard 20888 (US); Prov. Leoncio Prado: Distrito Rupa Rupa, al este de Tingo María, cerca del Cerro Quemado, Schunke 10164 (MO). Dpto. Junín: Cahuapanas, on Río Pichis, Killip & Smith 26782 (NY, US). Dpto. Loreto: Chacra de César Vela, sudeste de la granja del Sr. Barrera (Aguatia), Coronel Portillo, padre Abad, Schunke 5495 (NY); Balsapuerto (lower Río Huallaga basin), Killip & Smith 24498 (NY, US); Amazonas expedition, Cerro de Ponasa, E. Ule s.n. (B). SURINAM. source of river Litani, Rombouts 871 (US). VENEZUELA. Estado Bolívar: Cerro El Picacho, N of Las Nieves and Las Chicharras, 45 Km N of Tumaremo, vicinity of Deborah, altiplanicie de Nuria, Steyermark 89177 (NY).

In shape of the frond and disposition of the indument some specimens of this species resemble E. apodum. It differs from E. apodum in its apically narrower, darker rhizome scales which appear to be resinous toward the apex (bicolorous), larger fronds with a long-caudate apex, and broader fertile frond with an acuminate apex.

Fig. 33. Habit of E. raywaense.

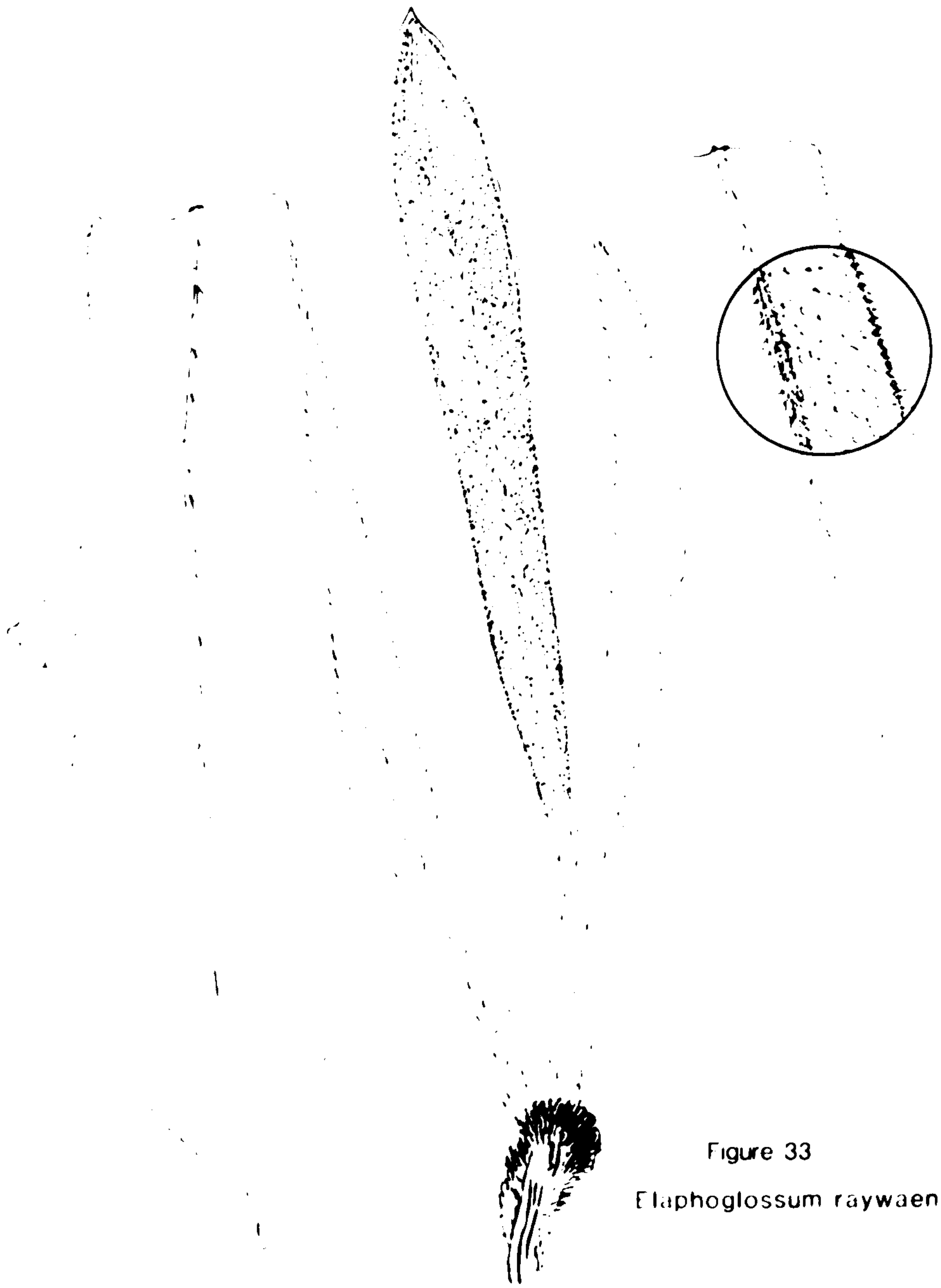


Figure 33

Elaphoglossum raywaense

SPECIES INCERTAE

1. WEST INDIES. CUBA. Oriente: deep ravine on the southern side of the crest of the Sierra Maestra, West of Aserradero, San Antonio de las Cumbres, region of La Bayamesa, 1400-1500 m elevation, 23-24 Jan 1956, Morton 9577 (US). This collection may be a large form of *E. cubense*. However, the sample consists of a single sterile specimen. It can be distinguished from *E. cubense* by its sterile oblanceolate frond, acuminate apex, larger size, (7-36 x 1.2-3.7 cm) and longer stipe (3.5-12 cm long).

2. CENTRAL AMERICA. COSTA RICA. Cocos Island: epiphyte, 80-100 m elevation, 9 March 1964, Fournier 351 (NY); 18 July 1898, Pittier 12359 (US); sea level to 500 m elevation, Gómez 3347 (F, US); along brook flowing into Wafer Bay, 305 m elevation, 19 April 1930, Svenson 403 (UC); 3 Sept 1967, Klawe s.n. (US).

These specimens are very similar to *E. auripilum* and *E. cubense*, but differ in their rhizome scales, petiole length, and altitudinal distribution. Since most of the samples consist only of sterile material, I prefer not to include them with any species until fertil material is available for study. They may represent new species

LIST OF TAXA

1. *E. amazonicum* Atehortúa
2. *E. apodum* (Kaulf.) Schott ex J. Smith

3a. *E. auripilum* Christ var. *auripilum*

3b. *E. auripilum* Christ var. *longipilosum* Atehortúa

4. *E. backhousianum* Moore
5. *E. cubense* (Mett. ex Kuhn) C. Chr.
6. *E. latum* (Mickel) Atehortúa
7. *E. procurrens* (Mett. ex D.C. Eat.) Moore
8. *E. raywaense* (Jenm.) Alston

LIST OF EXCCICATAE

Abbott, W. L. 276 (2)

Acuña, J. 9965 (5)

Allard, H. A. 20888 (8)

Alston, A. H. G. 8704 (6)

Anderson, W. R. et al. 3139 (2)

Balch, A. s. n. (2)

Bell, P. R. 244 (6), 272 (6)

Bernal, H. Y. & A. Sudgen 62 (6)

Brandbyge, J. et al. 32531 (8), 32577 (8), 33826 (8)

Box, H. E. 501 (2), 278 (2)

Brade, A. 276 (3a), 16813 (3b)

Britton, E. G. 2668 (2)

Bües, C. 1737 (1)

Chase, A. 6213 (2)

Chickering, A. M. 109a (6)

Clément, F. 711 (5), 731 (5), 944 (2), 948 (5), 1247 (5)

Correa, M. 187 (4)

Correa, M. & R. L. Dressler 186 (2), 192 (4)

Correa, M. et al. 1886 (4)

Croat, J. B. 863 (3b), 21255 (8)

Crosby, M. R. 2546 (3a)

Dodson, C. H. et al. 7246 (6), 9143 (6), 10346 (6)

Duss, P. 1621 (2), 4321 (2), 4577 (2)

Ekman, E. L. 2102 (2), 2987 (2), 3489 (6), 4729 (2), 5093 (5), 7024 (4), 9217 (7), 10259 (7), 11562 (2), 12857 (2), 13406 (6) 14416 (2).

Eggers, H. F. A. 2745 (2), 4997 (5), 5168 (7), 5328 (7)

Fanshawe, D. B. 5166 (8)

Fredholm, A. 3218 (2)

Folsom, J. P. 3576 (4)

Garnier, G. 290 (2)

Guilding, L. s. n. (2)

Guppy, N. G. L. 377 (8)

Harris, W. 7432 (2), 7444 (5), 7501 (2)

Hatschbach, G. 36206 (1)

Hart, J. H. 117 (2), 168 (5), s. n. (2)

Hioram, Bro. et al. 257 (2), 2428 (7), 4710 (2), 6353 (2), 7016 (5)

Hess, W. E. 216 (2), 355 (2)

Holdridge, L. R. 2199 (2)

Husnot, T. s. n. (2)

Jack, J. G. 8058 (5)

Jenman, D. D. 2158 (8), s. n. (2), s. n. (5), s. n. (8)

Jiménez, A. 790 (3a)

Kanehira, R. 151 (8)

Killip, E. P. 5014 (3a), 5030 (3a), 5262 (3a), 5277 (3a), 5298 (3a) 5369 (3a)

Killip, E. P. et al. 26782 (8), 28498 (8)

Kimnach, M. 59042-1 (3a)

Kennedy, H. 2497 (4)

Klug, G. 3330 (1)

Lankester, C. H. 829 (3b)

Lellinger, D. B. & de la Sota. 106 (6), 571 (6), 649 (4), 1383 (3a)

Lloyd, R. M. 4148 (6), 4159 (6), 4162 (6), 4226 (3b), 4227 (3b), 4242 (3b)

León, Fre. et al. 9841 (5), 10524 (2)

Leprieur, T. 58 (8), 244 (8), 316 (8)

Linden, J. 2156 (2)

Lundell, C. L. 16456 (6)

Luteyn, J. et al. 8549 (8), 9014 (8), 9112 (8)

Maxon, W. R. 402 (3a), 882 (2), 1526 (2), 1740 (2), 1827 (2), 1914 (2), 2248 (2), 2395 (2), 2782 (5), 4071 (2), 4173 (2), 4334 (7), 4335 (2), 5035 (3a), 5036 (3a), 5239 (3a), 5512 (3a) 5522 (3a), 5820 (2), 8520 (2), 8834 (2), 8930 (2), 9138 (2), 9379 (2), 10545 (2)

Maxon, W. R. & A. D. Harvey 7962 (3a), 8184 (3a), 8348 (3a), 8443 (3a)

Maxon, W. R. & Killip. 171 (2), 818 (2), 1313 (5), 1453 (2)

Mélinon, M. s. n. (8)

Mickel, J. T. 2657 (3a), 3098 (3b)

Miller, G. S. 1722 (2)

Morely, B. D. & C. Whiteford 548 (2), 921 (2)

Morton, C. V. 9507 (5), 9577 (5)

Morton, C. & J. Acuña 3194 (2)

Morton, C. V. et al. 1067 (2)

Nicholls, H. A. 193 (2)

Øllgaard, B. et al. 3426 (8), 35254 (8), 35312 (8)

Pennington, C. D. 46 SD (6)

Perkins, J. R. 1042 (5)

Pinkley, H. V. 482 (8)

Pollard, C. L. et al. 152 (2)

Porter, D. M. et al. 4791 (4), 4793 (6), 4828 (4), 4937 (6), 4938 (6)

Prance, G. et al. 10113 (8)

Proctor, G. R. 4125 (2), 5457 (2), 17323 (2), 17759 (2), 25660 (2)

Raven, P. H. 21966 (3b)

Riodoutt, C. A. 11562 (1)

Rombouts, H. E. 871 (7)

Scamman, E. 7161 (3a), 7700 (3a)

Schott, H. W. 85 (6)

Schramm, E. E. 29 (2)

Schunke, J. 5495 (8), 10164 (8)

Seidenschnur, C. 13 (3a), 108 (6), 109 (6), 131d (3b), 132 (3b), 135 (3b), 150 (3b), 161 (3b), 185 (3b), 200 (3b)

Shafer, J. A. 3222 (2), 3714 (2), 3715 (2), 8862 (7)

Sherring, R. V. 130 (2), 357 (2), s. n. (5)

Sintenis, P. 523 (2), 1338 (2), 4277 (2), 6443b (2)

Smith, A. C. 3011 (8)

Smith, A. C. & F. W. Smith 380 (2), 1137 (2)

Smith, H. H. 2688 (6)

Sytsma, K. J. 1356 (4)

Skog, L. E. 4163 (4)

Stork, H. E. & J. P. Folsom 1370 (3a)

Sodiro, A. 5(6), 13 (6), 36 (6), s.n. (8)

Spruce, R. 16 (8), 2186 (8), 4639 (1), s.n. (8)

Standley, P. 7679 (6), 5298 (6), 35571 (3a), 38187 (3a), 39876 (3a), 51767 (3a), 52258 (3a), 52981 (6)

Steyermark, J. A. 41554 (6), 44475 (6), 46368 (6), 89177 (8)

Ule, E. 6893 (8)

Underwood, L. 1330 (2), 1358 (5), 1526 (5), 1589 (2), 2027 (2), 2067 (2), 2599 (5), 2698 (2), 3259 (5)

Underwood, L. et al. 924 (2)

Valerio, M. A92 (3a)

Valeur, E. J. 657 (2)

Von Tuerckheim, H. 1465 (6), 8351 (6)

Walker, T. G. 38 (2)

Watt, M. D. 3 (5)

Werklé, C. s.n. (3a)

Whaston, P. s.n. (2)

Wiles, s.n. (2)

Williams, R. S. 1027 (1)

Wilson, P. 253 (2), 321 (2)

Wilson, K. A. et al. 553 (2)

Wright, C. 793 (7), 967 (2), 1040 (5)

Wurdack, J. J. 1858 (8), 1989 (8)

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