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A TAXONOMIC REVISION OF THE FERN GENUS *CAMPYLONEURUM* (POLYPODIACEAE)

by

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Afhandling indleveret til det Naturvidenskabelige Fakultet ved Aarhus Universitet til bedømmelse for Ph.D. graden

Vejleder: Lektor Benjamin Øllgaard

To my parents, Efrain León and Lucila Bocángel de León, and

to my husband, Kenneth R. Young.

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Note: Nomenclature novelties herein are not presented for purposes of valid publication.

Dansk Sammenfatning

Campyloneurum er en af de få slægter i bregnefamilien Polypodiaceae *s. str.*, der kun forekommer i den Nye Verdens Troper. Slægten blev grundlagt af Prel (1836), på basis af arternes særlige nervation; Presl medregnede både arter med hele og pinnate blade. Definitionen af *Campyloneurum* forblev uændret indtil Tryon & Tryon (1982a) udelukkede de pinnate arter og medregnede en art, der tidligere var henført til slægten *Hyalotrichopteris*.

Nærværende afhandling har til formål at afklare slægtens afgrænsning, og at gøre slægten til genstand for en taxonomisk revision, at definere arterne ved hjælp af morfoloiske karakterer og belyse deres indbyrdes slægtskab.

Omkring 4000 eksemplarer blev unersøgt, især ved Biologisk Institut, Aarhus Universitet (AAU), og ved det Nationale San Marcos Universitet (USM) i Lima, Peru. Mange af disse eksemplarer blev udlånt til projektet fra de følgende herbarier: B, BM, BR, CAY, F, GB, GH, HJBLH, LD, MICH, MO, MU, P, S, UC, US, og W, eller blev undersøgt under besøg på folgende herbarier C, CUZ, F, GH, HUT, K, LOJA, LPB, MO, NY, QCA og UC (herbarieakronymer ifølge Holmgren et al. 1990. Index Herbariorum Part I. 8th ed.).

Campyloneurum er defineret af en speciel (cyrtophleboid) nervation (Kap. III og VIII); det vigtigste traek ved denne er, at de costale areoler har en fri udløbende nerve, og at de extra-costale areoler har (1-) 2-5 fri udløbende nerver. Slægten omfatter 47 arter og 4 varieter (Kap. VIII), både arter med hele og med pinnate blade, forunden en art, den har været henført til slægten *Hyalotrichopteris*.

Slægtens morfologi gennemgås, og visse kritiske karakterer, såsom behåring, sporangier og parafyser, beskrives for første gang (Kap. IV). Slægten deler mange karakterer med andre slægter i Polypodiaceae. Stænglen (rhizomet) hos *Campyloneurum* er krybende, med skæl og

dorsiventralt arrangerede rødder og blade. Rhizomskæl har spillet en vigtig rolle for mange Polypodiace-slægters taxonomi, fordi de leverer mange konstante bygningstræk. Dette gælder også *Campyloneurum*, hvor materiale uden stængel ofte ikke kan bestemmes til art. Sterile og fertile blade er ens i form og størrelse; de er i reglen anbragt i to rækker langs stænglen, og falder af ved et distinkt løsningslag. Bladpladen er hel hos de fleste arter; kun *C. decurrens* og *C. magnificum* har fjersnitdelte bladplader. Med undtagelse af en enkelt art, *Campyloneurum aphanophlebium*, beskrives arterne som glatte. Imidlertid er der her påvist tre typer behåring hos flere arter, samt tidligt affaldende skæl. Fuldt udvoksede blades nervation kan inddeles i 4 typer, der danner grundlag for en inddeling i artsgrupper (Kap. VIII). Sporehushobene er afrundede eller elliptiske, uden indusier, og 1-2 (-3) mm i diameter. Sori sidder på bladundersiden, på afrundede eller elliptiske områder i niveau med bladoverfladen, oftest i to rækker mellem primærnerverne, men undertiden tre eller flere hos *C. brevifolium* gruppen, og undertiden i en enkelt række hos *C. anetioides* og *C. falcoideum.* Forekomsten af parafyser, organer der kan findes blandt sporangierne, blev undersøgt hos alle arterne. De findes hos 9 arter, og er gerne mindre end sporangierne, og tyndere end sporangiestilkene; der findes to typer: simple og dendritiske. Sporerne er ellipsoidale, de aborterede dog mere afrundede og kollaberede, 40—100 x 30—60 µm; deres overflade er forsynet med spredte sfæriske legemer eller granuli under under et tyndt perispor. Exosporet er mere eller mindre vortet.

Campyloneurum er tidligere anset for at stå nærmest de andre neotropiske slægter *Microgramma* og *Niphidium*, men anses her for at stå særlig nær *Pleopeltis* (Kap. IV).

De fleste af arterne hører til i skov-vegetation (Kap. VI), især stedsegrøn skov, men *C. xalapense* findes i delvis løvfældende skov i Mexico. De fleste arter forekommer på mange forskellige mikrohabitater på forstyrrede eller uforstyrrede skov-arealer. Seksogtyve arter hører til på skyggede og fugtige mikrohabitater i sluttet skov. De fleste af disse arter er epifyter på lavtsiddende grene eller på træstammer i de lavere etager af skoven. Nitten arter forekommer almindeligvis i lysåbne skove eller rydninger, på klipper, i klipperevner og i skovkanter. De er bredt tilpassede og kan vokse som epifyter, på jorden og klipper (f.eks. *C. cochense, C. ensifolium*). Det er ikke overraskende at finde de videst udbredte arter blandt disse 19 (f.eks. *C. angustifolium* og *C. phyllitidis*). De fleste arter vokser i højdeintervallet 1000—4500 m o.h. Kun syv er almindelige under 1000 m o.h. De fleste arter har en vid højde- og nord-syd-udbredelse. Seksogtyve arter har en højdeudbredelse på over 1000 m; de geografisk vidtudbredte arter er blandt disse arter (f.eks. *C. angustifolium, C. brevifolium, C. phyllitidis*). Tilsyneladende har de arter, der har en højdeudbredelse på under 1000 m, også en relativt begrænset geografisk udbredelse; de kræver derfor særlig bevågenhed i forbindelse med naturbevarelse (Kap. VII).

De fleste af arterne forekommer i mere end 3 lande, og the artsrigeste områder er i de tropisk sydamerikanske bjerge, mens de artsfattige områder er i subtroperne, på små øer og i ikke-montane områder.

I fem hovedområder er slægten særlig rigt repræsenteret: Mexico, Mellemamerika, Andes, Brasilien, og Caribien. Den Mexikanske region omfatter 12 arter, hvoraf to er endemiske; regionens affinitet er nærmest til Mellemamerika og den Caribiske region. Den Mellemamerikanske region har 16 arter, hvoraf en er endemisk; denne regions affinitet er nærmest til

den Mexicanske region, Andes, og den Caribiske region. I Andes forekommer 35 arter og 14 af disse er endemiske. Det nordlige Andes har 32, det centrale Andes 23 arter og det sydlige Andes kun fire arter. I den Brasilianske region findes ni arter, hvoraf fem er endemiske; denne regions største affinitet er til Andes. Kun tretten arter forekommer i de sydamrikanske subtroper; fire af disse arter forekommer også i de nordamerikanske subtroper, og de er alle vidtudbredte. I Caribien har de Store Antiller 10 arter, hvoraf 2 er endemiske, mens de Små Antiller kun har fire arter, alle vidtudbredte. Denne behandling af slægten *Campyloneurum* er baseret på herbarie- og feltstudier, og den morfologiske artsopfattelse er anvendt. Kategorien varietet er anvendt i to tilfælde, for mindre distinkte elementer i *C. amphostenon* and *C. nitidissimum.* To nye arter er beskrevet: *C. ensifolium* og *C. oellgaardii*.

Jeg anvender en uformel inddeling af slægten i ti artsgrupper (Kap. VIII); arterne i hver gruppe har en række fælles morfologiske karakterer og voksestedspræferencer, og formodes at repræsentere selvstændige udviklingslinier i slægten. I alfabetisk orden er de:

1) *C. amphostenon* gruppen, bestående af *Campyloneurum amphostenon, C. asplundii, C. chlorolepis, C. densifolium, C. fallax, C. lorentzii, C. rigidum* og *C. solutum*;

2) *C. angustifolium* gruppen, der består af *C. aglaolepis, C. angustifolium, C. angustipaleatum, C. angustifoliaceus, C. austrobrasilianum*, *C. centrobrasilianum*, og *C. ensifolium*.

3) *C. brevifolium* grupppen, der består af *C. brevifolium, C. pascoense, C. nitidissimum* og *C. tucumanense*;

4) *C. magnificum* gruppen, bestående af *C. decurrens* og *C. magnificum*;

5) *C. aphanophlebium* gruppen, bestående af *C. anetioides* og *C. aphanophlebium*;

6) *C. phyllitidis* gruppen, med fire arter: *C. abruptum, C. nitidum, C. phyllitidis, C. tenuipes* og *C. wurdackii*;

7) *C. repens* gruppen, bestående af *C. acrocarpon, C. fasciale, C. fuscosquamatum, C. minus, C. ophiocaulon* og *C. repens*;

8) *C. sphenodes* gruppen, med *C. sphenodes, C. chrysopodum, C. coarctatum, C. falcoideum, C. inflatum, C. sublucidum*, og *C. oellgaardii*;

9) *C. vulpinum* gruppen, med *C. vulpinum, C. cubense,* og *C. oxypholis*, og

10) *C. xalapense* gruppen, der består af *C. cochense, C. costatum* og *C. xalapense*.

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I. **INTRODUCTION**

Campyloneurum is one of the few genera of the Polypodiaceae (s. str.) restricted to the New World. This genus was erected by Presl (1836), who included in it both entire and one-pinnate leaved species, and who defined it by its reticulate venation . The definition of *Campyloneurum* went unchanged until Tryon & Tryon (1982a) proposed the exclusion of the one-pinnate species and the inclusion of the genus *Hyalotrichopteris* based on soral position.

In this study, *Campyloneurum* is again defined by its reticulate areolate venation. Important characters of the venation are the presence of costal areoles carrying one excurrent free veinlet, and of non-costal areoles carrying (1-) 2-5 free excurrent veinlets.

Most species of *Campyloneurum* were described during the middle of the 19th and the beginning of the 20th century. Circumscriptions of the species were based on foliar morphology and/or venation (cf. Mettenius, 1864; Hooker, 1864; Hooker & Baker, 1874; Christ, 1902; Rosenstock, 1909; Hieronymus, 1904). During that time no monographic treatement was attemped for the genus, although accounts for number of species in the genus were available because of the work of Fée (1852), Moore (1861), and Smith (1875), and also because of floristic studies done by Mettenius (1864), Sodiro (1893), and Christ (1902).

Difficulties at the species level were indicated by Fée (1852, 1864) and Smith (1875). Both authors mentioned problems in defining the species based on leaf morphology (Fée, 1852, 1864) and/or pattern of venation (Smith, 1875).

During the last 30 years, several pteridologists have contributed to a better understanding of species circumscription in *Campyloneurum*. Sota (1960) treated the meridional South American species. He was one of the first pteridologists to recognize the value of stem scale characteristics in the genus. He recognized 36 species. Later, Meyer (1964) made a first attempt to review the genus; based mostly on foliar morphology, she recognized 29 species. Lellinger (1977, 1984) called attention to several Andean and Central American species when he made new nomenclatural combinations. Recently Lellinger (1988) presented a general overview of the genus, wherein he recognized 50 species, including several new species, based on characters found on the scales of the stem (cf. Sota, 1960). Although there has been an improvement on the use of more reliable characters for species limitation, controversy in the number of species recognized in the genus, and in their nomenclature has persisted. For these reasons, a monographic revision was badly needed in the genus.

II. **MATERIALS AND METHODS**

MATERIALS

About 4000 specimens were examined at the Herbarium of the Institute of Biological Sciences of the University of Aarhus (AAU), Aarhus, Denmark, and the Herbario San Marcos (USM) in Lima, Peru. Loans were obtained from the following herbaria: B, BM, BR, CAY, F, GB, GH, HJBLH, LD, MICH, MO, MU, P, S, UC, US, and W, or were seen on visits to B, C, CUZ, F, GH, HUT, K, LOJA, LPB, MO, NY, QCA and UC (abbreviations according to Holmgren et al., 1990. Index Herbariorum Part I. 8th ed.).

Live material from five taxa (*Campyloneurum amphostenon*, *C. angustifolium*, *C. nitissimum* var. *latior*, *C. phyllitidis*, and *C. repens*) was examined for morphological and cytological studies. These plants were cultivated in Lima and Aarhus. The specimens cultivated in Lima, consisting of four of the species (excluding *C. angustifolium*), came from my collection in Peru, while the specimens cultivated in Aarhus (*C. angustifolium* and *C. phyllitidis*) were collected by Danish botanists in Ecuador.

METHODS

Measurements of macroscopic characters (stem diameter, distance between phyllopodia, petiole length and width, lamina width and length, angle of divergence of the primary veins, and the distance between primary veins) were made on five to thirty complete representative herbarium specimens of each species.

Microscopic characters (width and length of the stem scales, width of the cell walls of selected representative stem scales, width and length of

the cellular lumen of stem scales, sporangia length, number of cells of the sporangial annulus, width and length of the spore) were measured on ten representative specimens from each species using a compound microscope.

Material for anatomical observations was obtained from both live and herbarium specimens. Sections were made from the roots, stems, and leaves of seven species: *Campyloneurum amphostenon*, *C. angustifolium*, *C. aphanophlebium*, *C. densifolium*, *C. fuscosquamatum*, *C. sphenodes*, and *C. vulpinum*. Dried material was rehydrated in an aqueous solution of ethanol before it was embedded in paraffin. Sometimes before embedding, the samples required extraction of air bubbles using a vacuum chamber. Sections were made using an automatic microtome. For fresh material, small samples were first cut using a freezing microtome; then the sections were dyed with Chlorazol-black and mounted in Euparal (cf. Radford et al. 1964). Stem indument was obtained from herbarium specimens. Scales were mounted directly in Hoyer's solution or Glycerine jelly. Some mounted samples in Hoyer's solution were left in the oven at 60°C for two days allowing liberation of air bubbles from the sample.

Foliar epidermal samples were obtained from herbarium specimens for indument and stomata examination. Small sections were taken from the middle of the lamina, and then treated with fuchsin-KOH at 60°C for two to four days, depending on the thickness of the lamina. The sections were cleaned in absolute ethylic alcohol, then small drops of hydrocloric acid were added before they were cleaned again in alcohol and mounted in Euparal.

The pattern of lamina venation was examined in adult samples from herbarium specimens. Cleared leaves were obtained following the fuchsin-KOH technique used for epidermal studies, as mentioned above. Heteroblastic development was studied in *Campyloneurum amphostenon*, based on specimens collected in Peru.

Measurements of sporangia, spores, and paraphyses were made on material mounted in Hoyer's solution. This material was collected from herbaria specimens. Spores were treated following the acetolysis technique (Erdtman, 1943). Pretreated spores were mounted in ethylacetate for observation under a compound microscope. Others were treated for observation under the scanning microscope (JEOL JSM-840 at the University of Aarhus) using gold coating; photographs were made using AGFA PAN 100 film. Additional spore material was studied with Dr. Alice F. Tryon at the Gray Herbarium of the University of Harvard. Photographs of spores at Harvard were processed with Polaroid film.

Microphotographs were taken of most of the morphological characters and were procesed at the laboratory of the Biological Institute in Aarhus, Denmark.

Phylogenetic analyses were performed using PAUP version 3.0 (Swofford, 1990) in a Macintosh II computer.

Two cladistic analyses were performed using the heuristic search method, and without ordered states or weighted characters (Wiley et al., 1991). In this way "a priori" inferences were avoided. The first analysis was done for the species based on a matrix of 23 morphological characters. The second analysis was done for the species groups, based on a matrix of 12 characters. In both cases an ancestor was defined.

Descriptive morphological terms are used according to the Systematics Association Committee (Taxon 9: 245-257. 1960), except for the use of linear-lanceolate instead of narrow elliptic and lanceolate instead of elliptic, when both ends are gradually narrowed.

In this study, the species are presented in alphabetical order. Lists of selected revised specimens are included after the morphological descriptions and distribution information.

Abbreviations of bibliographic references follow those of Stafleu & Cowan (1976) for books, and those of the Botanico Periodicum Huntianum (Lawrence et al.,1968) for periodicals. Author's name abbreviations follow those of the Authors of Plant Names (Brummit & Powell, 1992).

III. **TAXONOMIC HISTORY**

The genus *Campyloneurum* ("kampylos" arched and "neuron" nerve) was described by Presl (1836) in his work Tentamen Pteridographiae, together with other genera considered before as *Polypodium*. Presl characterized his new genus by areolate venation with two or more free excurrent veinlets per areole and by mainly entire leaves.

Brown (Bennet & Brown, 1838) proposed in Polypodium the section *Cyrtophlebium*, placing in it the American plants with the characters of the genus *Campyloneurum* proposed by Presl, i.e. leaves mostly entire, reticulate venation, areoles formed by arching veins, and always two series of sori except next to the costa. Smith (1841) raised Brown's *Cyrtophlebium* to genus level, citing *Campyloneurum* as a synonym. Thus, the name proposed by Smith was nomenclaturally illegitimate. Mettenius (1856) proposed *Cyrtophlebium* as a subgenus, but he included within it species from tropical America and Asia that belong today to such different genera as *Pyrrosia*, *Polypodium*, and *Campyloneurum*. Later, however, Mettenius (1857) used the subgenus *Cyrtophlebium* as the section proposed by Brown, i.e. for tropical American plants.

Among the first authors to accept *Campyloneurum* as a genus were Link (1841), Hooker & Bauer (1842), Fée (1852, 1857, 1869), Smith (1854, 1875), Hooker (1859), and Moore (1861), among others. Fée (1852) added some species previously in *Marginaria*, under the ortographic variant *Campyloneuron*.

Presl (1836) had published *Campyloneurum* without designating a type. In 1875, Smith made the typification, selecting *Polypodium repens* (*C. repens*).

During the 19th century, other authors placed the species of *Campyloneurum* in different subgeneric categories, thus as a section of *Polypodium* by Klotzsch (1847) and Diels (1899); and as a subgenus of *Polypodium* by Kunze (1850, 1853), Eaton (1860), Hooker (1864), Baker (1870), Hooker & Baker (1874), Sodiro (1893), and Christ (1897).

In this century, there were still diverse criteria for the treatment of the group. It was considered a subgenus of *Polypodium* by Christensen (1906), Kramer (1954), Proctor (1977), Stolze (1981), and Hoshizaki (1982). It was considered as a genus by Ching (1940), Copeland (1947), Sota (1960, 1973), Duek (1971), Long & Lakela (1971), Crabbe et al. (1975), Pichi-Sermolli (1977), Lellinger (1977, 1984, 1985, 1988), Smith (1981), Tryon & Tryon (1982a, 1982b), Proctor (1985), Mickel & Beitel (1988), and León (1993).

The interpretation of *Campyloneurum* as a genus including species with one-pinnate and entire leaves has been used by most pteridologists. However, Tryon & Tryon (1982a) proposed a new generic concept based on the soral position, which allowed them to exclude species with 1-pinnate leaves and to include the monotypic genus *Hyalotrichopteris* W. Wagner.

The exclusion by Tryon & Tryon (1982a) of the one-pinnate species (*Campyloneurum decurrens* and *C. magnificum*) was based on the sori, which are born at the tip of the excurrent veinlets. This character was considered by Tryon & Tryon (1982 a) to ally those species with *Polypodium*. However, this exclusion has not been widely accepted (e.g. Lellinger, 1988; Hennipman et al., 1990; León, in press) because other characters such as the areolate venation and stem scales ally the one-pinnate species with *Campyloneurum* .

The inclusion of *Hyalotrichopteris anetioides* by Tryon & Tryon (1982a, b) was due to the medial position of the sori on the excurrent veinlets, together with the presence of reticulate venation and leaf indument formed by branched hairs. Lellinger (1988) did not accept this inclusion, although he did accept a close link between both genera, calling *Hyalotrichopteris* a "satellite genus" of *Campyloneurum*. However, Hennipman et al. (1990) and León (in press) have included *Hyalotrichopteris* in the synonymy of *Campyloneurum*.

In this treatment, *Campyloneurum* is considered a genus defined by its reticulate venation, with primary parallel veins from which curved veins arise and anastomose to form primary areoles, and by costal areoles bearing one included excurrent veinlet, and non-costal areoles, entire or divided, with most included free veinlets excurrent. The genus consists of species with entire and one-pinnate leaves.

IV. **MORPHOLOGY**

ROOTS

The roots are located opposite the leaves on the ventral side of the stem (Fig. 1 a-c). The roots usually form two rows, although three can be found in some individuals of *Campyloneurum amphostenon*. The diameter and branching of the roots are variable, as is the distance between roots. The abundance of roots appears indirectly related to the degree of creeping; also habitat conditions may influence it, similar to the case of *Pyrrosia* as described by Hovenkamp (1986). Short-creeping stems in close contact with the substrate tend to develop abundant, spongy-looking roots (e.g. *C. brevifolium*, *C. pascoense*, *C. phyllitidis*), while long-creeping stems in loose contact with the substrate (e.g. *C. coarctatum*, *C.fasciale* , *C. repens*) tend to have fewer roots.

The roots are endogenous (cf. Ogura, 1972) and the epidermis has numerous root hairs. The vascular strand is diarch (Figs. 2 a, b) and is surrounded by a cortex or stereom (*sensu* Ogura, 1972), (Fig. 2 b), which is differentiated into an external parenchymatous cortex and an internal schlerenchymatous cortex. The anatomy of the roots in *Campyloneurum* is similar to that of other genera in the Polypodiaceae, such as *Microgramma*, *Niphidium* and *Pleopeltis*, as was shown by Zlotnik (1991).

STEM

The stem in *Campyloneurum* is characterized by a creeping habit, by its dorsiventrality, and by having an indument of scales (Fig. 1 a-c). The stem is terete and usually has two rows of alternate phyllopodia on the dorsal side, while the ventral side supports the roots. Three discontinuous rows of phyllopodia are unusual in the genus. This phenomenon was observed only in *C. angustifolium* ; similar observations in this species were reported by Hovenkamp (1990).

The diameter of the stem ranges from 1 to 20 mm (Table 1). For example, in *Campyloneurum vulpinum* the stem is 1-2 mm wide and in *C. pascoense* it is 15-20 mm.

The color of the stem in most species is green, and usually turns brown or atropurpureus when dry. However in some species, such as *Campyloneurum sphenodes*, the green color is persistent in most herbarium specimens. Pruinosity is present in some species; a persistent whitish wax covers the surface of the stem of *C. amphostenon*, *C. angustifolium*, *C. densifolium*, and *C. solutum*, while in *C. cochense* and *C. lorentzii* it is less common.

The distance between neighboring phyllopodia is variable (Table 1), for example in *Campyloneurum angustifolium* the distance is 1-4 mm, and in *C. coarctatum* it is 10-15 mm. As in other genera of the Polypodiaceae (e.g. in *Pyrrosia*, Hovenkamp, 1986), this distance allows the recognition of two states of stem morphology: long-creeping and short-creeping, based on the relation between phyllopodium distance and stem diameter. Long-creeping stems (Fig. 1 b) are here defined by the smallest phyllopodium distance being larger than the smallest stem diameter (e.g. *C. falcoideum and C. sphenodes*). In short-creeping stems (Fig. 1 a), the largest phyllopodium distance is equal to or smaller than the largest stem diameter (e.g. *C. angustifolium and C. costatum*). A few species (*C. acrocarpon*, *C. amphostenon*, *C. asplundii*, *C. densifolium*, *C. lorentzii*, *C. minus*, and *C. nitidum*) may exhibit both states, which can be interpreted as an adaptation to different habitat conditions, such as rock crevices or tree branches.

The stem frequently branches laterally along its axis. Branching was observed in *Campyloneurum amphostenon*, *C. asplundii*, *C. coarctatum*, *C. cochense*, *C. densifolium*, *C. falcoideum*, *C. lorentzii*, *C. ophiocaulon*, *C. pascoense*, *C. solutum*, *C. sphenodes* , and *C. vulpinum*. Also, Sota (1960) observed branching of the stem in *C. aglaolepis* and *C. tucumanense*, and Wagner & Farrar (1976) in *C. anetioides*.

The stem in all species of *Campyloneurum* has the cortex and pith consisting mostly of parenchyma, a group or nest of sclereids in the cortical parenchyma, and a dictyostele (Fig. 3 a-d). The stele in the genus was defined as a perforated dictyostele by Ogura (1972).

The epidermis is formed by a single layer of regular, oblong cells with a thin cuticle (Fig. 3 a). The scales are appendages of the epidermis.

The parenchyma in *Campyloneurum* is found in the cortex and pith, and is characterized by cells with thin walls (Fig. 3 b, d), bearing granules of starch and tanines (Fig. 3 a-d). These features

were also observed by Zlotnik (1990). Sometimes a collenchyma occurs only in the cortex, beneath the epidermis; it has thicker walls, as observed in *C. fuscosquamatum* and *C. sphenodes* (Fig. 3 a-c).

The presence of nests of sclereids is one striking character in the cortex and pith. The color of these sclereid cells is brown as a result of a pigment called phlobaphene, which may prevent the decay of the tissue (Ogura, 1972). The presence of nests of sclereids has been related to the age of the stem by Wagner & Farrar (1976) in *Campyloneurum anetioides*, with young plants having fewer nests. In this study it was observed, however, that the size and abundance of nests are variable among examined species (Fig. 3 a-d). It appears that the patterns observed may be related instead to the thickness of the endodermis. Sometimes nest of sclereids are few, small, formed by 2-4 cells, and scattered among the parenchyma cells in those species with vascular bundles surrounded by thick endodermis (*C. angustifolium*, *C. densifolium*, and *C. sphenodes*, Fig. 3 a). Nests of sclereids are more numerous and formed by more than 4 cells in species with vascular bundles without a thick endodermis (*C. fuscosquamatum* and *C. vulpinum*, Fig. 3 b-d). It remains to be clarified if the arrangements observed here have some taxonomic value, as was shown by Hovenkamp (1986) in *Pyrrosia*.

In cross section, the perforated dictyostele shows (3-) 5-11 meristeles arranged in an elliptical ring (Figs. 1 c; 3 a, b). The vascular bundle is composed of xylem surrounded by phloem. The pericycle consists of three layers of cells (Fig. 3 b). The endodermis usually appears as a protecting sheath with strongly differentiated thick cell walls surrounding the vascular bundle (Fig. 3 a, b). However, in *Campyloneurum vulpinum* (Fig. 3 d) the endodermis appears slightly differentiated from the pericycle.

INDUMENT OF THE STEM

Scales of the stem have played an important role in the taxonomy of many genera of the Polypodiaceae because they are the main source of characters with taxonomic value (e.g. Sota, 1960, 1973; Lellinger, 1972; Bir & Trikha, 1979; Hennipman & Roos, 1983; Hovenkamp, 1986). Similarly, the stem scales are very valuable in *Campyloneurum*, as was recently corraborated by Lellinger (1988).

In *Campyloneurum*, the persistence of the scales of the stem varies among species. Those species with long-creeping stems have mostly caducous scales, although they persist or are more abundant on young parts, such as the stem apex and lateral branches (e.g. *C. repens* and related species). The stem scales partially overlap each other in three or four layers, but the apices are usually spread or, in a few species, adpressed.

The scales of the stem have a wide range of variation in shape, from linear, as in *Campyloneurum angustipaleatum* and *C. coarctatum* (Fig. 5 i), to broadly ovate, as in *C. fallax* and *C. nitidum*. The most common shapes in the genus are narrowly ovate, as for example in *C. costatum* and *C. nitidissimum*, or ovate as in *C. aglaolepis*, *C. amphostenon*, and *C. solutum* (Fig. 5 h). The shape of the scale of the stem is usually constant within a species. Rarely two shapes can be found in the stem of an individual, as was observed in some individuals of *C. xalapense* with both linear and narrowly ovate scales. Rare in the genus is the presence of bullate scales, as in *C. minus*, or slightly bullate, as in *C. acrocarpon*.

The area of attachment of the scale to the epidermis is differentiated in cell structure and coloration from the rest of the body of the scale (Fig. 4 a, b). The basal projection of the scale lamina and the position of the attachment allows the recognition of three types of scales: "pseudopeltate", "peltate", and "basifix", as was proposed by Hovenkamp (1986) for *Pyrrosia*. Pseudopeltate scales are the most common type in the genus (Fig. 4 a, 5 e), as are found in *Niphidium*, *Pleopeltis*, and some species of *Polypodium*. These scales have two separate auricles, usually overlapping. The two auricles may be the same size, or one of them may be longer than the other. Peltate scales are those with only one auricle; they are found in *Campyloneurum falcoideum*, and sometimes in *C. sphenodes* and *C. vulpinum* (Fig. 4 b, 5 e). Finally, the basifix scales, i.e. those without basal auricles, rarely occur in the genus. This type of scale was observed in young parts of the stem in several specimens of *C. amphostenon*, probably indicating an incomplete development of the scale.

The length of stem scales varies from 2 mm, as in *Campyloneurum chrysopodum*, to 15 mm, as in *C. magnificum*. The base of the scale can be abruptly wide, as in *C. aphanophlebium*, *C. centrobrasilianum* and *C. costatum*. The apex varies from obtuse as in *C. fallax*, *C. minus*, *C. nitidum*, *C. ophiocaulon*, and *C. wurdackii* (Fig. 5 a, b), to acute, as in *C. densifolium*, and acuminate, as in most of the remaining species (Fig. 5 e-j).

The margin of the scale in *Campyloneurum* can be entire to slightly dentate (Fig. 6 a-c). The teeth are composed of one to several protruding cells (Fig. 6 a-c). Some of the teeth look like the indument found in the leaves (Fig. 6 b); this type of tooth is formed of 1-3 cells, with apical cells as dark as glandular hair. Teeth along the margin of the stem scale are not restricted to any group of species or species in particular. However, they are more frequently found in *C. cochense*, *C. nitidissimum*, and *C. xalapense*.

The scales are one layer of cell, except at the point of attachment. The shape of the cells of the scales varies from narrowly oblong (Fig. 7 a, b), such as in *Campyloneurum aglaolepis* and *C. coarctatum*, to roundish (Fig. 7 c), as in *C. ensifolium* and *C. fallax*. Narrowly oblong cells are the most common type. The cell disposition and cell shape differentiation between margin and center of the scale can be used to recognize two types of scales: marginally nondifferentiated scales, i.e, those without major differences in shape and disposition between marginal and central cells (Fig. 7 a); and marginally differentiated scales, which have two or more rows of cells distinctive from the central cells in shape, cell wall thickness, and disposition (Fig. 7 c). Nondifferentiated scales are widely distributed in the genus (Table 1).

Most of the nondifferentiated scales have the cells arranged along the main axes, but for some species the narrow rectangular cells appear irregularly arranged, either in the main body of the scales, as in *Campyloneurum amphostenon* var. *irregulare* (Fig. 5 f), or at the base of the scale, as in *C. centrobrasilianum*. Differentiated scales occur in all species groups except in *C. angustifolium* and related species. The differentiated scale type shows the presence of heterocellularity in *Campyloneurum*. This is similar to *Microgramma* as discussed by Sota et al. (1982) and *Niphidium* by Lellinger (1972).

In mass the scales of the stem are almost concolorous, and for most species the color of the scales is brown, except in *Campyloneurum chlorolepis*, which has stramineous scales due to the hyaline cell walls. The color in the walls of the cells is usually homogeneously distributed, although along the scale margins, the cells have very thin and colorless outer walls. The lumen of the cells is for most species translucent and colorless, but in some species all cells or some of them may have dark yellow brown or yellowish lumen, as in *C. asplundii*, *C. inflatum*, *C. macrosorum*, *C. nitidissimum*, *C. solutum*, and *C. vulpinum*, or completly occluded, as in *C. fuscosquamatum*.

Three main types of scales can be recognized based on the thickness and coloration of the cell wall: clathrate, slightly clathrate and non-clathrate. In the clathrate scale type (heterotoechous of Pichi-Sermolli, 1972), the cell wall is usually brown and has a clearly defined lumen. This clathrate type scale is the most common in the genus, and occurs in differentiated and nondifferentiated stem scales (Fig. 7 a). In marginal differentiated scales the well-defined cells are located in the middle of the scale. Slightly clathrate scales occur in *Campyloneurum macrosorum* and *C. vulpinum* (Fig. 7 b), where the brownish cell walls are not clearly defined from a colored lumen. Non-clathrate scales (isotoechous, Pichi-Sermolli, 1972) occur in *C. asplundii*, *C. chlorolepis*, and *C. fuscosquamatum*; of these species, *C. chlorolepis* has stramineous scales with hyaline cell walls.

As mentioned by Moran (1987), there is not a satisfactory explanation for the adaptive advantages of stem scales. Their most common attribute has been claimed to be protection. Thus *Campyloneurum* stem scales are mostly restricted to the young parts. However, Muller et al. (1981, *in* Bosman, 1991) has attributed to them a physiological role influencing evaporation, water absorption, and temperature regulation. In the case of pruinose stems with caducous scales, Bosman (1991) has suggested the same role with regard to the whitish wax.

LEAVES

In *Campyloneurum*, sterile and fertile leaves are similar in shape and size. Leaves are articulate to the stem, and they are usually arranged in two rows on the adaxial side. Leaves are frequently curved in most species; sometimes they are erect, as in *C. abruptum*, overhanging as in *C. anetioides* or pendent as in *C. sublucidum*.

Petiole

The petiole is always present. It ranges in length from 0.3 mm, as in *Campyloneurum anetioides*, to 95 cm in *C. magnificum*. The petiole is usually terete and wider at its base, becoming slightly ranurate and narrow toward the distal portion.

In *Campyloneurum*, distal portions of the petiole have narrow lateral expansions that result from the decurrency of the lamina. These lateral lamina expansions may consist of parenchyma, usually at the most distal parts, or sclerenchyma, in the proximal ones, similar to other fern genera (Lin & De Vol, 1977). In most species the lamina expansions are not strikingly conspicuous, except in *C. abruptum*.

In herbarium specimens the color of the petiole varies from brown to stramineous; in living plants it is usually a deeper green on the adaxial side.

The indument of the petiole is composed of deciduous and scattered scales and hairs. Scales are similar in cell structure and shape to those of the stem. Hairs are found during juvenile stages in *Campyloneurum amphostenon*, *C. anetioides*, and *C. aphanophlebium*. In *C. amphostenon* hairs are deciduous, but in *C. anetioides* and *C. aphanophlebium* they are persistent. Hairs may also occur in juvenile leaves of other species with hairs in adult stages, such as for example in *C. cochense* and *C. repens* (Table 1).

In general, the petiole has anatomical features similar to those of the stem (Fig. 8 a, b). The epidermis is formed by a single layer of cells, with a very thick cuticle. The parenchyma, however, does not present nests of sclereids, and it is spongy with many intercellular spaces. Under the epidermis lies a 6-15 cell-thick layer of sclerenchyma. There are 3-7 meristeles; two of them are usually larger than the rest, and occupy a dorsal position. The anatomical structure of the petiole has recently been described by Zlotnik (1990), based on a study of three Mexican species.

Lamina

In *Campyloneurum*, the lamina of most species is simple and entire (Fig. 9 a-i, k-l); only in *C. decurrens* and *C. magnificum* is the lamina one-pinnate (Fig. 9 j). Pinnate leaves are here interpreted as a primitive character in the genus.

As with other genera in the Polypodiaceae (Hovenkamp, 1986; Bosman, 1991), aberrant lamina shapes are occasionally found, as in *Campyloneurum amphostenon* (Fig. 9 e). The aberrant laminae occur in simple-leaved species, and are characterized by irregular lobes either laterally or distally. Aberrants were described by Mettenius (1864) as *Polypodium angustifolium* var. *monstruosum* (=*C. cochense*) and by Poiret (1804) as *P. conjugatum* (=*C. phyllitidis*).

The size of the lamina varies within a species; thus it has reduced taxonomic value. The smallest leaves in the genus are found in *Campyloneurum anetioides*, and in *C. chrysopodum* and *C. falcoideum* with leaves sometimes less than 10 cm long. The largest leaves are found both in one-pinnate species, as in *C. magnificum* (2.5-3 m long), and in simple-leaved species, as in *C. pascoense* (2 m) and *C. oellgaardii* (1.5 m).

Shape varies little within a species, and is therefore more valuable taxonomically (Fig. 9). The most common shapes are linear-lanceolate to lanceolate (Fig. a-d, f-l), as in *Campyloneurum amphostenon*, *C. angustifolium*, and related species. Other shapes include oblong leaves, as in *C. coarctatum* and *C. inflatum*; narrowly obovate leaves, as in *C. aphanophlebium*, and spathulate leaves, as in *C. anetioides*. Spathulate is the basic shape found in young leaves, as illustrated in Figure 15 (a-c) and by Mitsuta (1983). Spathulate leaves of adult *C. anetioides* may represent a neotenic condition.

The base of the lamina is most often narrowly cuneate or attenuate, and is usually unequal. In *Campyloneurum abruptum*, the base is cuneate, before abruptly becoming long decurrent on the petiole (Fig. 9 l).

The margin of the lamina is well defined by a cartilaginous tissue. It is usually entire and slightly sinuate. Most of the species have a plane margin; in *Campyloneurm angustifolium* and

closely related species however, the margin can become revolute, probably as a response to environmental factors, such as low humidity and wind exposure.

The apex for most species is acuminate to subcaudate (Figs. 9 f-l), forming a "drip-tip". Only in *Campyloneurum anetioides* and juvenile specimens is it obtuse.

The texture of the lamina is usually herbaceous-chartaceous. Leaves are thickly chartaceous or sub-coriaceous, as in *Campyloneurum nitidissimum* and *C. rigidum*. Rarely leaves are thinly papyraceous, as in *C. tucumanense* .

In most species the abaxial surface of the lamina is usually a dull green, while the adaxial side is bright and usually shiny. In *Campyloneurum rigidum* and *C. sublucidum* however, both sides have the same degree of shininess.

The indument of the lamina is composed of hairs and scales. The lamina scales are scattered and deciduous along the costa. The hairs, however, tend to persist in most species either on the lamina surface or along the costa (see below for a description of hairs).

Leaf anatomy

The leaves have a single layer of epidermis cells with a thick cuticle; the outline shape of the cells is sinuose (Fig. 10 a-d), similar to other polypodiaceous genera (e.g. Barrera, 1981; Bosman, 1991).

The leaves in *Campyloneurum* are hypostomatic, i.e. the stomata are located on the abaxial surface. Following Van Cotthem's (1970, 1973) definitions, three types of stomata were found in the genus: polocytic, copolocytic (Figs. 10 a-c, 11 a-b) and anomocytic (Fig. 10 d).

Polocytic stomata is the most common type (Table 1), and it occurs in single strands (e.g. in *C. abruptum*) or mixed with copolocytic stomata (e.g. in *C. angustifolium*, *C. phyllitidis*, and *C. tenuipes*). Copolocytic stomata predominate only in *C. decurrens* (Fig. 11 a). Anomocytic stomata are rare; they have been observed in *C. cubense* (Fig. 10 d) and *C. nitidum* (Sen & Hennipman, 1981).

Abortive stomata have been observed in *Campyloneurum cubense* (Fig. 10 c), which may indicate a hybrid origin for this species. Polar contiguous stomata had not been previously observed in the family (Sen & Hennipman, 1981), however, during this study contiguous stomata were found in *C. cubense* (Fig. 10 b).

Hydathodes occur in all species of the genus. They appear at the tip of the free veins, on the adaxial surface of the lamina (Fig. 11 b). The enlarged tip consists of numerous tracheids and cells of the epidermis arranged concentrically. Active hydathodes are recognizable by the whitish surface covering. This probably results from the secretion of water and salts from root pressure, as was observed in *Blechnum* by Sperry (1983). Although functional hydathodes are present during juvenile stages of leaves, only rarely do they continue functioning in adult leaves, as sometimes occurs in *Campyloneurum brevifolium* and *C. xalapense*. As Bosman (1991) observed for *Microsorum*, non-functioning hydathodes are usually sunken into the epidermis.

Foliar nectaries were observed in recently developed adult leaves of *Campyloneurum phyllitidis* and *C. xalapense*, and have also been reported in *C. repens* by Mickel and Beitel (1988). These structures are located abaxially, on the acroscopic side at the joint of the costa with primary veins. In herbarium specimens these structures appear as dark spots. Koptur et al. (1982), working with other polypodiaceous species, found that the secretion is composed of aminoacids and sugars. Although no chemical tests were done, the exudate of *C. phyllitidis* had a sweet taste. It was observed both in the field and in cultivation that during the production of exudates *C. phyllitidis* was visited by ants, but no damage was noticed on the leaves. The role of nectaries in ferns is still unresolved; as discussed in Koptur et al. (1982), foliar nectaries may be associated with protection from predators or due to some other adaptation to the environment.

The mesophyll in *Campyloneurum* is composed of 4-7 cell layers of parenchyma. On the adaxial side of the leaf the parenchyma has cells closely arranged, with small intercellular spaces; these cells contain numerous chloroplasts. On the abaxial side is a spongy parenchyma, characterized by more loosely cells arranged, with conspicuous intercellular space. Some individuals of *C. phyllitidis* growing in a

greenhouse, however, showed cells of the parenchyma from both adaxial and abaxial sides that resembled one another in shape and disposition. Yet another type of parenchyma, with large polygonal spaces was reported in *C. anetioides* by Wagner & Farrar (1976). Schlerenchyma is found at the costa and margins of the lamina.

The vascular tissue is represented by 1-2 large meristeles located in the costa (Fig. 12 b). In the lamina (Fig. 12 a), there are small meristeles that correspond to the subsidiary veins.

Indument of the lamina

Leaves in *Campyloneurum* species, except *C. aphanophlebium* (as *C. occultum*) are commonly described as glabrous (e.g. Mickel & Beitel, 1988; Lellinger, 1988). During this study, however, indument consisting of scattered hairs and scales was observed in several species.

Scales are only found along the costa, and their features are similar to those of the stem, although size in costal scales is very reduced. Because most of these scales are deciduous, their taxonomic value is limited. They are, however, usually persistent in *Campyloneurum lorentzii*. They can be basifix, as was also observed by Baayen & Hennipman (1987) in *C. angustifolium*.

During this study, representatives of three types of hairs were found in the genus. They are described according to their complexity. The first type (Fig. 13 a) consists of two cells with the apical cell slightly enlarged, as in *Campyloneurum decurrens* and *C. nitidum*. The second type (Fig. 13 b) is branched, composed of three cells, one forms the base, another is small, lateral and glandular, while the third is an enlarged cell with a gradually obtuse apex. This was observed for example in *C. aphanophlebium*, *C. repens* , and *C. sphenodes*. The third type (Fig. 13 c) is branched, and also has a basal glandular cell, plus one or two pluricellular branches, as in C. anetioides.

In most species, inconspicuous and scattered hairs are found on the abaxial surface of the lamina (Table 1). *Campyloneurum anetioides* and *C. aphanophlebium* have hairs scattered on both surfaces. In a few species, such as *C. amphostenon*, *C. angustifolium* and closely related species, hairs are usually absent on the lamina tissue of adult leaves. But in juvenile leaves of *C. amphostenon*, numerous hairs cover the tip of the lamina on the abaxial side, and are sometimes scattered along the costa on the adaxial side.

The types of hairs found in *Campyloneurum* are not exclusive to the genus. The same type of hairs are found in *Grammitis* (Parris, pers. comm., 1985), *Microgramma* and some species of *Polypodium* (Sota 1960), *Pecluma* (Baayen & Hennipman, 1987), *Platycerium* (Hennipman & Roos, 1982) and *Pyrrosia* (Hovenkamp, 1986).

Venation

The pattern of venation has been a very important feature in the taxonomy of the Polypodiaceae (e.g. Presl, 1836; Pichi-Sermolli, 1977). This character is a basis for establishing generic limits in *Campyloneurum* (Chapter III).

In *Campyloneurum* the pattern of venation of adult leaves has been briefly described by various authors, while the venation found in juvenile plants has been described for a very few species by Wagner & Farrar (1976) and Mitsuta (1981, 1983).

Campyloneurum is characterized by a reticulate venation, with areoles between parallel primary veins, and by excurrent free veinlets included in most areoles.

The costa is prominent in most species (Fig. 14), and can be rounded, angular abaxially, and slightly sulcate adaxially. In *Campyloneurum anetioides*, it is only conspicuous at the base of the lamina and then becomes immersed in the lamina tissue.

The primary veins (Fig. 14) run parallel, slightly sinuate or straight from costa towards the margin. The distance between two neighboring primary veins varies from 4-10 (-15) mm. The angle of divergence between the costa and primary veins at the middle of an adult leaf ranges from 40 to 75º. There is no aparent relationship between lamina width and this angle, as was also observed in *Microsorum* (Bosman, 1991).

In most species, primary veins become immersed in the tissue toward the margin, except in *Campyloneurum nitidissimum* var. *nitidissimum* and *C. pascoense* where they are prominulous from the costa to the margin. Primary veins can be totally immersed, becoming inconspicuous, except in dry herbarium specimens, as in *C.*

angustifolium and related species. They can also be slightly prominulous, or prominulous, with dark green or stramineous color on one side of the lamina. These primary veins may have different degrees of prominence on each side of the lamina, as in *C. amphostenon* and related species, or similar degrees of prominence on both sides, as in *C. repens* and *C. phyllitidis*.

Primary veins always branch into secondary veins. Secondary veins run almost parallel to the costa, and they are mostly slightly arched. The acroscopic secondary vein unites with the basiscopic vein of the neighboring primary vein; the fusion of these secondary veins creates primary areoles, which vary in number from two to more than 15 between the costa and margin. The primary areoles are uniform in size and shape, although those close to the costa (costal areoles) are usually different from those found elsewhere (non-costal areoles). These costal areoles can be larger and more polygonal than the non-costal areoles, as in *Campyloneurum angustifolium* and related species, or they can be shorter and wider as in *C. magnificum*, *C. repens*, and related species. In most species, secondary veins are immersed in the tissue, except in *C. nitidissimum* var. *nitidissimum* and *C. pascoense*, where they are prominulous.

Secondary veins usually form tertiary veins. Tertiary veins are veinlets inside the primary areoles. Tertiary veins or veinlets may be simple or furcate. They are mostly excurrent and parallel to the primary veins, especially at the marginal areoles, however, they may also be recurrent (Fig. 14 k).

Tertiary veins may be free as in *Campyloneurum magnificum*, *C. repens*, *C. sphenodes*, and allied species, or may connect with the arched secondary veins forming secondary areoles.

Some secondary marginal areoles do not have included veinlets (Fig. 14 a, b). Costal areoles without veinlets are rare in the genus. Alston (1957) showed this type of areoles in *Campyloneurum chlorolepis*, Sota (1960) observed them at the base of the lamina of *C. tucumanense* and Mitsuta (1983) in *C. angustifolium*.

Marginal free veinlets are excurrent and usually undivided. They may occur in several unrelated species, such as *Campyloneurum anetioides* (Fig. 14 i), *C. angustifolium* (Fig. 14 c), *C. brevifolium* (Fig. 14 j), and *C. decurrens* (Fig. 14 h).

The development of the venation in juvenile plants was studied in *Campyloneurum angustifolium*, *C. caudatum* (here under*C. costatum*),*C. phyllitidis*, and *Polypodium vexatum* (here under *C. cubense*) by Mitsuta (1981). Figure 15 shows a similar pattern of the development in *C. amphostenon*. Collectively, these studies show that the costal vein is formed by forked veinlets, where one of the branches run along the main axis of the lamina (Figs. 15 a-d); that the lateral veins continue branching and anastomose to form areoles (Fig. 15 e-f); that free excurrent included veinlets are present in the areoles (Fig. 15 g, h); and that the more complex anastomosing occurs later in more mature leaves.

In adult leaves, the pattern of venation is an important taxonomic character. The pattern of venation together with other important feautures has allowed the recognition of ten species groups during this study (see Chapter VIII), based on four types of venation in adult leaves. These types are used for descriptive purposes only. However, some evolutionary tendencies were inferred during their recognition, and they will be discussed in the chapter on phylogeny.

Type 1 is characterized by immersed primary veins, less than two rows of non-costal areoles on each side of the lamina, and one free excurrent veinlet in each areole (Fig. 14 a-c). The areoles are usually longer than wide. Type 1 is mostly found in narrow leaves, as in *Campyloneurum angustifolium*, *C. vulpinum*, and allied species.

Type 2 is characterized by slightly prominulous or prominulous primary veins, more than two rows of non-costal areoles, primary areoles divided symmetrically into secondary areoles with one or two free excurrent veinlets (Fig. 14 d-f). Type 2 is found in *Campyloneurum amphostenon*,*C. phyllitidis*, *C. xalapense*, and allied species.

Type 3 resembles type 2 in having more than two rows of non-costal areoles. However, it differs by the immersed or prominulous primary veins, by the predominance of undivided primary areoles, usually with 2 (-5) excurrent veinlets, and by areoles usually wider than long (Fig. 14 g-i). Type 3 occurs in *Campyloneurum aphanophlebium*, *C. magnificum*, *C. repens*, *C.*

sphenodes, and allied species, and it may represent a less advanced type of venation in the genus. Three species (*C. anetioides*, C. *chrysopodum* and *C. falcoideum*) that also belong to this venation type, have non-costal areoles usually with only one free excurrent veinlet, and they appear to represent a reduced pattern of this type of venation.

Type 4 is characterized by prominent primary veins, more than two rows of non-costal areoles, and asymmetrical secondary and tertiary areoles with more than two free mostly excurrent veinlets in each primary areole (Fig. 14 j-k). Type 4 corresponds to the venation found in *Campyloneurum brevifolium* and allied species.

Some general features of the pattern of venation in *Campyloneurum*, such as costal areoles with one excurrent veinlet, or the presence of excurrent and sometimes recurrent veinlets in non-costal areoles, are shared with three other neotropical polypodiaceous genera, *Pleopeltis*, *Microgramma* and *Niphidium*, and these may reflect the closest affinities of *Campyloneurum*.

SORI

In *Campyloneurum*, sori are round to elliptical, 1-2 (-3) mm across, and on the surface of the lamina. They usually occur in two rows between primary veins, but three or more are common in *C. brevifolium* and allied species, while one row of sori may occur in *C. anetioides* and *C. falcoideum*. Each sorus is innervated by a solitary excurrent free veinlet, however, rarely two or three sori occur together in *C. brevifolium*.

The position of sori on the veinlet is subapical or medial for most species. Terminal sori occur in the one-pinnate species, rarely in some individuals of *Campyloneurum aphanophlebium* and *C. falcoideum*, and it was shown by Mitsuta (1983) in *C. angustifolium*. The terminal position of sori is considered to be a primitive character state in the genus. Sori at the junction of two veinlets may occur in *C. brevifolium* and related species, correlated with the more complex venation (Fig. 14 k), although it was also observed by Mitsuta (1983) in *C. angustifolium*. The range of variation of sorus position (medial, subapical or terminal) in the genus is similar to that in other genera in the family (e.g. *Pyrrosia*, Hovenkamp, 1986), and in this study the soral position is considered of limited value for generic definition.

Paraphyses

The presence of paraphyses (sensu Wagner, 1964) in *Campyloneurum* was noticed earlier by Mettenius (1864) in *Polypodium lindigii* (=*C. macrosorum*). Wagner & Farrar (1976) observed them in *C. anetioides*; Tryon & Tryon (1982a) in *Campyloneurum occultum* (=*C. aphanophlebium*), and Lellinger (1988) in *C. cooperi* (=*C. amphostenon*). Baayen & Hennipman (1987), however, did not find these structures in *C. angustifolium* and *C. phyllitidis*.

During this study, each species was examined for paraphyses. They were observed in nine species (Table 1). Paraphyses are most often smaller than the sporangia, and more slender than the stalk. Two types of paraphyses are recognized here: simple and dendritic. Simple paraphyses are composed of one unbranched row of 2-3 cells (Fig. 16 a), as occurs in *Campyloneurum acrocarpon*, *C. pascoense*, and some individuals of *C. amphostenon* and *C. angustifolium*. Dendritic paraphyses are composed of a row of 5-7 cells with 3-5 unicellular branches (Fig. 16 b), as seen in *C. aglaolepis*, *C. aphanophlebium*, *C. nitidum*, and *C. vulpinum*. Dendritic paraphyses in *Campyloneurum* resemble those found in *Microgramma ciliata*, as described by Baayen & Hennipman (1987). In *C. macrosorum*, simple paraphyses are common in addition to dendritic ones.

Sporangiasters or abortive sporangia (Wagner, 1964) are frequently found on the receptacle.

Sporangia

Sporangia are characterized by a spherical capsule supported by a slender stalk of 2 (-3) rows of cells. Sporangia are numerous in the sori. They appear to mature in a centripetal order. They are mixed with abortive sporangia and sometimes with paraphyses. Abortive sporangia are easily recognized by the small size of the tannin-filled capsule.

The length of the capsule ranges from 330-460 µm. The annulus is composed by 12-18 bow cells. The faces of the capsule are similar to other genera in the family s.str., as described by Wilson (1959). The stalk is thin and well developed; it is

composed of two rows of cells, except below the capsule, where there are three rows.

Spores

Earlier observations of spores of *Campyloneurum* date back to Fée (1869). Since then, there have been several studies of the spore morphology in *Campyloneurum*, especially during the last 30 years, such as those of Nayar (1962), Tschudy & Tschudy (1965), Pal & Pal (1970), Kremp & Kawasaki (1972), Murillo & Bless (1978), Lloyd (1981), and Tryon & Lugardon (1991), among others. *Campyloneurum* spore morphology was examined here for each species when available (Figs. 17, 18, 19). Spores are reniform and ellipsoidal, although abortive spores may be rounded and collapsed. Size varies between 40-100 µm long and 30-60 µm wide (Table 1). For most species, spore sizes varies little intraspecifically; large differences in size, however, were observed in *C. angustifolium*, *C. repens*, and *C. vulpinum*. This variation may suggest the occurrence of different ploidy levels (cf. Tryon & Lugardon, 1991).

The laesura characterizes the monolete spore in the genus. It always protrudes from the surface (Fig 17, 18). Laesura sizes are usually constant among species. The laesura occupies between 1/4 of the spore length, as in *Campyloneurum costatum* (Fig. 17 c) and 3/4 of the length of the spore, as in *C. amphostenon* (Fig. 17 a). Rarely this range of size may occur within a single species, as in *C. phyllitidis* (Fig. 18 c, d).

The surface of the spore is covered by scattered spherical bodies or granules, which are located under a thin perispore (Fig. 19 b, 20 a, b). The exospore can be slightly verrucate or verrucate (Fig. 17, 18, 19). In a few cases, as in *Campyloneurum anetioides*, *C. aphanophlebium*, and *C. falcoideum*, the surface is rather smooth (Figs. 17 c, 18 e), supporting a probable affinity of these species.

Tryon & Tryon (1982a) and Tryon & Lugardon (1991), based on spore characteristics, have suggested generic relationships between *Campyloneurum* and *Niphidium*, and also with some species of *Polypodium*. In this study these relationships are considered, and it is suggested that the genus *Pleopeltis* is closely related to *Campyloneurum*, because many characteristics of spore morphology are shared, such as shape and surface.

GAMETOPHYTES

As Atkinson (1973) mentioned, features found in gametophytes may help to demonstrate the cohesiveness of a genus and to understand relationships. In *Campyloneurum*, little is known, however, of the development and characteristics of the gametophytes.

Spore germination has only been observed in *Campyloneurum anetioides* by Wagner & Farrar (1976).

The development and characteristics of the gametophyte has been observed in *Campyloneurum anetioides* (Wagner & Farrar, 1976) and *C. angustifolium* (Nayar, 1962). In both species the shape of the gametophyte was found to be thalloid, with a cordate apex and with a continuous or discontinuous midrib. The indument of the gametophyte was composed of bicellular glandular branched hairs, similar to those found in the sporophyte of most species of *Campyloneurum*.

V. **CYTOLOGY AND BIOCHEMISTRY**

CYTOLOGY

Chromosome numbers in *Campyloneurum* have been reported in at least ten taxa (Table 2), by several authors (see Fabbri, 1963, 1965; Walker, 1985). For most cases the basic chromosome number is x=37.

Three species (*Campyloneurum costatum*, *C. tenuipes*, and *C. xalapense*) are diploids with n=37 and 2n=74; five species (*C. acrocarpon*, *C. anetioides*, *C. minus*, *C. nitidum*, and *C. repens*) are tetraploids with n=74 and 2n=148; and in two species (*C. angustifolium* and *C. phyllitidis*) both tetraploids and diploids are found.

The presence of both diploid and polyploid populations within a species is not uncommon in ferns (e.g. Walker, 1985) and may occur in *Campyloneurum*. In *C. angustifolium* there is evidence of a wide variation in spore sizes, that may support the findings of two ploidy levels. A diploid was once reported by Evans (1963) from material collected in Peru, while tetraploids were recorded from specimens collected in Costa Rica

and Florida (Evans, 1963; Wagner, 1963). However, the evidence of different cytotypes within this species is not conclusive, due to the poor taxonomic understanding of the species at that time and the fact that vouchers specimens from those cytological studies were not examined for this treatment.

Campyloneurum brevifolium is a diploid species, as was reported by Evans (1963) for southern U.S.A. and by Smith & Foster (1984) and Walker (1985) for Trinidad. This is the only species thus far that is known to present two chromosomal satellites (Walker, 1985).

Campyloneurum phyllitidis is tetraploid, as reported by Evans (1963) and Wagner (1963) for southern U.S.A., by Jarrett et al. (1968) for the Galápagos in Ecuador, and by Walker (1973, 1985) for Jamaica and Trinidad. Similar to the case of *C. angustifolium*, *C. phyllitidis* appears to have two cytotypes, since Sorsa (in Fabbri,1965) registered a diploid from Peru, but no conclusions can be certain since no voucher specimens were cited. Allopolyploidy has been suggested by Walker (1985) to occur in *C. phyllitidis* from Jamaica based on the bimodal distribution of chromosomal length; however, no further information is available in relation to the probable parental species.

Campyloneurum nitidum is tetraploid, as reported by Smith & Foster (1984) from Paraguay.

In *Campyloneurum*, aneuploidy has been reported once (Pal, 1961 as cited by Fabbri, 1963) for a cultivated plant of *C. phyllitidis*. This phenomenon is not uncommon among ferns (Walker, 1985), however, further studies are neccesary to clarify its occurrence in the genus.

Based on the present cytological information, some *Campyloneurum* species present different cytotypes that may correlate with the morphological variation found in their leaves and spores. If allopolyploidy proves to be more widely distributed among species of *Campyloneurum*, it may be useful character for testing affinities among species.

BIOCHEMISTRY

The biochemistry of ferns has been recognized as less variable than that of angiosperms (Swain & Cooper-Driver, 1973). During the last 20 years, there has been an increase in the study of fern biochemistry (Soeder, 1985).

Several works in different genera of the Polypodiaceae s.str., as mentioned by Soeder (1985), have revealed the presence of alkaloids, flavonoids, terpenoids, sterols, and other compounds. According to Swain & Cooper-Driver (1973), flavonoids and terpenoids are widespread in ferns.

Very little is known about the biochemistry in *Campyloneurum*. Lynch et al. (1970) reported the presence of saponins (terpenoid) and the absence of anthocyanin (flavonoid) and triterpenoids in *Polypodium latum* (=*C. brevifolium*).

VI. **ECOLOGY AND DISTRIBUTION**

ECOLOGY

Most *Campyloneurum* species are found in forests, in the tropics and subtropics of the New World. These forests are often spatially discontinuous and have been classified in numerous life zones and with many types of vegetation (cf. Gómez-Pompa, 1965, 1973; Walter, 1971; Oldeman 1990). Most *Campyloneurum* species inhabit evergreen forest, but *C. xalapense* is also found in drier semideciduous forests in Mexico.

Most species in *Campyloneurum* may occur in disturbed sites, both natural, such as landslides, treefalls and streamsides, and those made by humans, such as roadcuts. Some species, however, such as *C. anetioides*, *C. aphanophlebium*, *C. falcoideum*, *C. inflatum*, *C. macrosorum*, *C. oellgaardii*, and *C. sublucidum* occur only in forest environments not modified by humans.

Twenty-six species occur in shady and moist microhabitats inside forests (Table 3). Most of these species are low branch epiphytes or trunk climbers, and they occupy the lower zones of the forest strata. Epiphytes or climbers usually have erect leaves, rarely pendent leaves, as in *Campyloneurum sublucidum*, are found. Among terrestrial species are *C. abruptum*, *C. decurrens*, and *C. magnificum*, which are usually distributed in lowland forests below 1000 m elevation, while *C. pascoense* and *C. tucumanense* are frequently found as terrestrials, but in montane forests. Other species may occur as terrestrials, but only

on forest floors covered by thick layers of debris and mosses.

Nineteen species generally inhabit either exposed areas or open forests (Table 3). These species occur on cliffs, in rock crevices, and in the ecotone between forests and grasslands. In one locality in Costa Rica, *Campyloneurum angustifolium* has been recorded inhabiting tree canopies (Grayum & Churchill, 1989). These 19 species have wide environmental adaptations, and they can grow as epiphytes, epipetrics or terrestrials (e.g. *C. cochense*, *C. densifolium*). It is not surprising to find among these species the most widely distributed species (e.g. *C. angustifolium* and *C. phyllitidis*).

Two species, *Campylonerum cubense* and *C. oxypholis* (Table 3) occur only outside forests, i.e. cliffs in partially protected microsites.

Adaptations to strongly mesic conditions are found in *Campyloneurum anetioides*, the only species in the genus with spongy mesophyll (Wagner & Farrar, 1976). Most species occurring in forested areas have a "drip-tip" and/or curvate or hanging leaves; these adaptations probably allow draining of the leaf surface (Jungner, 1891; Richards, 1952; Dean & Smith, 1978). In species occurring in exposed areas, leaves are usually thickly chartaceous, with well-developed cartilaginous margins. In some species inhabiting different kinds of exposed areas, margins of the leaf are partially revolute (e.g. *C. angustifolium*, *C. densifolium*). Some species growing above 3000 m elevation (*C. amphostenon*, *C. cochense*, *C. densifolium*, and *C. lorentzii*) have stems covered by a white wax, which, as suggested by Bosman (1991) for *Microsorum*, may protect the stem from dessication.

Most *Campyloneurum* species inhabit montane areas between 1000 and 4500 m elevation (Fig. 21). Only eight species (*C. abruptum*, *C. acrocarpon*, *C. austrobrasilianum*, *C. coarctatum*, *C. cubense*, *C. decurrens*, *C. rigidum*, and *C. wurdackii*) frequently occur below 1000 m.

Elevational range differs among species (Fig. 21). Twenty-three species have a greater than 1000 m altitudinal range (Fig. 21; Table 9); among these species are the widely distributed species (e.g. *Campyloneurum angustifolium*, *C. brevifolium*, *C. phyllitidis*). It appears that for species growing with a less than 1000 m elevational range, their latitudinal range is more restricted than for those species having a large elevational range. Fourteen species (*C. abruptum*, *C. acrocarpon*, *C. austrobrasilianum*, *C. chrysopodum*, *C. coarctatum*, *C. costatum*, *C. decurrens*, *C. fallax*, *C. macrosorum*, *C. nitidum*, *C. ophiocaulon*, *C. pascoense*, *C. rigidum*, and *C. sublucidum*) have an altitudinal range between 600 and 1000 m, and most of them have a latitudinal range of 15º to 40º. On the other hand, ten species in the genus have a narrow altitudinal range (Fig. 21), thus *C. anetioides*, *C. centrobrasilianum*, *C. cubense*, *C. inflatum*, *C. oelgaardii*, *C. oxypholis*, *C. tenuipes*, *C. tucumanense*, *C. vulpinum*, and *C. wurdackii* occur with less than a 500 m elevational amplitude, and all are latitudinally restricted species, with less than 15º of range.

DISTRIBUTION

Campyloneurum ranges from southern Florida, the Caribbean Islands and Mexico, throughout Central America, the Andes to northern Argentina, eastern Brazil and Uruguay (Fig. 22). This genus is predominantly tropical, with occurrences in adjacent subtropics.

Most species are widespread (Table 4). The countries with more than five species are located in mountainous tropical areas; while the countries with five or fewer species are located in non-mountainous areas, mostly in the subtropics and/or on small islands (Fig. 22). Only ten species (*Campyloneurum acrocarpon*, *C. austrobrasilianum*, *C. centrobrasilianum*, *C. chrysopodum*, *C. cubense*, *C. fallax*, *C. oellgaardii*, *C. oxypholis*, *C. rigidum*, and *C. wurdackii*) are geographically restricted (i.e. found within a single political boundary).

Disjunct distributions occur in *C. inflatum* and *C. sublucidum*. These disjunctions may be explained by a lack of collections, or by specialized biological and habitat requirements. For example, *C. sublucidum* is found on calcareous rocks.

Patterns of distribution of species

The distribution of fern species has been used by Tryon (1972, 1979, 1985, 1986) to discuss the relation of geographic features to speciation. For tropical American ferns, those features were

discussed in terms of the concentration of species and of endemism in regions or regional centers.

Here the geographic information of *Campyloneurum* species is presented according to biogeographical regions (modified from Tryon, 1972), relating their floristic affinities with the history of the area, and thus allowing speculation on geographic speciation.

The six biogeographical regions are: Mexico, Central America, Caribbean Islands, Andes, Guayana and Brazil.

The Mexican region lies north of the Isthmus of Tehuantepec. Present conditions of climate and vegetation in the area are diverse (see Rzedowski, 1978). *Campyloneurum* species occur mainly in conifer, *Quercus-Liquidambar*, and tropical evergreen forests. This region contains 12 species and no endemics (Table 5). Nine of these species (*C. amphostenon*, *C. angustifolium*, *C. aphanophlebium*, *C. brevifolium*, *C. costatum*, *C. densifolium*, C. *fasciale*, *C. phyllitidis*, and *C. repens*) are widely distributed, occurring in another two or three regions more. On the other hand, three species (*C. ensifolium*, *C. tenuipes*, and *C. xalapense*) occur in one other region, the Central American. This region's affinities are closer with the Central American and Caribbean than with the Andean and Guayanan regions (Table 6). These affinities and distribution patterns may be interpreted as a result of geological events in the past. Data on the geological history of the area suggest that from the Permian to the early Cretaceous the area was separated from South America, which caused a separation of the floras. During the early Eocene, the Mexican region was closer to the Greater Antilles, and probaby, due to orogenesis and volcanism, cycles of contact may have occurred with northern Central America (cf. Coney, 1982; Savage, 1982). These Cenozoic events and changes in climate conditions, as summarized by Savage (1982), may account for the closer affinities with the northern Central American region.

The Central American region runs between the south of the Isthmus of Tehuantepec and the Isthmus of Panama. The present climate and vegetation in the area are also as varied as those found in the previous region, and they can be related to the presence of two important Cordilleras: Guatemalan and Costa Rican. The Central American region has a *Campyloneurum* flora of 18 species (Table 5), with one endemic (*C. anetioides*). Eleven of these species (*C. amphostenon*, *C. angustifolium*, *C. aphanophlebium*, *C. brevifolium*, *C. coarctatum*, *C. costatum*, *C. densifolium*, *C. fasciale*, *C. magnificum*, *C. phyllitidis*, and *C. repens*) occur in another two or more regions. This region has greater affinities with the Mexican and Andean, than with the Caribbean and Guayanan regions (Table 6). In the Central American region, two main subdivisions were recognized by Savage (1966, 1982), based on the herpetofauna: a Nuclear or Upper Central America (from southern Mexico to northern Nicaragua) and the Isthmian link or Lower Central America (from southern Nicaragua to Panama), with a different geological history (cf. Coney, 1982). These two subdivisions appear to be also important in the analysis of *Campyloneurum* regional distribution and speciation. Two species (*C. ensifolium* and *C. tenuipes*) are only found in the northern subdivision. These two species occur also in the Mexican region, reflecting perhaps the early Eocene connection between this region and the northern Central American subdivision (cf. Taylor, 1991). The northern subdivision may also have been an important source area for the flora of the southern subdivision. *Campyloneurum anetioides*, is endemic to the whole region, and probably arose in the oldest northern subdivision not long before the connection occurred between the northern subdivision and southern Central American subdivisions during the Pliocene. On the other hand, three species (*C. falcoideum*, *C. sphenodes*, and *C. sublucidum*) are restricted to the Isthmian link subdivision. These species are Andean in origin and they reflect the Pliocene contact between South and Central America.

The Caribbean region comprises the islands of the Greater Antilles, excluding the Lesser Antilles. There are four main islands (Cuba, Hispaniola, Jamaica and Puerto Rico) which have a wide variety of environments due to changes in altitude, soil types, temperature ranges and vegetation as mentioned by Howard (1973). In this region *Campyloneurum* is represented by 10 species of which two are endemics (*C. cubense*, *C. oxypholis*). Seven species (*C. amphostenon*, *C. angustifolium*, *C. brevifolium*, *C. costatum*, *C.*

densifolium, *C. phyllitidis*, *C. repens*, and *C. vulpinum*) are distributed in another two or more regions. The floristic affinities of this region are closer to the Mexican and Central American regions. These affinities may be a result of connections among these regions during the late Cretaceous (Coney, 1982). The richness of this zone appears to be related to its diversified habitats (Tryon, 1979) and its geological history of isolation after the late Eocene from the Lesser Antilles-South America and the north Central America.

The Andean region, as defined by Tryon (1972), includes the area along the Andes from 10ºN to 25ºS. The implications of the geological history of the Andean region related to biogeography and evolution have been discussed for different organisms (e.g. angiosperms, Simpson, 1975, 1979; Berry, 1982; Gentry, 1982; Molau, 1988; reptiles and amphibians, Duellman, 1979). *Campyloneurum* has wind-dispersed spores and belongs to an older group of plants, and thus it differs from many other organisms studied in the Andes. These and other intrinsic characteristics of the genus (e.g. the possibility of polyploidy), together with dynamic changes in the past, may have offered a wide range of possibilities for speciation. In the Andes, *Campyloneurum* is represented by 33 species of which 15 are endemics (*C. aglaolepis*, *C. asplundii*, *C. chrysopodum*, *C. cochense*, *C. fuscosquamatum*, *C. inflatum*, *C. lorentzii*, *C. macrosorum*, *C. nitidissimum*, *C. oellgaardii*, *C. ophiocaulon*, *C. pascoense*, *C. solutum*, and *C. tucumanense*). Both total number of species and number of endemics are higher than in any other region (Table 5). In order to understand the richness of this area *Campyloneurum* species distribution is analyzed within three subdivisions in the Andes: Northern (10°N-6°S), Middle (6-18°S) and Southern (south of 18°S). Each of the these subdivisions have a complex geology, mountain building history and paleofloristic history, as discussed in detail by Taylor (1991). Major events presented by Taylor (1991) that may have influenced speciation events in this genus are 1) in the middle and southern subdivisions mountains probably existed from the early Cretaceous, 2) the northern subdivision had mountains probably later, during the early Tertiary, 3) the cordilleras that form the Andes today had extensive uplift in the Oligocene, and 4) the last phase of the uplift of the Andes began in the Upper Pliocene. In the northern subdivision, *Campyloneurum* is represented by 31 species, five of them (*C. chrysopodum*, *C. cochense*, *C. inflatum*, *C. macrosorum*, and *C. oellgaardii*) only occur in this subdivision (Fig. 23). The Middle subdivision has 24 species and the Southern subdivision 4, both subdivisions without restricted species (Fig. 23). These results differ from the general patterns provided by Berry (1982) for *Fuchsia* sect. *Fuchsia*, and by Molau (1988) for *Calceolaria*. The richness of the Northern Division in the Andes may be a result of the presence of younger zones in the area compared to rest of the Andes (e.g. Taylor, 1991). Besides, the Northern Division is characterized by three cordilleras with humid montane vegetation that could have offered more suitable environments for diversification of *Campyloneurum*. The affinities of the whole region are closer to the Mexican and Central American, although these affinities are low (less than 25%), which may reflect the long isolation of South America.

The Brazilian region is here interpreted to include the central Brazilian shield and the south-eastern mountains ranging to 30ºS. This region is characterized by the presence of nine species, five of which are endemics (Fig. 22). The highest affinity of this region is with the Guayana, although it is low (Table 6). The high endemism in the region has also been observed in other groups of plants (angiosperms, Smith, 1962; pteridophytes in general, Brade, 1942; Tryon, 1972; and in the fern genus *Polybotrya* Moran, 1987), and may also be related to the high ecological diversity in the area as shown by Brade (1942). Another important factor that may allow the explanation of the richness of endemism in the Brazilian region is its geological history, which dates back from the Cretaceous (cf. Novaes Pinto, 1990) and also its isolation from other mountain systems in the continent.

The Guayanan region, as defined by Tryon (1972), is located on the Roraima shield. It contains six species (Table 5) of which one is endemic (*Campyloneurum wurdackii*). Its closest affinities are with the Central American and

Mexican regions. The importance of the region for species diversification has been shown for flowering plants (Maguire, 1970; Huber, 1988) and for certain fern genera (Lellinger, 1967; Tryon, 1972). For *Campyloneurum* speciation events appear to have occurred in the more isolated areas.

The Amazon area, not included in the above regions, has a flora of widely distributed *Campyloneurum* species, which mostly inhabit the foothills of the Andes and the Cordilleras of Central America. Most of the discussion of the geological history of the basin is centered around the last five million years, associated with changes in climate and vegetation in the Pleistocene (see Prance, 1982). Assuming that time is a important factor for speciation in the genus, then the evidence from the Pleistocene may account for the low endemism reported by Tryon & Conant (1975) for the Amazonian fern flora in general. In the case also of *Campyloneurum*, the Amazon area does not have endemics.

Only thirteen species occur in the subtropics of South America. Four of these species also inhabit the subtropics of North America and all of them are widely distributed. In the subtropics of South America, nine species (*Campyloneurum acrocarpon*, *C. aglaolepis*, *C. austrobrasilianum*, *C. fallax*, *C. minus*, *C. nitidum*, *C. lorentzii*, *C. rigidum*, and *C. tucumanense*) have a restricted geographic distribution.

Other non-continental areas in the Neotropics are the Lesser Antilles and other small islands of the West Indies. The Lesser Antilles have only four species (*Campyloneurum angustifolium*, *C. brevifolium* , *C. fasciale*, and *C. phyllitidis*), all of them widely distributed elsewhere. The *Campyloneurum* flora of the West Indies islands is depauperate, with only three species (*C. angustifolium*, *C. brevifolium*, and *C. phyllitidis*). These species are the ones that can grow at low altitudes in their range, as was also mentioned by Correll (1976).

In the Neotropics there are few islands isolated from the continent. The *Campyloneurum* flora of the Cocos has one species, *C. phyllitidis* (Gómez, 1975) and the Galápagos islands have two widely distributed species (*C. amphostenon* and *C. phyllitidis*). As Tryon (1970; 1972) observed, no endemics are found in these islands, which are located less than 1500 km from the mainland. These islands are also relatively young in geologic age, which may have not allowed time for speciation.

Distribution of species groups and a general overview of speciation

In this study, ten informal species groups are recognized in *Campyloneurum* (Chapter VIII) that are interpreted as evolutionary lineages.

Each of the biogeographical regions differ in the number of species groups. The Mexican region has seven species groups, the Central American has nine, the Caribbean has seven, the Andean has all ten, the Brazilian has five and the Guayanan has four (Table 7).

The common species groups for the regions are the *Campyloneurum phyllitidis* and the *C. repens* groups, which represent two succesful groups regarding dispersal, with numerous species. The *C. phyllitidis* group seems to have originated in continental America; four species in this group are restricted to one of the oldest biogeographical regions. The Brazilian has*C. nitidum*, the Andean has *C. abruptum*, the Mexican has *C. tenuipes* and the Guayanan has *C. wurdackii* . The group is presently associated with low to middle elevations and forested areas. It seems that the environment suitable for this group was partially available in most parts of America since the late Cretaceous, as can be inferred from the work of Gentry (1982) for angiosperms; although in some parts the origin of the present vegetation where the *C. phyllitidis* group is found may be recent in origin (e.g. Toledo, 1982).

The *Campyloneurum repens* group probably had a continental origin and successfully reached the Antillean region like the *C. phyllitidis* group. The former group seems to have radiated in two main mountain systems, the Andes and the eastern Brazilian Cordillera, with an ancient geological history. The Andean region has more species (*C. fuscosquamatum*, *C. macrosorum*, *C. ophiocaulon*) than the Brazilian (*C. acrocarpon* and *C. minus*). Since the former region has suffered more continuous dramatic geological changes since the early Cretaceous, it seems that speciation in this group can be due to geographic isolation. However, speciation by peripheral

divergence (Tryon, 1972), may have also ocurred within each region.

The available information indicates that the elements of the *Campyloneurum brevifolium* group occur widely in all regions, except the Brazilian. This group appears to have been succesful in radiating in different parts of tropical continental and insular America. However, its absence from the Brazilian region may be interpreted as the result of a recent origin outside of this region, since it is assumed here that all biogeographic regions were available for ancestral populations of the genus before they became isolated. The *C. brevifolium* group appears also to have a high rate for speciation, especially in the dynamic Andean region, where most of its endemic species are found.

Two species groups, the *Campyloneurum aphanophlebium* and the *C. xalapense*, are presently distributed in the Mexican, the Central American and the Andean regions. The *C. aphanophlebium* group has a clear continental origin; its present distribution is limited to the Central American and Andean regions. The center of endemism in this group seems to be the north Central American-Mexican region, an area emergent since the early Eocene. One feature of this group is the paucity of species, that can be interpreted as the result of a recent origin and the short time available for speciation.

The *Campyloneurum xalapense* group is a heterogeneous one. The pattern of regional distribution appears similar to that found in the *C. phyllitidis* group. The *C. xalapense* group occurs in all regions except in the Brazilian and Guayanan. Its elements presently grow at high-middle (*C. cochense* and *C. xalapense*) or low altitudes (*C. costatum*). It appears that this group diverged in the Mexican-Caribbean (*C. costatum* and *C. xalapense*) and in the Andes (*C. cochense*).

The elements of the *Campyloneurum amphostenon* and the *C. angustifolium* groups show a similar pattern of distribution in five of the regions (Brazilian, Andean, Caribbean, Central American and Mexican). Both are more speciose in the Andean and Brazilian region. Both groups seem to have speciated and radiated in middle to high altitude environments. The*Campyloneurum amphostenon* group seems to combine two important intrinsic features, high rate for speciation and high capacity for dispersal. These features, combined with regional isolation and geological changes has resulted in the presence of vicarious species between the oldest mountainous regions in South America: the Brazilian (*C. fallax*) and the Andean (*C. lorentzii*) regions. These features, together with the geologic dynamism of the areas, may account for the presence of extreme variation within some taxa, as for example in *C. amphostenon* and *C. densifolium*.

The *C. angustifolium* group seems to have similar intrinsic characteristics as discussed for the *C. amphostenon* group. Vicarious species are found between the Mexican-north Central American (*C. ensifolium*) and the central Brazilian Plateau (*C. centrobrasilianum*). High speciation rate appears to occur in the Andes, but is not necessarily related to geographic isolation, as seen in the case of *C. aglaolepis* and closely related species (*C. angustipaleatum*, *C. austrobrasilianum*).

The elements of the *Campyloneurum sphenodes* group occur in three regions, Central American, Andean and Guayanan, all of them in continental America. This group has a great number of species in the Andean region, where they presently occur from middle to low elevations. It seems that this group migrated to the Guayanan and Central American regions recently since there are no endemics there.

The *Campyloneurum vulpinum* group has an unclear origin. It may be the only lineage that may have arisen in the Caribbean region. *Campyloneurum vulpinum* may later have migrated to South America. On the other hand, if this lineage was of South American origin, it may had enough time since the late Eocene for dispersal and speciation by isolation. This group apparently had a low rate of speciation.

The *Campyloneurum magnificum* group has several primitive characteristics in the genus, such as division of the lamina, undivided primary areoles and terminal position of the sori, as was discussed in Chapter IV. The elements of this group occur today in the Andean and Central American region, mostly in mesic environments. The present distribution of the two species may support the idea that this group migrated recently from South America to the

Lower Central America and Lesser Antilles, areas geological younger (Figs. 35, 41). It appears that this group has not been succesful in colonizing different habitats, and that his capacity of dispersal is rather low.

In conclusion, the distribution of the species groups in the regions suggests that the genus may have arose before the late Jurassic. Post Jurassic geological and environmental changes may have allowed the speciation by isolation in the regions. The genus appears to have a middle elevation origin, and may have had a high rate of speciation, at least in some of the lineages. The Pliocene changes allowing the connection of South with Central America have allowed the exchange of floras between regions, but the lapse of time has probably not been sufficient for numerous speciation events to have occurred in the newly connected areas.

VII. **USES AND CONSERVATION**

USES

Campyloneurum species are occasionaly used for decorative, therapeutical or religious purposes.

The use of *Campyloneurum* as a decorative plant has not reached the degree of acceptance found with polypodiaceous Asian genera. Only two species of the 47 in the genus are cultivated as garden or interior plants; Hoshizaki (1982) and Jones (1987) listed *C. amphostenon* and *C. phyllitidis* in cultivation in temperate zones.

Only four *Campyloneurum* species have popular names or are probably used as medicine for a disparate assortment of illnesses. The common names and uses of some species of *Campyloneurum* were recorded from herbaria labels (Table 8). All these are widespread, lowland species, common in the areas that they are used. The common name "calaguala" is applied in the Andes to different genera of Polypodiaceae with entire leaves. In Paraguay this name is used for *C. nitidum*.

CONSERVATION

In the Neotropics, major efforts in conservation and protection of the environment have been focused on the tropical lowland rain forests. However, other habitats in the region, including disturbed sites, should be incorporated into efforts to protect and preserve biotic resources. One reason for this approach is the fact that species such as those of the genus *Campyloneurum* occur in a great variety of mountainous environments from rock crevices in grasslands to evergreen or semi-deciduous forests, as was discussed in Chapter VI.

Based on taxonomic and biogeographical information, conservation issues for *Campyloneurum* are here tentatively addressed, recognizing endangered species, species with an unknown conservation status, and species with probably adequate and unthreatened populations. In the future, it will be necessary to reevaluate these categories with empirical data on the size and status of populations.

Those species with small latitudinal and altitudinal ranges, and growing in habitats that are being destroyed are considered to be probably endangered. Twelve species belong to this category: *Campyloneurum acrocarpon*, *C. anetioides*, *C. centrobrasilianum*, *C. chrysopodum*, *C. fallax*, *C. inflatum*, *C. macrosorum*, *C. oellgaardii*, *C. oxypholis*, *C. sublucidum*, *C. tucumanense*, and *C. wurdackii*. All these species appear to be restricted to forested areas, except *C. acrocarpon*, which occurs in exposed slopes (Table 9). Some species, such as *C. oellgaardii*, *C. sublucidum*, and *C. wurdackii* are currently known from fewer than three localities. Among these endangered species are also those that inhabit the forest in southeastern Brazil, an area with high deforestation rates (Mori et al., 1988; Prance & Campbell, 1988).

Six species (*Campyloneurum decurrens*, *C. falcoideum*, *C. lorentzii*, *C. magnificum*, *C. minus*, and *C. rigidum*) are here considered species with populations of unknown status. They have larger altitudinal and latitudinal ranges than those of the previous category, but are known from a rather small number of localities. They inhabit either forests or open forested areas (as defined in Chapter VI).

The majority of species do not appear to be endangered since they have large altitudinal and latitudinal distributions , and occur in a wide variety of habitats.

VIII. **INFRAGENERIC GROUPS AND PHYLOGENY**

SPECIES CONCEPT

The available data for *Campyloneurum* comes from the study of field and herbarium specimens, and from distributional and ecological information. Based on these sources, the morphological species definition (Haufler, 1989) is employed in this treatment.

The infraspecific category of variety has been used here in two cases, for *Campyloneurum amphostenon* and *C. nitidissimum*. The use of variety has been applied when some morphological characters differences are obvious but still overlap.

INFRAGENERIC GROUPS

Campyloneurum has never been formally subdivided, and that is not the intention here either. Herein are presented ten informal species groups, based on the sharing of at least three morphological characters.

The groups are intended to represent a hypothesis of evolutionary relationships within the genus (Fig. 51). In this study, it is considered that all descend from a common ancestor characterized by pinnatifid leaves, and undivided primary areoles with 2-4 excurrent free veinlets. This ancestor may have been a terrestrial plant, growing in humid low to middle elevations. Each group then independently followed speciation at different rates and with individualistic patterns.

1. The *Campyloneurum magnificum* group. This group is composed of *Campyloneurum decurrens* and *C. magnificum*. These species are the only ones with pinnatifid leaves. Their stem diameter is more than 10 mm wide, short-creeping, and the stem scales are broadly ovate, clathrate with differentiated margins. The venation in this group is that described as type 4, which is interpreted as the least advanced in the genus. This species group is restricted to low elevation forest habitats, and might represent an old evolutionary line in the genus. Pinnate leaves are commonly considered a primitive character state among Polypodiaceae (e.g. Hovenkamp, 1986), and this view is probably true for *Campyloneurum*, too.

2. The *Campyloneurum repens* group. *Campyloneurum acrocarpon*, *C. fasciale*, *C. fuscosquamatum*, *C. macrosorum*, *C. minus*, *C. ophiocaulon* and *C. repens* have long-creeping stems, usually less than 5 mm wide, distant leaves (except in *C. acrocarpon* and *C. minus*), short petiolate lamina with decurrent lamina bases, and undivided non-costal primary areoles. This group occurs today from low to middle elevations, and most species inhabit disturbed areas. The undivided primary areoles are considered to be a less advanced character in the genus. However, in the *C. repens* group other characters such as the medial position of the sori, entire leaves and climbing habit are considered to be more advanced. Here, this group is considered closer to the *C. sphenodes* and the *C. aphanophlebium* groups than to the *C. magnificum* group.

3. The *Campyloneu*rum *sphenodes* group. This group includes *Campyloneurum chrysopodum*, *C. coarctatum*, *C. falcoideum*, *C. inflatum*, *C. oelgaardii*, *C. sphenodes*, and *C. sublucidum* , which are characterized by a stem diameter less than 5 mm wide, more than 3 areoles between costa and margin, areoles rarely undivided and usually carrying two excurrent veinlets, and broadly oblong-lanceolate leaves with cuneate bases. This group shows some morphological similarities with the *C. repens* species group, but differs by the long petioles, broadly oblong-lanceolate lamina, and cuneate bases. All species are restricted to continental tropical America, where they occur in mountainous areas of Central and South America as climbing epiphytes. The position of this group appears to be close to the *C. repens* group, but more advanced.

4. The *Campyloneurum aphanophlebium* group. This includes *Campyloneurum anetioides* and *C. aphanophlebium*. They both have undivided primary non-costal areoles, closely spaced leaves, free veinlets along the margin, and medial sori. This group is also characterized by a specialized

indument of branched pluricellular hairs that occupy both sides of the leaf. It appears from the venation pattern and indument features that this group has affinities with the *C. repens* and *C. sphenodes* groups.

5. The *Campyloneurum phyllitidis* group. *Campyloneurum abruptum*, *C. nitidum*, *C. phyllitidis*, *C. tenuipes*, and *C. wurdackii* are characterized by a short-creeping stem, stem diameter more than 4 mm wide, prominent primary veins, more than 5 rows of areoles between costa and margin, and usually symmetrically divided primary areoles, or rarely undivided. All species occur typically at low elevations as terrestrials or low trunk climbers. This group is interpreted as a line independent from the *C. amphostenon* group because of the more complex venation, and separate from the *C. brevifolium* group because of the equal division of areoles.

6. The Campyloneurum brevifolium group. This includes *Campyloneurum brevifolium*, *C. nitidissimum*, *C. pascoense*, and *C. tucumanense*. These species are terrestrial or creeping trunk epiphytes, characterized by a stem diameter more than 6 mm wide; large leaves, non-costal areoles asymmetrically divided, with prominent primary and secondary veins. *Campyloneurum nitidissimum* is the only species with non-clathrate scales. This group resembles the *C. phyllitidis* group in stem diameter and stem scale characters. The complexi pattern of venation of the *C. brevifolium* group is interpreted as highly specialized.

7. The *Campyloneurum amphostenon* group. *Campyloneurum amphostenon*, *C. asplundii*, *C. chlorolepis*, *C. densifolium*, *C. fallax*, *C. lorentzii*, *C. rigidum*, and *C. solutum* have a stem diameter less than 6 mm wide; lamina with 2-5 rows of areoles between costa and margin, divergent angle of primary veins less than 50º, and primary non-costal areoles symmetrically divided with one veinlet per areole. In *C. amphostenon*, *C. rigidum* and *C. solutum* stem scales are clathrate or slightly clathrate, while in *C. asplundii* and *C. chlorolepis* they are non-clathrate. This group is widespread in mountainous environments of continental and insular tropical America, where it occurs from middle to high elevations. Because of the dynamic geological history of mountain environments in the Neotropics, populations of this group may have repeatedly had contacts and isolations, which is now reflected in the high number of species. The *Campyloneurum amphostenon* group is considered to be one of the advanced groups in the genus.

8. The *Campyloneurum xalapense* group. This group includes *Campyloneurum costatum*, *C. cochense*, and *C. xalapense*. This is a heterogeneous group; most of the characters appear intermediate between *C. amphostenon* and *C. phyllitidis*, and for this reason is located among them in the evolutionary diagram (Fig. 51). The *C. xalapense* group is characterized by having the stem usually more than 5 mm wide, leaves with more than 5 areoles between the costa and margin, and primary veins inconspicuous or partially prominulous on one side of the lamina.

9. The *Campyloneurum angustifolium* group. This group includes *Campyloneurum aglaolepis*, *C. angustifolium*, *C. angustipaleatum*, *C. austrobrasilianum*, *C. centrobrasilianum* and *C. ensifolium*. This is a very homogeneous group that shares stem diameters less than 4 mm wide, lamina with 1-3 rows of areoles between costa and margin, and inconspicuous primary veins. They are epiphytes that occur mostly at middle elevations.

10. The *Campyloneurum vulpinum* group. This is composed of *Campyloneurum cubense*, *C. oxypholis*, and *C. vulpinum*, and is related to the *C. angustifolium* and the *C. repens* groups. The three species are characterized by primary veins 50-65º divergent from the costa, with undivided primary non-costal areoles, and narrowly lanceolate, thin chartaceous leaves.

PHYLOGENY

During the last thirty years many genealogical relationships in different kinds of organisms have been discussed on the basis of hypotheses generated by cladistic analyses under the assumption of parsimony. The results of this kind of analysis have been compared to the

current classification and/or to other hypotheses. Here a cladistic analysis is attempted for the first time for *Campyloneurum*.

Species level

Twenty-three characters were used in the analysis (Table 10). A hypothetical polypodiaceous ancestor was included in the analysis as an outgroup, because earlier attempts using *Microgramma*, *Niphidium*, *Pleopeltis*, and *Pyrrosia* as outgroups produced more than 1000 unresolved polytomic trees.

The characters used in this analysis were mostly qualitative. Most characters had binary states and only six characters had multistate conditions (Table 10). Not all characters found in the genus were used because of a lack of information for the majority of species. Examples include, for example, chromosome number, spore morphology, and anatomical details of the stem and leaf. The data matrix used for this analysis (Table 11) has very few missing data, and these correspond to characters where the states were defined with a binary condition rather than a multistate.

A consensus tree for the species (Fig. 52) was obtained from the first 600 trees; the length of the shortest tree was 86, and the consistency index was 0.326. The low value of the consistency index may suggest high homoplasy in the characters used. Homoplasy is one of the problems that was encountered by Hovenkamp (1986) and Bosman (1991) while performing cladistic analyses in other polypodiaceous fern genera.

The consensus tree for the species shows a major polytomy at the base of the tree, with one branch going to the hypothetical ancestor, one to *Campyloneurum magnificum*, another to *C. decurrens* and another to the entire-leaf species (Fig. 52). Other polytomies are found among the species with narrow leaves, those with divided areoles and others with undivided areoles.

When the ideas of phenetic relationships, as presented before (Fig. 51) are compared to the results of the cladistic analysis, consistency is found to some extent. For example, according to both approaches *Campyloneurum brevifolium* comes out with *C. pascoense* and *C. tucumanense*, and *Campyloneurum aphanophlebium* comes out near to *C. anetioides*.

Other groups are different. For instance *Campyloneurum aglaolepis*, *C. ensifolium*, *C. angustipaleatum*, *C. austrobrasilianum*, and *C. centrobrasilianum* are separated from *C. angustifolium*, which on the other hand is placed closer to *C. amphostenon*, perhaps indicating a close relationship .

In the cladogram *Campyloneurum phyllitidis* seems closer to the clade of *C. brevifolium*. Two of the species (*C. nitidissimum*, *C. tenuipes*) that were assumed to be allies of *C. phyllitidis* are located closer, while others are scattered in the tree: *C. abruptum*, *C. nitidum*, and *C. wurdackii*. *Campyloneurum xalapense* is located close to *C. tenuipes* as was anticipated (Fig. 51). Allied species of *C. xalapense*, however, are separated: *C. cochense* comes out closer to *C. densifolium* and *C. nitidum* , and *C. costatum* between *C. amphostenon* and allied species, and *C. cubense*, *C. leuconeuron* and *C. rigidum*.

In the cladogram (Fig. 52), the species with undivided primary areoles (*Campyloneurum acrocarpon*, *C. chrysopodum*, *C. coarctatum*, *C. falcoideum*, *C. fasciale*, *C. fuscosquamatum*, *C. inflatum*, *C. minus*, *C. oellgaardii*, *C. ophiocaulon*, *C. repens*, *C. sphenodes* and *C. sublucidum*) are located closely together, as was previously anticipated; however, they come out far away from the ancestor. Species with undivided areoles come out together with species considered to be closely related to other species: *C. abruptum*, *C. cochense*, *C. densifolium*, *C. lorentzii*, *C. oxypholis*, and *C. wurdackii*. Some of these species were difficult to assess in regards to their affinities, such as *C. cochense* and *C. oxypholis*.

Although the cladistic analysis was not completely satisfactory due to homoplasy, in general the results support the classification presented in this revision.

Species-group level

Twelve characters were used for this analysis (Table 12). These characters were chosen because most of them only allowed two conditions in six groups in the data matrix (Table 13). Three of these characters had a multistate condition (Table 12). Similar to the species analysis, a hypothetical ancestor was defined and the character states were given based on

comparisons to other genera of the Polypodiaceae.

A consensus tree (Fig. 53) was obtained from a total of 149 trees; the length of the shortest tree found was 28, and the consistency index was 0.536. Polytomies were found at the base of the tree and in two other places.

The information from the tree shows that the *Campyloneurum magnificum* group is closer to the ancestral type of the genus than any other group (Fig. 53). This agrees with the analysis performed for the species (Fig. 52), and also with the phenetic hypothesis (Fig. 51). The positions of the *C. angustifolium* and *C. amphostenon* groups are interesting. The former appears closer to the ancestral type than the *C. amphostenon* group, which previously had four of its components closer to the species of the former group (Fig. 52). The position of the *C. angustifolium* group may be interpreted as representing ancestral features for all simple leaf species; this idea was intuitively proposed by Lellinger (1988).

The *Campyloneurum xalapense* group was placed twice in the data matrix (Table 13) because character #6, stem diameter, was variable within the group. It is difficult to interpret the position of this group in the tree: the group was heterogeneous, with features found in both *C. amphostenon* and *C. phyllitidis* groups, but it did not occur among them (Fig. 53).

The closeness of the groups with long-creeping stems and mostly undivided areoles (*Campyloneurum aphanophlebium*, *C. repens*, *C. sphenodes*, and *C. vulpinum* groups) shows that they in fact represent close lineages, as previously anticipated. The position of the *C. aphanophlebium* group closer to the *C. sphenodes* group than to the *C. repens* group is very similar to the taxonomic interpretation at the species level (Chapter IX).

The *Campyloneurum phyllitidis* and the *C. brevifolium* groups appear together and far away from the ancestor of the groups (Fig. 53). These positions differ from that of the species-level analysis (Fig. 52), where most of the species belonging to both groups appeared near the hypothetical ancestor.

Phylogenetic interpretation

During the last ten years the generic concept of *Campyloneurum* has been discussed among pteridologists (cf. Tryon & Tryon, 1982 b; Lellinger, 1988, León, in press). The scope of this discussion has implications in the phylogenetic interpretation of the genus because it deals with its monophyletic status. The two cladistic analyses made here showed that the pinnate species are not totally incorporated in the clade of the entire-leaf species. This can be used to support the idea of the exclusion of those species with pinnate leaves. However, both analyses are problematic because of homoplasy and polytomies. This classification, as presented in Chapter IX and as was discussed earlier, accepts the entire genus as monophyletic, based on morphological similarities, without considering that only apomorphies have to define the clade.

IX. **TAXONOMIC TREATMENT**

Campyloneurum C. Presl, Tent. Pterid. 189. 1836.
Lectotype: (chosen by J. Smith, 1875) *Campyloneurum repens* (Aublet) C. Presl.
*Polypodium*_ subg. Cyrtophlebium R. Brown, *in* Bennet & Brown, Pl. Jav. Rar. 4. 1838.
Cyrtophlebium (R. Br.) J. Sm., J. Bot. 4: 58. 1841.
Hyalotricha Copel., Amer. Fern J. 43: 12. 1953.
Type: *Hyalotricha anetioides* (Christ) Copel. (*Polypodium anetioides* Christ), not Dennis, 1949.
Hyalotrichopteris W. Wagner, Taxon 27: 548. 1978. *Nom. nov.* for *Hyalotricha* Copel.

Stem short or long creeping, sometimes branched, with clathrate or non-clathrate scales, phyllopodia present. Leaves simple or 1-pinnate, homophyllous, 10-300 cm long, glabrate or pubescent, or scales on the costa; petiole usually present and articulate. Costa usually prominent on both sides of the lamina, veins areolate, primary veins usually parallel, divergent from the costa, secondary veins transverse, forming primary areoles, these with 1-6 included veinlets, tertiary veins or veinlets free or anastomosing, simple or furcate, excurrent, transverse, rarely recurrent; excurrent veinlets connected sometimes to secondary veins forming secondary areoles, in a few cases veinlets in secondary areoles forming tertiary areoles, apex of free

veinlets with hydatodes. Sori exindusiate, usually medial to apical on the free veinlet, or at the junction of two veinlets, in 2-4 (-6) series between secondary veins; paraphyses simple, filamentous or dendritic, or absent. Spores monolete, slightly verrucate or verrucate. Basic chromosome number: 2n= 74, 148.

The genus comprises epiphytic, creeping or terrestrial plants. It grows from southern U.S.A., Mexico, Central America, Antilles, Colombia, Venezuela to Bolivia and Brazil. In this treatment, forty-seven species are recognized, most of them from the American tropics.

The characters of the key apply to mature leaves and individuals. Complete specimens are required, especially among narrow leaved species, where stem scales have many valuable characters.

The number of areoles between the costa and the leaf margin includes both costal and non-costal areoles. Prominence of the veins and angle of divergence of the primary veins from the costa should be examined at the central part of the leaf, and does not usually require the use of a microscope. However, a stereomicroscope will be required to examine the indument and stem scales.

Some species are mentioned two or more times in the key when characters may overlap.

Key to species

1. Leaves 1-pinnate 2
1. Leaves simple. 3
2. Areoles of the pinna with 2-3 excurrent veinlets; pinna width less than 4 cm (Colombia, Venezuela, Martinica, southern Brazil). 19. *C. decurrens*
2. Areoles of the pinna with 3-5 excurrent veinlets; pinna width more than 5 cm (Panama to Bolivia, Trinidad, southern Brazil). 29. *C. magnificum*
3. Stem usually more than 6 mm wide. 4
3. Stem usually equal or less than 5 mm wide. 17
4. Primary veins inconspicuous, or conspicuous and prominulous in different degrees on each side of the lamina, or prominulous near the costa on both sides of the lamina. 5
4. Primary veins conspicuous, prominulous or prominent to the same degree on each side of the lamina. 9
5. Lamina lanceolate or narrowly obovate; bases narrow cuneate (southern U.S.A. to Panama, Greater Antilles, Trinidad, Venezuela and Ecuador). 17. *C. costatum*
5. Lamina linear-lanceolate or narrowly lanceolate, bases attenuate. 6
6. Primary veins conspicuous, prominulous from the costa to the margin on one side of the lamina; 4-7 primary areoles between the margin and costa. 7
6. Primary veins inconspicuous; 2-5 primary areoles between the margin and costa. 8
7. Stem scales subadpressed, with well differentiated margins, 2-3 (-4) mm long; stem usually pruinose (Colombia to Ecuador). 16. *C. cochense*
7. Stem scales spreading, without differentiated margins, 3-6 mm long; stem not pruinose (Mexico to Costa Rica). 47. *C. xalapense*
8. Stem scales with acuminate apices, 4.5-7 mm long, cells oblong or broadly oblong (Mexico to Bolivia). 20. *C. densifolium*
8. Stem scales with acute or obtuse apices, 3-4 mm long, cells broadly ovate (Bolivia to Argentina). 27. *C. lorentzii*
9. Stem scales narrowly ovate, three times or more longer than broader. 10
9. Stem scales ovate or broadly ovate, less than three times longer than broader. 12
10. Lamina bases cuneate; lamina long petiolate, petiole length 1/4-1/2 of the lamina (Mexico to Honduras). 43. *C. tenuipes*
10. Lamina bases abruptly cuneate then decurrent or attenuate; lamina short petiolate, petiole length less than 1/5 of the lamina. 11
11. Stem scales distinctly clathrate, cell lumen translucent; lamina herbaceous-chartaceous; primary non-costal areoles usually undivided, rarely symmetrically divided. (Colombia to Bolivia and western Brazil). 1. *C. abruptum*
11. Stem scales non-clathrate, cell lumen dark yellow brown; lamina subcoriaceous or

coriaceous; primary non-costal areoles asymmetrically divided (Colombia to Bolivia). 32. *C. lucidum*

12. Primary non-costal areoles undivided or symmetrically divided only to secondary areoles. 13
12. Primary non-costal areoles asymmetrically divided to secondary and tertiary areoles. 15
13. Lamina bases cuneate, long petiolate; petiole length more than 1/3 of the lamina; more than 16 areoles between the costa and margin (northwestern Ecuador). 33. *C. oellgaardii*
13. Lamina bases attenuate, short petiolate; petiole length usually less than 1/3 of the lamina; equal or less than 16 areoles between the costa and margin. 14
14. Primary areoles undivided; lamina apices and bases attenuate; stem scales slightly bullate, 1-2 (-3) mm long (southeastern Brazil). 2. *C. acrocarpon*
14. Primary areoles usually divided; lamina apices acuminate and bases attenuate; stem scales flattish, 4-8 mm long (southern U.S.A., Mexico, Central America, Antilles to Bolivia and central Brazil). 37. *C. phyllitidis*
15. Secondary veins inconspicuous or slightly prominulous, same color as the leaf tissue. (Mexico, Central America, Antilles, Venezuela to Bolivia). 11. *C. brevifolium*
15. Secondary veins conspicuous, prominulous, usually stramineous. 16
16. Stem scales 8-10 mm long, more than 2.5 mm wide; laminae chartaceous or subcoriaceous (Ecuador to Bolivia). 36. *C. pascoense*
16. Stem scales 5-6 mm long, 1-2.5 mm wide; laminae herbaceous (northern Argentina). 44. *C. tucumanense*
17. Phyllopodia distance more than 7 mm apart. 18
17. Phyllopodia distance 6 mm apart or less. 36
18. Primary veins 40-55° (-60°) divergent from the costa, inconspicuous or sometimes slightly prominulous abaxially. 19
18. Primary veins 60-80° divergent from the costa, prominulous or prominent to the same degree on both sides of the lamina. 26
19. Lamina broadly lanceolate, shining on both sides of the lamina; 5-6 primary areoles between the costa and margin (Costa Rica and Ecuador). 42. *C. sublucidum*
19. Lamina lanceolate or narrowly lanceolate; dull on one side of the lamina; 2-5 primary areoles between the costa and margin. 20
20. Primary non-costal areoles mostly undivided; stem 1-2 mm wide. 21
20. Primary non-costal areoles divided; stem more than 2 mm wide. 22
21. Primary veins 50-70° divergent from the costa; stem scales clathrate, peltate, falcate (Costa Rica, Panama, southwestern Colombia). 22. *C. falcoideum*
21. Primary veins 30-40° divergent from the costa; stem scales non-clathrate, mostly pseudopeltate, narrowly ovate (Haiti, Dominican Republic, and from Ecuador to Bolivia, and central Brazil). 45. *C. vulpinum*
22. Stem scales spreading, narrowly ovate. 23
22. Stem scales subadpressed or adpressed, ovate or ovate lanceolate. 24
23. Stem scales distinctly clathrate, cell lumen usually transparent; scales with oblong cells (Mexico, Central America, Antilles, Venezuela to northern Argentina). 4. *C. amphostenon*
23. Stem scales slightly clathrate, cell lumen usually yellowish; scales with narrowly oblong cells (Colombia, Venezuela to Peru). 40. *C. solutum*
24. Apices of stem scales acute or obtuse; stem scales 3-4 mm long (Bolivia and northern Argentina). 27. *C. lorentzii*
24. Apices of stem scales acuminate; stem scales 4-7 mm long. 25
25. Lamina linear-lanceolate; cells of stem scales oblong or broadly oblong; stem scales light brown in mass (Mexico to Panama, Cuba, and from Colombia to Bolivia). 20. *C. densifolium*
25. Lamina lanceolate; cells of stem scales roundish or broadly oblong; stem scales pinkish brown in mass (southeastern Brazil). 23. *C. fallax*
26. Stem scales with obtuse apices. 27
26. Stem scales with acuminate apices. 28
27. Stem scales slightly bullate, with non-differentiated margins; stem scales broadly ovate (southeastern Brazil).

2. *C. acrocarpon*

27. Stem scales flat, with differentiated margins; stem scales ovate (Colombia and Venezuela to Bolivia). 34. *C. ophiocaulon*
28. Margins of stem scales differentiated in color and cell disposition. 29
28. Margins of stem scales not differentiated. 32
29. Petiole length more than 1/3 of the lamina; lamina base cuneate, if narrowly cuneate then stem scales narrowly ovate. 30
29. Petiole length less than 1/3 of the lamina; lamina base decurrent or narrowly cuneate. 31
30. Leaves more than 50 cm long; stem scales 2 mm or more wide (northwestern Ecuador). 33. *C. oellgaardii*
30. Leaves less than 50 cm long; stem scales less than 1 mm wide (Costa Rica to Peru). 41. *C. sphenodes*
31. Stem scales clathrate, subadpressed, caducous; sori without paraphyses (Mexico, Central America, Greater Antilles to Bolivia and central Brazil). 38. *C. repens*
31. Stem scales slightly clathrate, spreading, persistent; sori with long filamentous paraphyses (Colombia and Venezuela). 28. *C. macrosorum*
32. Lamina ovate, long petiolate, petiole usually more than 10 cm long. 33
32. Lamina lanceolate, short petiolate, petiole usually less than 5 cm long. 34
33. Cell lumen of stem scales translucent colorless; cells narrowly oblong; stem scales dark brown in mass. Costa Rica to Bolivia dark brown in mass (Costa Rica to Bolivia and western Brazil). 15. *C. coarctatum*
33. Cell lumen of stem scales yellowish; cells roundish; stem scales brown in mass (Colombia and Peru). 26. *C. inflatum*
34. Stem scales peltate, base with one long auricle; stem 1-2 mm wide; lamina base narrowly cuneate (Costa Rica, Panama, southwestern Colombia). 22. *C. falcoideum*
34. Stem scales pseudopeltate, base with two symmetrical auricles; stem 2-3 mm wide; lamina base decurrent. 35
35. Stem scales distinctly clathrate, cell lumen translucent (Mexico to Bolivia). 24. *C. fasciale*
35. Stem scales non-clathrate; cell lumen dark yellow or obsolete (Colombia to Bolivia). 25. *C. fuscosquamatum*
36. Primary areoles 6 or more between the costa and margin. 37
36. Primary areoles 5 or less between the costa and margin. 46
37. Leaves puberulous; hairs spreading on both sides of the lamina (Belize to Bolivia and western Brazil). 8. *C. aphanophlebium*
37. Leaves glabrous or glabrescent; hairs if present spreading abaxially. 38
38. Primary veins inconspicuous or slightly prominulous near the costa, and with same color as the leaf tissue. 39
38. Primary veins prominulous or prominent; stramineous or darker than the leaf tissue. 42
39. Lamina oblanceolate or narrowly obovate (southern U.S.A. to Panama, Greater Antilles, Trinidad, Venezuela and Ecuador). 17. *C. costatum*
39. Lamina linear-lanceolate or narrowly lanceolate. 40
40. Scales of the stem with acuminate apices; cells of stem scales narrowly oblong (Mexico to Costa Rica). 47. *C. xalapense*
40. Scales of the stem with obtuse or short acuminate apices; cells of stem scales oblong or roundish. 41
41. Scales of the stem slightly bullate, with obtuse apices, 2-2.5 mm long; primary non-costal areoles undivided (southeastern Brazil, Argentina and Paraguay). 30. *C. minus*
41. Scales of the stem flattish, with short acuminate apices, ca.4 mm long; primary non-costal areoles usually divided (Cuba, Jamaica and Haiti. 18. *C. cubense*
42. Apices of the scales of the stem obtuse or acute. 43
42. Apices of the scales of the stem long acuminate. 44
43. Stem scales ovate; primary veins 65-70º divergent from the costa (southeastern Brazil. 2. *C. acrocarpon*
43. Stem scales broadly ovate; primary veins 50-60° divergent from the costa (southeastern Brazil, Argentina, Uruguay, and Paraguay). 31. *C. nitidum*
44. Petiole length 1/4-1/2 of the lamina; lamina

base cuneate (Mexico, Guatemala and Honduras). 43. *C. tenuipes*
44. Petiole length less than 1/8 of the lamina; lamina base attenuate. 45
45. Primary veins prominulous or prominent to the same degree on both sides of the lamina, approximately straight (southern U.S.A., Central America, Antilles, Colombia to Bolivia and central Brazil). 37. *C. phyllitidis*
45. Primary veins prominulous usually adaxially, slightly prominulous abaxially, conspicuously sinuous (Mexico to Costa Rica). 47. *C. xalapense*
46. Leaves puberulous; hairs scattered on both sides of the lamina. 47
46. Leaves glabrescent; hairs if present scattered abaxially. 48
47. Lamina spathulate, apex obtuse; plants usually less than 10 cm long (Nicaragua, Costa Rica and Panama). 5. *C. anetioides*
47. Lamina narrowly obovate, apex acuminate or subcaudate; plants usually more than 10 cm long (Belize to Bolivia and western Brazil). 8. *C. aphanophlenium*
48. Primary non-costal areoles undivided; stem 1-2 mm wide. 49
48. Primary non-costal areoles mostly divided; if primary areoles undivided then stem more than 3 mm wide. 50
49. Stem scales ovate, slightly bullate (Brazil, Argentina and Paraguay). 30. *C. minus*
49. Stem scales narrowly ovate, plane (western Venezuela). 14. *C. chrysopodum*
50. Lamina ovate with a cuneate then decurrent base; some primary areoles asymmetrical divided (southern Venezuela). 46. *C. wurdackii*
50. Lamina linear or linear-lanceolate, base attenuate; primary areoles symmetrically divided. 51
51. Lamina linear-lanceolate, more than 1.5 cm wide. 52
51. Lamina linear or narrowly obovate, less than 1.5 cm wide. 62
52. Stem scales non-clathrate; cell lumen same color as the cell wall. 53
52. Stem scales slightly or distinctly clathrate; cell lumen translucent or yellowish. 54
53. Stem scales dark brown in mass; phyllopodia 4-7 mm apart (Venezuela to Bolivia). 9. *C. asplundii*
53. Stem scales whitish or light brown in mass; phyllopodia 1-2 mm apart (Colombia, Venezuela to Bolivia, and central-southern Brazil). 13. *C. chlorolepis*
54. Stem scales broadly ovate, with obtuse apices. 55
54. Stem scales ovate or narrowly ovate, with acute or acuminate apices 56
55. Lamina dull, dark green adaxially; usually 5 or more areoles between costa and margin (southern Brazil to Argentina). 31. *C. nitidum*
55. Lamina bright light green on both sides; usually 3 or less areoles between costa and margin (southeastern Brazil). 39. *C. rigidum*
56. Primary veins 60-75º divergent from the costa; primary areoles 4-7 between the costa and margin. Mexico to Costa Rica. 47. *C. xalapense*
56. Primary veins 40-55º (-60º) divergent from the costa; primary areoles usually 1-5 between costa and margin. 57
57. Stem scales adpressed, broadly lanceolate; 2.5-3 mm wide (Mexico, Central America to Bolivia). 20. *C. densifolium*
57. Stem scales spreading or subadpressed, ovate or narrowly ovate. 58
58. Stem usually long-creeping; stem scales dark brown, bright, cell lumen yellowish; lamina base usually narrowly cuneate (Venezuela to Bolivia). 40. *C. solutum*
58. Stem usually short-creeping; stem scales brown, dull; cell lumen usually translucent; lamina base decurrent. 59
59. Stem scales with differentiated margins (Cuba, Jamaica and Haiti). 18. *C. cubense*
59. Stem scales without differentiated margins. 60
60. Lamina linear or linear lanceolate; primary areoles 1-3 between costa and margin (southern U.S.A. to Bolivia, Antilles, central Brazil). 6. *C. angustifolium*
60. Lamina lanceolate or narrow lanceolate; primary areoles 2-5 between costa and margin. 61
61. Stem scales 1.5-2 mm wide; stem usually pruinose, 3-5 mm wide (Mexico, Central

America, Antilles, Venezuela to Argentina). 4. *C. amphostenon*

61. Stem scales 1-1.5 mm wide; stem never pruinose, 2-2.5 mm wide (Haiti). 35. *C. oxypholis*
62. Lamina yellow bright green to the same degree on both sides (southeastern Brazil). 39. *C. rigidum*
62. Lamina dark bright green or dull to different degrees on either side. 63
63. Lamina lanceolate or linear-lanceolate, more than 1 cm wide. 64
63. Lamina linear, less than 1 cm wide. 68
64. Lamina narrowly obovate; stem scales with differentiated margins; stem never pruinose (Cuba, Jamaica and Haiti). 18. *C. cubense*
64. Lamina linear-lanceolate; stem scales with or without differentiated margins; stem usually pruinose. 65
65. Stem scales whitish (Colombia, Venezuela to Bolivia and central-southern Brazil). 13. *C. chlorolepis*
65. Stem scales brown. 66
66. Stem scales adpressed, broadly ovate or ovate (Mexico, Central America to Bolivia). 20. *C. densifolium*
66. Stem scales spreading, narrowly ovate. 67
67. Stem scales 3-5 mm long, 1-1.5 mm wide, cell lumen occluded; lamina base usually decurrent (Venezuela, Ecuador to Bolivia). 9. *C. asplundii*
67. Stem scales 4-7 mm long, 1.5-2.5 mm wide, cell lumen yellowish or transparent; lamina base usually narrowly cuneate (Colombia, Venezuela to Peru). 40. *C. solutum*
68. Base of scales of stem 1 mm or less wide. 69
68. Base of scales of stem more than 1 mm wide. 71
69. Base of stem scales with outline of cells contorted (central Brazil). 12. *C. centrobrasilianum*
69. Bases of stem scales without contorted cells (Mexico to Panama, Greater Antilles, and from Colombia to Bolivia, southeastern Brazil). 70
70. Stem scales subulate from a roundish base; scale cells narrowly oblong; cell walls usually brown (Costa Rica, Ecuador to Bolivia). 7. *C. angustipaleatum*
70. Stem scales narrowly ovate; scale cells oblong; cell walls ferrugineus (southeastern Brazil). 10. *C. austrobrasilianum*
71. Stem scale cells roundish; stem scale apex shortly acuminate (Mexico to Guatemala, Nicaragua). 21. *C. ensifolium*
71. Stem scale cells oblong; stem scale apex long acuminate. 72
72. Stem scales 6-10 mm long, 1.5-2 mm wide, persistent, cells oblong usually with iridescent lumen (central Ecuador, southern Peru to Argentina). 3. *C. aglaolepis*
72. Stem scales 3-6 mm long, 1-1.5 mm wide, caducous, cells narrowly oblong, lumen usually not iridescent (southern U.S.A., Antilles to Bolivia, and central Brazil). 6. *C. angustifolium*

1. *Campyloneurum abruptum* (Lindman) B. León, Fieldiana Bot. n.s. 1993: in press.

Polypodium repens Aublet var. *abruptum* Lindman, Ark. Bot. 1: 245. 1903. Lectotype (chosen here). Brazil: Matto Grosso, Serra do Itapirapuam, ad arbores, 28 Apr. 1894, *Lindman (Regnell Exped. I) 3345* (type S!, isotype K!).

Campyloneurum nitidissimum var. *abruptum* (Lindman) B. León, Ann. Missouri Bot. Gard. 77: 212. 1990. p.p.

Stem creeping, not pruinose, 5-10 mm wide. Stem scales dark brown in mass, linear-lanceolate or narrowly-ovate, 5-7 mm long, 1-1.5 mm wide; scale bases short auriculate, apices acuminate, scales distinctly clathrate, cells narrowly oblong, cell walls 6-13 µm wide, some times with spreading hair-like teeth on the margins. Phyllopodia 1-2 mm long, 4-5 mm wide, 2-7 mm apart. Leaves erect, 60-110 cm long; petiole 2-7 cm long, stramineous, slightly ranurate adaxially; lamina lanceolate or ovate, (4.5-) 6.5-13.5 cm wide, chartaceous or herbaceous-chartaceous, lamina base abruptly cuneate or attenuate, then long-decurrent, apex usually acuminate, margins of the lamina slightly sinuate, cartilaginous, lamina puberulous, indument of inconspicuous, bicellular hairs, 70-75 µm long, scattered abaxially, stomata polocytic; costa prominent, slightly sulcate adaxially, indument of caducous scales at the base; primary veins prominent,

diverging (60º-) 65-70º from the costa, straight, lighter in color than the adjacent tissue, (3-) 5-7 (-10) mm apart, with 9-15 areoles between costa and margin, with 2-4 excurrent veinlets in each non-costal areole, veinlets entire or furcate, usually free, rarely forming regular secondary areoles. Sori subterminal on the excurrent veinlet, paraphyses inconspicuous or lacking; only abortive spores seen. Figs. 9 a; 19 a.

South American species, distributed from Colombia and Venezuela, south to Bolivia and Brazil, where is found between 100 m and 650 m elevation. It grows mostly as terrestrial in shady and humid places, on abundant organic debris, and sometimes on rocks.

REPRESENTATIVE SPECIMENS: COLOMBIA. MAGDALENA: La Jagua, 11 Sep. 1924, *Allen 655* (MO); on Quebrada Santa Cruz, 5 km N of La Jagua, 3 Aug. 1943, *Haught 3582* (GH, US). BOLIVAR: Boca Verde, on Río Sinu, 13-14 feb. 1918, *Pennell 4216* (NY). SUR DE SANTANDER: vicinity of Barranca Bermeja, Magdalena valley, between Sogamoso and Colorado rivers, 19 Feb. 1935, *Haught 1567* (US). BOYACA: Casanare, Tauramena, 13 Apr. 1963, *Uribe 4281* (US). META: Río Guatiquia, near Villavicencio, 18 Mar. 1939, *Alston 7597* (US). WHITOUT EXACT LOCALITY: Llanos de San Martín, *Stübel 598* (B). VENEZUELA. MERIDA: s.d. *Karsteinley s.n.* (W); ESE of Santa Bárbara, 9 Mar. 1980, *Liesner & Gonzales 9236* (MO). TACHIRA: ESE of la Fundación, 0-3 km below Represa Dorada, 29 Apr. 1981, *Liesner & Guariglia 11539* (MO, UC); W of Pinal, W of bridge over Río Frío, 27-30 Aug. 1966, *Steyermark & Rabe 96710* (GH); dist. Uribante, from La Siberia to entrance to Represa Las Cuevas, 10 Jul. 1983, *Werff & Gonzalez 5241* (MO). BARINAS: dist. Pedraza, above El Algarrobo, 3 Aug. 1983, *Werff & Ortiz 5810* (MO, UC).
ECUADOR. NAPO: 1.1 km E of Río Conejo on road to Lago Agrio, 31 Mar. 1972, *Dwyer & Mac Bryde 9769* (MO); Napo-Pastaza, Cantón Napo, Zatzayacu, 22 Mar. 1935, *Mexia 7065a* (UC).
PERU. SAN MARTIN: Chazuta, Río Huallaga, Apr. 1935, *Klug 4080* (F, GH, MO, S, UC, US); 15 km E of Shapaja on road to Chazuta, along Quebrada Chumia 4 Aug. 1986, *Knapp 7867* (F, MO, USM); Mariscal Cáceres, dist. Campanilla, Mashuyacu, 12 Aug. 1970, *Schunke V. 4226* (F, US); Moyobamba, Huallaga, Potrero to Tabalosos, *Stübel 1101* (B). HUANUCO: Pachitea, Panguana, 1983, *Seidenschwarz 100/34* (USM). MADRE DE DIOS: Río Manu, Cocha Cashu Biological station, Jul. 1978, *Foster & Terborgh 6559* (F); Tambopata, SE Puerto Maldonado, Albergue "Cuzco Amazónico", Apr. 1986, *León 884* (F, USM).
BOLIVIA. LA PAZ: Provincia Larecaja, Casanavi, 27.8 km Guanay, 28 Nov. 1980, *Beck 3784* (F, LPB); Caranavi and Guanay, 28 Nov. 1980, *Croat 51658* (MO, UC); Nor Yungas, 4.5 km below Yolosa, 19-20 Oct. 1982, *Solomon 8549* (MO).
BRAZIL. RORAIMA: Posto Mucajaí, Rio Mucajaí, vic. Mucajaí airstrip, 13 Mar. 1971, *Prance et al. 10923* (K, MO, NY, S, US). AMAZONAS: Matto do Curupira, 18 Feb. 1894, *Lindman 3075* (S, B); Rio Curuquete, Cachoeira República, 25 Jul. 1971, *Prance et al. 14584* (NY, US). PARA: W bank of Rio Maicurú, ca. 23 km from Lageira, 29 Jul. 1981, *Strudwick et al. 3702* (F, NY). RONDONIA: basin of Rio Madeira, 2 km below confluence of Río Abunã, 12 Nov. 1968, *Prance et al. 8341* (K, MO, S, US). MATTO GROSSO: between S. Cruz and Jairip, 1891-92, *Moore 370* (BM); gorge of Véu de Noiva, Chapada dos Guimarães, 17 Oct. 1973, *Prance et al. 19105* (K, US). GOIAS: Mun. Jataí, Bálsamo, 9 Feb. 1895, *Macedo 2148* (S, US). MINAS GERAIS: Distrito Rio Branco, 13 Nov. 1930, *Mexia 5298* (BM, NY, S). Without locality: *Glaziou 15755* (B).

Campyloneurum abruptum can be distinguished by the abruptly cuneate or attenuate leaf bases that are then long-decurrent, and by the stem scales dark brown in mass, distinctly clathrate, with a clear cell lumen. *Campyloneurum abruptum* belongs to the *C. phyllitidis* group.

2. *Campyloneurum acrocarpon* Fée, Cr. Vasc. Br. 1. 35., t. 115. 1869. Type. Brazil: Serra dos Orgãos, *Glaziou 2801* (probably P).
Campyloneurum wacketii Lellinger, Amer. Fern J. 78: 27. 1988. Type. Brazil: São Paulo, Río Grande, *Wacket (Ros. Fil. Austrob. Exsc. 213)* (holotype US!, isotypes B!, S!, UC!).

Stem long-creeping, not pruinose, black or stramineous, 3-6 mm wide. Stem scales partly persistent, light brown in mass, 1-2 (-3) mm long, 0.5-1 (-1.5) mm wide, ovate, slightly bullate, base auriculate, apex obtuse, clathrate, the cells oblong, irregularly arranged, cell walls 8-10 µm wide, scales sometimes with teeth on the margins. Phyllopodia 2-4 mm long, 4 mm wide, 3-8 mm apart. Leaves 45-92 cm long; petiole 1-3 cm long, stramineous, slightly ranurate

adaxially; lamina narrowly lanceolate to oblanceolate, 4-7 cm wide, herbaceous-chartaceous to chartaceous, lamina bases and apices attenuate, lamina margins sinuate, cartilaginous, indument of inconspicuous simple glandular hairs, scattered abaxially, stomata polocytic; costa prominent; primary veins prominulous on both sides of the lamina in the same degree, slightly stramineous, 65-70º divergent from the costa, slightly sinuate, (4-) 5-8 mm apart, (5-) 7-12 areoles between costa and margin, 2-3 (-4) excurrent veinlets in each noncostal areole, veinlets entire or furcate, usually free; sori medial or subterminal, paraphysis scarce, simple, 11 µm long; spores 45-50 µm long, 25-30 µm wide. Fig. 25.

Species restricted to southeastern Brazil, where it is usually found from sea level to 800 m. It grows mostly terrestrial in disturbed forests.

REPRESENTATIVES SPECIMENS: BRAZIL. SÃO PAULO: Arariba, 1926, *Brade 8443* (UC); Tietê, 16 Oct. 1904, *Gerdes 39a* (UC); Estação Sagrado do Coração, Linha Sorocobana, 3 Oct. 1979, *Mizoguchi 1043* (MO); Santos, 1 Apr. 1875, *Mosen 3744* (B). PARANA: Yacarehy, 20 Mar. 1914, *Dusen 97a* (MO); 18 Jul. 1914, *Dusen 15311* (B); Yacarehy, 7 Aug. 1914, *Dusen 15345* (BM, MO, S); Mun. Guaraqueçaba, Serrinha, *Hatschbach 16314* (F); Mun. Paranaguá, Ilha do Mel, 28 Nov. 1970, *Hatschbach & Guimarães 25680* (UC); Mun. Morretes, Ilha do Turco, 2 Dec. 1975, *Hatschbach 37834* (MU); Mun. Morretes, Ilha do Malha, 12 Nov. 1975, *Kummrow 988* (MU). MINAS GERAIS: dist. Rio Branco, 13 Nov. 1930, *Mexia 5298* (MO). SANTA CATARINA: Itajubá, 29 Jan. 1988, *Krapovickas & Cristóbal 42140* (F); Santa Catarina, 10 Jul. 1901, *Schmalz 13* (F); Antonio Carlos, Biguassú, Feb. 1943, *Reitz 274* (US); Brusque, Mata Hoffman, 10 Oct. 1949, *Reitz 3091* (S, US); Indayal, 1904, *Vierdel 15* (S).

Campyloneurum acrocarpon is characterized by its long-creeping stem, with stem scales ovate, slightly bullate, and by the herbaceous leaves, which are lanceolate with a long decurrent base.

Because of the characters in the pattern of venation and those of the stem, this species is placed in the *C. repens* group. Although the type of *C. acrocarpon* was not located, its description and illustration undoubtedly apply to this taxon.

3. *Campyloneurum aglaolepis* (Alston) Sota, Opera Lilloana 5: 96. 1960.

Polypodium aglaolepis Alston, J. Bot. 77: 346. 1939. Type. Argentina: Tucumán, Siambón, Sierra de Tucumán, *Lorentz & Hieronymus 948* (holotype BM!; isotype B! CORD).

Stem short-creeping, sometimes slightly pruinose, 1-3 mm wide. Stem scales brown or dark brown, iridescent in mass, (4.5-) 6-10 mm long, (1-) 1.5-2 (-2.5) mm wide, narrowly ovate, scale base auriculate, apex long acuminate, clathrate, the cells oblong, cell walls 10-15 µm thick. Phyllopodia 1-2 mm long, 1-1.5 mm wide, 2-4 (-6) mm apart. Leaves (10-) 40-60 cm long; petiole green stramineous, (0.2-) 0.5-3 (-8) cm long, slightly ranurate adaxially, convex abaxially, glabrate; lamina linear, bases and apices attenuate, 0.3-0.8 (-1.2) cm wide, herbaceous-chartaceous, lamina margins cartilaginous, slightly revolute, indument absent, stomata polocytic; costa prominent on both surfaces; venation areolate, primary veins inconspicuous, 2 areoles between the costa and margin, undivided, marginal areoles smaller than costal areoles, excurrent veinlets one in each areole, sometimes marginal free veinlets. Sori subterminal or medial, paraphyses scarce, dendritic, smaller than the sporangia; spores (60-) 65-70 µm long, 40-42 µm wide. Figs. 6 c; 7 a; 14 b; 26.

South American species known from central Ecuador, southern Peru to Argentina and southern Brazil, where is found between 1000 m and 3600 m elevation. It grows as an epiphyte or in crevices among rocks.

REPRESENTATIVE SPECIMENS: ECUADOR: PICHINCHA: Hacienda Margarita, 35 km S of Santo Domingo at Puerto Ila, 3 Jun. 1980, *Balslev & Quintana 24163* (AAU).
PERU. CUSCO: Piñasniocj, Panticalla (Pantiacolla) Pass, 14 Jul. 1915, *Cook & Gilbert 1826* (US); Quispicanchis, Marcapata, Cadena, 24 Jul. 1957, *Vargas 11665* (F). PUNO: Carabaya, Ollachea, *Vargas 6885* (CUZ, MO).
BOLIVIA. LA PAZ: Sud Yungas, La Paz-Calacoto, 31 Dec. 1980, *Beck 3909* (F, LPB); Quime, 5 May 1949, *Brooke 5441* (BM, F); Bautista Saavedra, Charazani, Charazani to Khata, 19 Apr. 1982, *Feurer 11258a* (F); Charazani, Río Curva, 17 May 1985, *Feurer 22332a* (F);

Bautista Saavedra, Curva, 30 Oct. 1979, *Krach & Feuerer 6563a* (F) Larecaja, Sorata, 7 Dec. 1981, *Sperling & King 5386* (MO); Sorata, 1901-1902, *Williams 2574* (MO). COCHABAMBA: Ayopaya, ca. 10 km NW Independencia, 9 May 1988, *Beck & Seidel 14476* (LPB); Choro, ca. 100 mi NW of Cochabamba, 18 Jan. 1950, *Brooke 6005* (BM, F, S); Sailapata, Dec. 1934, *Cárdenas 3084* (US); Carrasco, 19 km W from Epizana,11 Feb. 1987, *Solomon & Nee 16048* (MO, USM); Socaba, 11 Oct. 1921, *Steinbach 5847* (F, MO); *Steinbach 5848* (F, MO). SANTA CRUZ: Caballero, above Tunal, 30 km NE of El Tambo School, 11 Jun. 1987, *Killen 2556* (F, MO); Vallegrande, Vallegrande to Piraimiri, 31 Jan. 1987, *Nee & Coimbra 33913* (MO). CHUQUISACA: Luis Calco, 5 km N of Muyumpampa (Vaca Guzman), Sep. 1986, *Willian 275* (F). TARIJA: Pinos near Tarija, 6 Jan. 1904, *Fiebrig 2474* (BM, F, MO, S); O'Connor, Rancho Huayco, W of Entre Ríos, 4 Sep. 1987, *Killeen 2705* (F, MO); O'Connor, 73.1 km E of Tarija-Padcaya road, ca. 1 km below Narvaez, 1-2 May 1983, *Solomon 10350* (LPB, MO, UC).
BRAZIL. PARANA: Mun. Bocaiuva do Sul, Bacaetava, 30 Dec. 1980, *Kummrow 1423* (MO). SÃO PAULO: Campos do Jordão, Apr. 1947, *Leite 3467* (GH, MO, UC). MINAS GERAIS: Mun. Ouro Preto, São Sebastião, *Macedo 3046* (MO). GOIÁS: Mun. Jataí, Fazenda Queizadu, 13 Dec. 1948, *Macedo 1480* (MO). RIO DE JANEIRO: Itatiaya, 23 Oct. 1927, *Zerny s.n.* (W).
ARGENTINA. JUJUY: Selva Río Grande, Troncoso, 17 Feb. 1940, *Burkart & Troncoso 11255* (MO); Jujuy, 6 Mar. 1937, *Castellanos 19972* (BM); Laguna de Yala, 25 km NW of Jujuy, 26 Sep. 1938, *Eyerdam & Beetle 22230* (F, MO, UC); dist. Santa Bárbara, 11 Feb. 1964, *Fabris 5102* (US); Jujuy de Yala to Laguna de Yala, 8 Apr. 1945, *O'Donnell 2899* (MO); road Lozano de Tiraxi, 3 Nov. 1974, *Schinini et al. 10211* (UC); Tiraxi, 17 Mar. 1982, *Schinini & Vanni 22459* (F). ROSARIO DE LA FRONTERA: Los Baños, 13 Jul. 1929, *Venturi 9198* (MO). SALTA: Salta,16 Sep. 1985, *Bonavia 74* (MO); Salta, Mar. 1907, *Hauman 339* (BM); San Lorenzo, Feb. 1936, *Schulz 906* (GH). CATAMARCA: Andalgalá, 2 May 1915, *Jorgensen 337* (BM). TUCUMAN: Quebrada Lules, Jul. 1928, *Burkart 3283* (GH); Valle Tafí, Dec. 1911, *Castillón s.n.* (GH); 1-5 km S of Anta Muerta, on road to Villa Nougués, 7 Feb. 1974, *Conrad & Dietrich 2599* (MO, UC); La Banderita, 14 Feb. 1971, *Ellenberg 4480* (LPB); Tafí, road Apachiri-Alto del Clavillo, 20 Sep. 1946, *Hunziker 6811* (US); valley of Río Cochuna, W vicinity of Concepción, 16 Oct. 1989, *Kramer et al. 10681* (F); Quebrada Monteros, 5 Apr. 1872, *Lorentz 791* (F); Quebrada de la Angostura, May 1945, *Lourteig 1045* (BM, MO); Tafí, Tafí del Valle to Los Nogales, 6 May 1947, *Meyer 12111* (BM); Chicligasta, Las Pavas, 16 Jun. 1949, *Meyer 15137* (BM); Chicligasta, Las Pavas, 15 Mar. 1961, *Meyer et al. 21977* (W); *Meyer et al. 21984* (W); *Meyer et al. 21988* (W); Cochuna, 4 Mar. 1941, *Ousset 135* (F); *Ousset 136* (F); San Javier, Cumbres Calchaquies-Amaicha to Siambón, 25 Jan. 1933, *Parodi 10659* (S); Quebrada de Las Sosas (Los Nogales); 12 Nov. 1952, *Petersen & Hjerting 608* (BM, C); Sierra de Aconquija, 14 Nov. 1948, *Skottsberg s.n.* (GB); Quebrada de los Sosa, km 25, 2 Sep. 1957, *Sota 1668* (S).

Campyloneurum aglaolepis is characterized by its brown stem scales with oblong cells and iridiscent cell lumen. The stem scales are persistent and numerous, slightly spreading. This species has dendritic paraphyses among the sporangia. It belongs to the *Campyloneurum angustifolium* group.

4. *Campyloneurum amphostenon* (Kunze ex Klotzsch) Fée, Gen. Fil. 258. 1852.
Polypodium amphostenon Kunze ex Klotzsch, Linnaea 20: 399. 1847. Type. Venezuela: Mérida, *Moritz 120b* (holotype B!; isotypes BM!).

Stem long-creeping, usually pruinose, (2-) 3-5 mm wide. Stem scales dark brown in mass, ovate, adpressed at their bases, with spreading apices, (3-) 5-6 (-8) mm long, (1-) 1.5-2 (-2.5) mm wide, the cell walls 8-10 µm thick. Phyllopodia 1-2 mm long, 2-3 mm wide, 2-5 (-10) mm apart. Leaves 30-70 cm long; petiole stramineous or brown stramineous, (2-) 5-10 (-30) cm long; lamina linear-lanceolate or lanceolate, bases attenuate, apices acuminate, (1-) 2-3 (-5) cm wide, chartaceous or subcoriaceous, margins slightly revolute or plane, cartilaginous, indument of simple trichomes scarce abaxially, stomata polocytic; costa prominent, with indument of caducous scales, primary veins obscure or prominulous adaxially, slightly prominulous abaxially, often concolorous with the adjacent tissue, straight or slightly flexuosus, 5-7 mm apart, 40-50º divergent from the costa, transverse secondary veins forming 2-4 (-5) areoles between the costa and margin, 1-2 free excurrent veinlets in each noncostal areole; sori medial or subterminal on the excurrent veinlets, paraphyses not seen, spores 62-70 µm long, 40-45 µm wide.

Campyloneurum amphostenon is characterized by linear lanceolate leaves with four or fewer rows of areoles between the costa and margin, by stems being frequently pruinose, and by its lanceolate stem scales with spreading apices.

This species is closely related to *Campyloneurum densifolium* and *C. fallax*. They are different from *C. amphostenon* by the adpressed, broadly ovate stem scales.

At middle elevational levels some individuals of *C. amphostenon* with narrow leaves and narrow stem scales are difficult to distinguish from *C. angustifolium*. They can be distinguished, however, because *C. amphostenon* presents more than three costal areoles between the margin and costa regardless of the width of the leaf.

Campyloneurum amphostenon is recognized here as a complex of populations that may have been subject to recurrent isolation and reconnection through time. This complexity is shown in the wide range of variation in stem morphology (short or long creeping stems) and structure of the stem scale (cell wall width and cell arrangement), especially in Central America and the north-central Andes. In this treatment two varieties are recognized.

-- Most of stem scales with elongate cells parallel to the main axis. var. *amphostenon*

-- Most of stem scales with cells irregularly ordered. var. *irregulare*

4A. *Campyloneurum amphostenon* var. *amphostenon*.

Polypodium angustifolium var. *amphostenon* (Kunze ex Klotzsch) Baker *in* C. Martius, Fl. Bras. 1(2): 530. 1870.

Campyloneurum angustifolium var. *amphostenon* (Kunze) Farwell, Amer. Midl. Naturalist 12: 296. 1931.

Polypodium leucorhizon Kunze ex Klotzsch, Linnaea 20: 400. 1847. Cyted Syntypes. Venezuela: *Moritz 83* (B!); *Moritz 135* (n.v.); *Moritz 136b* (B!, BM!). British Guiana: *Schomburgk 1145* (B!). Lectotype (chosen here). Peru: *Ruiz 10* (B!).

Campyloneurum leucorhizon (Kunze ex Klotzsch) Fée, Gen. Fil. 258. 1852.

Polypodium pittieri Christ *in* Pittier, Prim. Fl. Costa Rica 3: 16. 1901. Type. Costa Rica: El Páramo, E Cerro Buena Vista, Jan. 1897, *Pittier 10479* (holotype P ; isotypes US!, photo of P, BM!).

Campyloneurum pittieri (Christ) Ching, Sunyatsenia 5: 263. 1940.

Polypodium leuconeuron var. *latifolia* (*ibid*.) Rosenst., Fedde Rep. 11: 58. 1912. Type. Bolivia: La Paz, Yungas septentrionalis, Unduavi, Nov. 1910, *Buchtien 2759* (holotype, not seen; isotypes S!, US; photo of US at F!, USM!)

Polypodium poloense Rosenst., Repert. Sp. Nov. Fedde 12: 473. 1913. Type. Bolivia: La Paz, near Coroico, Polo Polo, Oct.-Nov. 1912, *Buchtien 3525* (holotype, S!).

Campyloneurum cooperi Lellinger, Amer. Fern J. 78: 19. 1988. Type. Costa Rica, Cartago, Cartago, *Cooper 6053* (holotype, US!).

Stem scales lanceolate (3-) 5-7 mm long, (1-) 1.5-2 mm wide; the cells oblong, arranged along the main axes, cell lumen transparent. Figs. 9 e; 10 d; 15; 27; 35.

Widely distributed in tropical America, from Mexico and the Antilles to Argentina. It usually grows above 1500 m elevation, in remnant forested areas or in shady rock crevices.

REPRESENTATIVE SPECIMENS. MEXICO. HIDALGO: Agua Blanca-Iturbide, 22 Jul. 1973, *Gimate 1065* (F). VERACRUZ: El Volcancillo, Las Vigas, 30 Oct. 1975, *Dorantes et al. 5120* (BM, F, NY); road Huayacocotla-Viborillas, 1 km from Huayacocotla, 14 Jul. 1977, *Fay & Calzada 898* (F, NY); 42 km W of Escola, on road to Jalcal, 12 Jan. 1981, *Nee & Schatz 19773* (F); crater of volcano Rafael Ramirez, 21 Jan. 1976, *Ortega et al. 132* (F); Mun. Chiconquiaco, Planta el Pie, 23 Mar. 1972, *Ventura 5123* (F, NY). CHIAPAS: Mun. San Cristóbal de las Cajas, 9 mi SE of San Cristobal, 20 Aug. 1966, *Breedlove 15109* (F); Mun. Tenejapa, Banabil, 7 Nov. 1971, *Breedlove & Smith 22021* (F, MO); Mun. San Cristóbal de las Casas, S of Zonthuitz, 8 Nov. 1971, *Breedlove & Smith 22066* (F); Mun. San Cristóbal de las Casas, 5 Dec. 1971, *Breedlove 22998* (F, MO); Cerro Huitepec, 20 Aug. 1972, *Breedlove 27219* (F); Cerro Huitepec, 4 Dec. 1983, *Cabrera & Cabrera 6000* (MO); above San Juan Chamula, 9 Jul. 1977, *Croat 40672* (AAU, MO); from Motozintla de Mendoza to Siltepec, 11 Feb. 1979, *Croat 47280* (MO); *Croat 47320* (MO); between Chiapa de Corzo and

Pichualco, 17 Feb. 1987, *Croat & Hannon 65142* (MO); NE side of Cerro Huiytepec, 19 Apr. 1945, *Little & Sharp 9885* (US); creek at Rincón Chamula, 12 km NW of Pueblo Nuevo Solistahuacan, 23 Jan. 1965, *Raven & Breedlove 19785* (F); Mun. Tenejapa, Paraje Balum k'anal, 13 Apr. 1966, *Ton 814* (F, US). OAXACA: Cumbre de los Frailes, 11 Dec. 1907, *Conzatti 2130* (F); Santa Ana, Cuicatlán, 23 Jun. 1909, *Conzatti 2364* (F); along Oaxaca-Tuxtepec road, beyond Cerro Pelón, 3 Jan. 1974, *Carlson 4151* (F); between Oaxaca and Pochutla, 19 Jan. 1979, *Croat 46052* (MO); vic. of Cerro Zempoaltepetl, E slopes at Patio de Arena, 8 Aug. 1950, *Hallberg 845* (US); dist. Ixtlan, Sierra de Juárez, Llano Verde, ca. 15 km NE de Calpulalpán, 9 Apr. 1981, *Lorence et al. 3267* (MO); dist. Central, N slope of Cerro San Felipe, 13 Oct. 1969, *Mickel & Hellwig 4038* (UC); dist. Teotitlán, 26-29 km NE of Teotitlán del Camino, 16 Oct. 1969, *Mickel & Hellwig 4127* (UC); between Teotitlán del Camino and Huautla de Juárez, 8 Jul. 1972, *Webster et al. 17274* (UC); ca. 24 km N of San Gabriel Mixtepec, 18 Jul. 1985, *Yatskievych et al. 85-205* (MO).

GUATEMALA. HUEHUETENANGO: between Paquix and Todos Santos, 25 Sep. 1944, *Melhus & Goodman 3569* (F). QUICHE: 1942, *Aguilar 1131*; *Aguilar 1165* (F). ALTA VERAPAZ: San Juan Chamelco, 12 Dic. 1973, *Dary-Rivera 1713* (F). BAJA VERAPAZ: San Rafael Chilascó, Salama, 10 Sep. 1973, *Dary-Rivera 541* (F); 10 Oct. 1973, *Dary-Rivera 970* (F); 10 Nov. 1973, *Dary-Rivera 1208* (F), *Dary-Rivera 1228* (F). SAN MARCOS: 10 mi S of San Marcos, along road from San Rafael, 13 Jul. 1977, *Croat 41013* (MO), *Croat 41303* (MO); Volcán Tacaná, 6 Feb. 1987, *Martinez et al. 19557* (F); *Martinez et al. 19576* (F), *Martinez & Ramirez 19588* (F); Barranco Eminencia, San Marcos-San Rafael Pie de la Cuesta, 6 Feb. 1941, *Standley 86545* (F); San Sebastián at km 21 and km 8, 15 Feb. 1940, *Steyermark 35658* (F); slopes of Cerro Tumbador, 15 Dec. 1962, *L.O. Williams et al. 23046* (F); near Aldea Fraternidad, between San Rafael Pie de la Cuesta and Palo Gordo, 10-18 Dec. 1963, *L.O. Williams et al. 25745* (F); Sierra Madre Mountains, 13 Dec. 1963, *L.O. Williams 25875* (F); between San Rafael Pie de la Cuesta and Palo Gordo, 10-18 Dec. 1963, *L.O. Williams et al. 26276* (F); on outer slope of Tujumulco volcano, ca. 10 km W of San Marcos, 3 Jan. 1965, *L.O. Williams et al. 27166* (F, NY), *L.O. Williams et al. 27206* (F).

QUEZALTENANGO: Quebrada El Pocito, S of San Martín Chile Verde, 27 Jan. 1941, *Standley 85078* (F, UC), *Standley 85108* (F); vic, of Fuentes Georginas, slopes of Volcán Zunil, 3 Feb. 1941, *Standley 86032* (F, UC); above los Bahos, Cerro Quemado, 5 Feb. 1941, *Standley 86087* (F); Volcán Zunil, 22 Jan. 1940, *Steyermark 34711* (F). TOTONICAPAN: Sierra Madre mountains, S of Totonicapán, 13 Dec. 1962, *L.O. Williams et al. 22922* (F). SOLOLA: Volcán Santa Clara, 5 Jun. 1942, *Steyermark 46945* (F); 5-10 km W of Los Encuentros, Cerro María Tecum, 24 Dec. 1972, *L.O. Williams et al. 41730* (AAU, F). CHIMALTENANGO: Santa Elena, 10 Aug. 1932, *Johnson s.n.* (F); Santa Elena, 12 May 1936, *Johnston 420* (F); Santa Elena, cerro Tecpám, 4 Dec. 1938, *Standley 58780* (F, MO); 26 Dec. 1938, *Standley 61081* (F); slopes of Volcán de Acatenango, above Las Calderas, 3 Jan. 1939, *Standley 61951* (F); cerro Chichoy, 26-27 Jan. 1949, *L.O. Williams & Molina 15403* (F). SACATEPEQUEZ: San Rafael, Feb. 1892, Smith 2741 (GH, NY). GUATEMALA: slopes of Volcán de Pacaya, 20 Dec. 1940, *Standley 80764* (F, UC). Volcán de Agua, 22 Mar. 1905, *Maxon & Hay 3742* (US).

HONDURAS. LEMPIRA: Montaña Celaque, 18-22 Nov. 1974, *Hazlett 2316* (F). San Pedro de Sula, 35 km NE Nuevo Ocotepeque, 12 Jun. 1985, *Martinez & Tellez 12954* (MO).

EL SALVADOR. SANTA ANA: Forest Montecristo, 15 Sep. 1977, *Seiler 89* (F); forest Montecristo, 19 Sep. 1977, *Seiler 113* (F); forest Montecristo-Los Planes del Miramundo, 6 Nov. 1977, *Seiler 187* (F, NY); Cerro El Pital, 10 Jun. 1978, *Seiler 392* (F), *Seiler 393* (F), *Seiler 395* (F); forest Montecristo, 10 Oct. 1978, *Seiler 656* (F, NY); forest Montecristo, 11 Oct. 1978, *Seiler 669* (F, NY, UC); Cerro El Pital, 16 Nov. 1978, *Seiler 755* (F); forest Montecristo, 31 Jan. 1979, *Seiler 848* (MO); forest Montecristo, 7 May 1979, *Seiler 1124* (NY, UC). CHALATENANGO: E slope of Los Esesmiles, 27 Mar. 1942, *Tucker 1151* (UC).

COSTA RICA. ALAJUELA: Varablanco de Sarapiquí, N slope of Cordillera Central, Feb. 1938, *Skutch 3539* (NY, S). HEREDIA: Sacramento, Volcán Barba, 18 Dec. 1983, *Givens 3372* (F). LIMON: Cordillera Talamanca, at cerro Bekom, 21-27 Mar. 1984, *Davidse et al. 25728* (MO); Cordillera Talamanca, Atlantic slope, Valle de Silencio, along the Río Terbi, 9 Sep. 1984, *Davidse et al. 28746* (MO); Cordillera between Río Terbi and Río Siní, 13 Sep. 1984, *Davidse 29003* (MO); Kámuk massif, NE of the main Kámuk peak, 17-18 Sep. 1984, *Davidse & Herrera 29328* (MO). PUNTARENAS: Cordillera Talamanca, upper slopes of Cerro Echandi, 23 Aug. 1983, *Davidse et al. 23965* (MO); slopes between cerro Echandi and cerro Burú, 24 Aug. 1983, Davidse et al. 24023 (UC). SAN JOSE: trail from Canaán to Chirripó, N of Río Talari, 19-22 Jan. 1970, *Burger & Liesner 7440* (F, GH, NY); from Canaán to Chirripó, *Burger 8323* (F); SW slopes from Canaan to summit, 23 Aug. 1967, *Lellinger et al. 92* (MO); upper slopes of Cerro Daser (Azulillo), 5 km S of Aserrí, 19 Mar. 1973, *Stolze 1405* (F); along Panamerican highway, Villa Mills, 15 Sep. 1961, *Weber 6239* (MO, US). CARTAGO: Cerro de la Muerte, near km 97 marker, 8-10 Aug. 1967, *Evans & Bowers 3169* (MO); side of Turrialba volcano, 26 Jul. 1965, *Lent 684* (F, NY); Cerro de la Muerte, 24.5 km NW of La

Asunción, 11 Aug. 1967, *Mickel 3330* (NY, US); 1 km N of Carretera Interamericana, 10 km SE of Empalme, 17 Mar. 1973, *Stolze 1388* (F), *Stolze 1390* (F); N of Irazú, 27 Mar. 1928, *Stork 1293* (UC); E of Irazú, 17 May 1928, *Stork 2027* (UC). SAN JOSE-CARTAGO: near El Trinidad and km 72, 25 May-19 Jun. 1968, *Burger & Stolze 5244* (F); near La Asunción, 21 Nov. 1969, *Burger & Liesner 6302* (F), *Burger & Liesner 6337* (F); SE of El Empalme, 27 Nov. 1969, *Burger & Stolze 6501* (F); upper slopes of Talamanca, W ridge of cerros Cuericí, 15 Sep. 1983, *Davidse 24661* (MO); *Davidse 24721* (AAU, UC); Parque Nacional Chirripó, 16 Sep. 1983, *Davidse 24813* (AAU, MO, UC); road Cartago-San Isidro del General, ca. 1 km NW of Asunción, 29 Jan. 1986, *Smith & Beliz 2022* (MO). PUNTARENAS-LIMON: between cerro Kasir and cerro Nai, 22 Mar. 1984, *Davidse et al. 25837* (MO).

PANAMA. CHIRIQUI: Monte Azul, 1.4 mi N of Entre Ríos on E slopes of Cerro Punta, 22 Nov. 1979, *Antonio 2738* (MO); Volcán Chiriquí, 7.3 mi from Boquete, 24 Jul. 1970, *Armond 533* (F); Guadalupe, Cerro Punta, 6 Mar. 1982, *Caballero 55* (MO); dist. Boquete, W end of Paso de Respingo, *Cochrane et al. 6313* (MO); Las Cumbres, N of Quebrada Iglesia, near town Cerro Punta, 22 Jul. 1971, *Croat & Porter 16170* (AAU, MO); 12 mi above Boquete on road to Volcán Baru, 18 May 1976, *Croat 34879* (MO); 7 km NW of Cerro Punta, Las Nubes region, 11 Feb. 1978, *Hammel 1395* (AAU, MO); lower N slope of Baru, E bajo Choro region, 7 May 1978, *Hammel 2995* (MO); W slopes of Cerro Respingo, Ne of Cerro Punta, ca. 15 Jun. 1971, *Webster & Breckon 16578* (UC). BOCAS DEL TORO: Cordillera Talamanca, 7-8 Mar. 1984, *Davidse et al. 25333* (MO); between Itamut and Bine, Fabrega massiff, 5-9 Mar. 1984, *Gómez et al. 22547* (MO); 1-2 km SWW of Itamut camp, 6-7 Mar. 1984, *Gómez et al. 22615* (MO). Isla Potrero, Changuinola valley, 6 Aug. 1923, *Dunlap 71* (F).

CUBA. GUANTANAMO: Sierra de Imías, Cabezadas del Río Jojo, 20 Aug. 1975, *Bisse & Meyer 27692* (HAJB); San Antonio del Sur, Puriales de Caujeri, Sierra del Purial, 30 May 1982, *Bisse et al. 47263* (HAJB); Palenque, Sierra de Frijol, loma Bernardo, 21 May 1983, *Bisse et al. 50051* (HAJB).

COLOMBIA. MAGDALENA: Sierra Nevada de Santa Marta, 1 km NW Quebrada de Laguna Río Trío, *Forero & Kirkbride 628* (F, MO); Sierra Nevada de Santa Marta, 3 Aug. 1972, *Forero & Kirkbride 655* (MO), *Forero & Kirbride 656* (MO); Serranía de Perijá, Cerro El Avión, 3 Mar. 1959, *Romero-Castañeda 7364* (MO); Santa Marta, 1898-1901, *H.H. Smith 945* (BM, F, S, US). NORTE DE SANTANDER: between Pamplona and Chorro Colorado, 4 May 1983, *Croat 56416* (MO); Quebrada Samaria, drainage of Río Chitagá, 19 Nov. 1942, *Fosberg 19200* (US); Pamplona, S of García, 18 Mar. 1945, *Garganta 975* (F). Cipacoa, *Lindig 241* (BM, GH, US). CUNDINAMARCA: Cordillera Oriental, Macizo de Bogotá, Quebrada de San Cristóbal, 4 Feb. 1940, *Cuatrecasas 8019* (F); about 5 km SW of Bogotá, on road to Usme, 4 Aug. 1950, *G. Smith & Idrobo 1319* (MO). DEL VALLE: Cordillera Occidental, Hoya del Río Sanquininí, 10-20 Dec. 1943, *Cuatrecasas 15428* (F); Los Farallones, Cerro Alto del Buey, 11-12 Oct. 1944, *Cuatrecasas 17969* (F, S, US); Río Palo, Quebrada de Santo Domingo, 13 Dec. 1944, *Cuatrecasas 19266* (F).

VENEZUELA. ANZOATEGUI: dist. Libertad, NE of Bergantín, NE of Buenos Aires, Serranía de Turimiquire, 28 Nov. 1981, *Davidse & González 19622* (MO). TERRITORIO FEDERAL AMAZONAS: Río Negro, Cerro de la Neblina, 5.1 km NE Pico Phelps, 2 Dec. 1984, *Bell 396* (UC); Departamento Atabapo, Cerro Marahuaca, 26-27 Feb. 1985, *Steyermark & Holst 130749* (MO), *Steyermark & Holst 130817* (MO). MERIDA: Páramo de La Negra, near Pregonero road junction, 21 Mar. 1947, *Box 3750* (BM), *Box 3751* (BM); Páramo de Los Leones, La Lagunita, W de Mucurubá, 31 May 1930, *Gehriger 141* (F); dist. Campo Elías, S de Pueblo Nuevo, entre Mucusus y Cerro La Becerrera, 18 Sep. 1984, *Ortega & Diaz 2142* (UC); dist. Campo Elías, La Carbonera, El Palmarito, 24 Nov. 1985, *Ortega & Werff 2939* (MO); dist. Libertador, Laguna Coromoto, 22 Feb. 1971, *Ruiz-Terán & López 1534* (UC); dist. Rangel, Quebrada Las Escaleras, ca. 10 km SE from San Rafael de Mucuchíes, 16-17 May 1972, *Ruiz-Terán 7239* (UC). ZULIA: dist. Mara, Puesto Guardia Nacional, 10-15 Nov. 1982, *Bunting et al. 12135* (UC). TACHIRA: Quebrada La Lejía, S of Quebrada Agua Azul, 25 Jul. 1979, *Steyermark & Liesner 118580* (MO). LARA: dist. Moran, trail from Humocaro to Buenos Aires, 25 Jun. 1979, *Liesner et al. 7974* (MO); dist. Moran, Páramo Las Rosas, 5 Dec. 1984, *Rivero 755* (UC). MONAGAS: Cerro Negro, above La Sabana de las Piedras, NW of Caripe, 15 Apr. 1945, *Steyermark 62070* (F, NY). SUCRE: Cerro Turumuquire, W of Boquerón, 8 May 1945, *Steyermark 62671* (F, MO, US). MIRANDA: Pico de Naiguatá, above Los Chorros, 16-17 Jun. 1945, *Steyermark 62975* (F, GH). BOLIVAR: Cerro Roraima, S border Guyana, Brasil andVenezuela, Río Arabapó, 26 Aug.-2 Sep. 1976, *Steyermark et al. 112602* (NY, UC); dist. Piar, Macizo del Chimantá, NE of Chimantá-tepui, 26-29 Jan. 1983, *Steyermark et al. 128057* (F, MO). TRUJILLO: Páramo de Guaracamal-Vega de Guaramacal, 23-24 Jul. 1984, *Ortega et al. 2022* (MO); Páramo de Guaracamal, 22 Nov. 1984, *Ortega & Werff 2274* (MO); dist. Boconó, ca. 10 mi SW Batatal, 3 Nov. 1982, *Smith et al. 921* (MO); Páramo de Guaramacal, 3 Feb. 1987, *Werff et al. 8805* (UC). Without locality: *Vogl 186* (F) Colonia Tovar, 1854-1855, *Fendler 226* (MO).

ECUADOR. CARCHI: El Angel-Tulcán, 14 May 1973, *Holm-Nielsen et al. 5235* (AAU, F, GB, MO); Valle de Maldonado, km 71 on road Tulcán-Maldonado, 20

May 1973, *Holm-Nielsen et al. 6092* (AAU, USM); *Holm-Nielsen et al. 6100* (AAU, USM); Páramo El Angel, 12 Jan. 1980, *Holm-Nielsen 20986* (AAU, USM). IMBABURA: SW slopes of volcano Cotacachi, 7 Nov. 1983, *Boysen-Larsen et al. 45583* (QCA); Cantón Ibarra, SW of Ibarra, 30 Jun. 1935, *Mexia 7402* (F). PICHINCHA: Los Alpes, 19 Jan. 1944, *Acosta-Solis 7094* (F); road Olmedo-Laguna San Marcos, 10 Jul. 1980, *Øllgaard et al. 34363* (AAU, USM), *Øllgaard et al. 34438* (AAU, USM). NAPO: junction of Río Borja and Río Quijos, 19 Sep. 1980, *Holm-Nielsen et al. 26230* (QCA); 6.6 km W of Papallacta, 26 Mar. 1972, *Mac Bryde & Dwyer 1242* (QCA). CAÑAR: north rim of the valley of Río Cañar, 25 Apr. 1945, *Camp 2883* (F). AZUAY: Gualaceo-Sigsig, 31 Ago. 1984, *Jaramillo 7156* (QCA); Hacienda Tarqui, 20 Ago. 1987, *Jaramillo 9998* (QCA); road Gima-Gualaquiza km 20.1, 28 Dec. 1990, *Øllgaard et al. 98628* (QCA). MORONA-SANTIAGO: trail Alao-Huamboya, 7 May 1982, *Øllgaard et al. 38277* (AAU, QCA). LOJA: muletrack Amaluza-Palanda, western slope Cerro Amarillo, 22 Sep. 1976, *Øllgaard & Balslev 9610* (AAU, QCA, UC, USM); Podocarpus National Park, Nudo de Cajanuma, around Centro de Información, 25-26 May 1988, *Øllgaard et al. 74487* (QCA). GALAPAGOS ISLANDS: Santa Cruz (Indefatigable), Cerro Colorado, 7 Feb. 1974, *Adsersen & Adsersen 205* (QCA)

PERU. PIURA: Huancabamba, Cuello El Indio, 13 Nov. 1981, *López et al. 8894* (GH, MO, UC). CAJAMARCA: Cajamarca-Celendín, 18 Oct. 1986, *Díaz 2159* (MO, NY); Santa Cruz, upper Río Zaña valley, 2-4 May 1987, *Dillon et al. 4896* (F, UC); jalca Kumulca, road to Celendín, 17 Jun. 1975, *Sagástegui et al. 8117* (NY); San Miguel, Llapa-Uchuquinua, 14 May 1977, *Sagástegui et al. 8907* (F, MO, UC); Contumazá, Guzmango, Cerro Chungarrán, 24 May 1978, *Sagástegui & Mostacero 9180* (F, MO, NY); Contumazá, Lledén, 3 Nov. 1979, *Sagástegui et al. 9404* (F, MO, NY); Contumazá, around Pozo Kuan, 13 Jun. 1981, *Sagástegui et al. 10068* (GH, UC); Quebrada Honda, Santiago-Yumal, 13 Jun. 1983, *Sagástegui & López 10616* (MO); Celendín, Sendamal, 17 Aug. 1984, *Sagástegui et al. 12093* (MO, NY); Contumazá, 6 Apr. 1985, *Sagástegui 12639* (NY, UC); Cajamarca, Cerro Cumbe Mayo, 9 Aug. 1969, *Sanchez Vega & Ruiz 7351* (GH). Chota, Chota-Tacabamba road, 20 Feb. 1983, *D.N. Smith & R. Vásquez 3618* (MO). AMAZONAS: Chachapoyas, jalca de Calla Calla, 23 Oct. 1965, *Sagástegui 6070* (GH, MO); Mendoza, 30 Jul. 1963, *Woytkowski 8062* (MO); Chachapoyas, Puma-urcu, ESE of Chachapoyas, 1 Jun. 1962, *Wurdack 707* (F, GH, NY, US, USM); Caño Santa Lucía, E of Chachapoyas, *Wurdack 736* (US, USM); Bongará, hill WNW of Pomacocha, 19 Jun. 1962, *Wurdack 948* (US); summit of Cerro Campanario, 3 Aug. 1962, *Wurdack 1574* (GH, NY, US). LA LIBERTAD: Sánchez Carrión, Huamachuco-Cajabamba road, Sausacocha-Cajabamba, 15 Feb. 1983, *D.N. Smith & Vásquez 3378* (F, UC); Pataz, 1985, *Young 2933* (USM). SAN MARTIN: Mariscal Cáceres, Parque Nacional Río Abiseo, Puerta del Monte, patch of forest P2, 1985, *Young 1685* (USM), *Young 1686* (USM); Parque Nacional Río Abiseo, forest patch P3, 1985, *Young 1722* (USM); forest patch P11, *Young 1994* (USM); forest patch C6, 25 Nov. 1985, *Young 2153* (USM); forest patch P5, *Young 2134* (USM); Parque Nacional Río Abiseo, forest patch C10, 24 Nov. 1985, *Young 2534* (F, USM); Chochos valley, *Young 3691* (USM); NW corner of Río Abiseo Nat. Park, Chochos, 14 Jul. 1987, *Young & León 4562* (USM); Parque Nacional Río Abiseo, Laguna de Chochos, Jul. 1987, *Young & León 4848* (USM, HUT). ANCASH: Cordillera Blanca, Quebrada Honda, small vally between Toqllarju and Pallkaraju, 8 Jul. 1979, *Gibby & Barrett 173* (BM); Yungay, Llanganuco, 9 Ago. 1986, *Mostacero et al. 1385* (F, MO, NY); Santa, Jalca Ultu Cruz (Jumbe), 3 May 1987, *Mostacero et al. 1869* (F, NY); Corongo, Nueva Victoria, 7 May 1987, *Mostacero et al. 2001* (F, UC); Huari, slopes valley of Laguna Ichicpotrero, 8 May 1986, *D.N. Smith et al. 12412* (F, MO); Huari, P. N. Huascarán, Quebrada Pachachaca, lateral valley of Quebrada Rurichinchay, 12 Jun. 1986, *D.N. Smith et al. 12539* (MO). HUANUCO: Mito, 8-18 Apr. 1923, *Bryan 204* (F); Cushi, trail to Tambo de Vaca, 19-23 Jun. 1923, *Bryan 620* (F); Tambo de Vaca, *Bryan 646* (F); Mito, 23 Jul. 14 Aug. 1922, *Macbride & Featherstone 1919* (US); Huacachi, near Muña, 20 May-1 Jun. 1923, *Macbride 4127* (F); 32 km de Huánuco, Huánuco-La Unión, 25 Jul. 1982, *D.N. Smith 2191* (F, USM). PASCO: Oxapampa, Río San Alberto, 28 Jun. 1985, *Foster et al. 10302* (F); Huariaca-Cerro de Pasco, 25 Jun. 1953, *Ferreyra 9502* (GH); 95 km S from Huánuco, 15 Jul. 1982, *Gentry et al. 37489* (F); trail to summit of Cordillera Yanachaga, via Río San Daniel, 17 Jul. 1984, *D.N. Smith et al. 7856a* (USM). JUNIN: Tarma, Incatacuna, Tarmatambo-Acolla, 29 Jun. 1954, *Constance & Tovar 2348* (UC); vicinity of La Oroya, 14 Jul. 1914, *Rose & Rose 18691* (US); Pampa Hermosa, Satipo, 17 Apr. 1965, *Saunders 1062* (GH), *Saunders 1068* (GH); Tarma, Incatacuna, 29 Jun. 1954, *Tovar 2351* (USM). LIMA: Huarochirí, Infiernillo, 17 Jan. 1949, *Ferreyra 5294* (GH); between San Mateo and Casapalca, 8 Aug. 1949, *Ferreyra 6236* (BM, USM); Huarochirí, Viso, 22 Apr. 1939, *Goodspeed et al. 11547* (GH, UC, US); Lima-La Oroya road, 76 km W of La Oroya, 29 Jan. 1983, *Gentry et al. 39747a* (MO); Río Blanco, 15-17 Apr. 1929, *Killip & Smith 21603* (NY, US); San Mateo, 1/2 km before Río Blanco, 1973, *Saunders 1161* (GH). HUANCAVELICA: Tayacaja, Huaribamba, 1km before Huari, 28 Jul. 1968, *Saunders 1147* (GH); Conaica, above Alauma, 22 Mar. 1952, *Tovar 796* (GH, USM); Pachaspampa, below Huando, 3 Apr. 1953,

Tovar 1230 (USM); Tayacaja, above Tocas, 20 Apr. 1954, *Tovar 2006* (GH); Tayacaja, Chuspi, near Tocas, 22 Apr. 1954, *Tovar 2039* (GH, USM); Tayacaja, Yacuhuanay, 16 Apr. 1962, *Tovar 3680* (GH). AYACUCHO: La Mar, E massif of the Cordillera Central, between Tambo San Miguel, Ayna and the Hacienda Luisiana, 24 Aug. 1968, *Dudley 12029* (GH, US); La Mar, road from Tambo to Ayna, above Jano, 3 Jan. 1975, *Plowman & Davis 4676* (GH). CUSCO: Anta, El Chaccan, 3 Jan. 1973, *Brunel 236* (F, MO); Urubamba, trail from Chincheros to Antakillqa, 13 Jan. 1982, *Davis et al. 1454* (F); Urubamba, Quebrada above Pojpoj waterfall, 14 Jan. 1982, *Davis et al. 1477* (F, NY, USM); Abra de Málaga, 15 km Quillabamba, 9 Mar. 1971, *Ellenberg 4777* (LPB); Cusco, *Herrera 2591* (F); Tres Cruces, upper edge of Parque Nacional de Manu, 29 Jun. 1978, *Gentry et al. 23450* (F); Urubamba, Chincheros, Titiqaqa Ch'impa, 3 Feb. 1982, *King et al. 128* (F); prov. Paucartambo, km 130 road to Kosñipata, 30 Oct. 1987, *Nuñez 8500* (F, NY, UC); Machu Picchu, above Pauqarcancha, 3 May 1982, *Peyton & Peyton 142* (MO); Machu Picchu, in Urcoscancha, above the village of Palcay, 4 Jul. 1982, *Peyton & Peyton 761* (GH, MO); Machu Picchu, Llactapampa, below Palcay, Acobamba river, 7 Jul. 1982, *Peyton & Peyton 810* (GH, MO); Machu Picchu, in the Pacasmayo river, 22 Aug. 1982, *Peyton & Peyton 1084* (GH); Quillabamba, Santa Teresa, Mandonilloc, 5 Sep. 1982, *Peyton & Peyton 1153* (GH, MO); Cusco, *Soukup 159* (F, GH, US); Hacienda Urco, 18 Sep. 1939, *Schmidt s.n.* (F).
BOLIVIA: Camacho, Ambana, 19 Dec. 1980, *Beck 4171* (LPB); Larecaja, Sorata, 16 Dec. 1981, *Beck 4985* (LPB); Nor Yungas, Chuspipata, 5 km vía Unduavi, 2 Apr. 1982, *Beck 7634* (LPB); Nor Yungas, between Unduavi and Chulumani, 25 Nov. 1980, *Croat 51465* (MO); Larecaja, 7 Mar. 1982, *Fernández-Casas 6537* (MO); Bautista Saavedra, Chullina, 30 Jan. 1979, *Krach & Feuerer 6573* (F, US); Inquisivi, between Pongo Chico and Laguna Naranjani, 27 Jun. 1988, *Lewis 88960* (F); Sud Yungas, Yanacachi, 3 Jan. 1981, *Liberman 241* (F); Yungas, 1885, *Rusby 350* (F, US); Nor Yungas, 22 km NE Unduavi, on road to Yolosa, 29 Feb. 1980, *Solomon 5181* (UC); Murillo, 27.4 km N of dam at Lago Zongo, 27-28 Nov. 1982, *Solomon 8970* (LPB, MO, NY, UC); Bautista Saavedra, Chajaya, near Charazani, 30 Mar. 1985, *Solomon 13345* (LPB); Sud Yungas, 1.4 km W of Unduavi, between Chuspipata and La Paz, 2 Jul. 1986, *Solomon 15403* (MO); Murillo, Valle of Río Zongo, 18 Mar. 1987, *Solomon 16384* (MO); Larecaja, Sorata, 7 Dec. 1981, *Sperling & King 5387* (MO). COCHABAMBA: Ayopaya, above Independencia, 20 Oct. 1986, *Linke 12* (LPB); Yungas de San Mateo, Pojos, 25 Oct. 1928, *Steinbach 8547* (MO). BENI: Ballivián, Puente Río Quiquibey, 14 Jul. 1979, *Beck 3899* (LPB).
ARGENTINA. JUJUY: Santa Bárbara, Cerro Centinela, 11 Feb. 1964, *Fabris et al. 5135* (UC, US).

Campyloneurum amphostenon var. *amphostenon* is characterized by its pruinose stem with caducous brown, clathrate scales, and the cells oblong arranged along the main axes of the scale.

Among the synonyms *Polypodium leucorhizon* is included. The protologue of this basionym is based on five syntypes, four of them were seen at the herbarium in Berlin. Three of those specimens (*Ruiz 10*, *Moritz 83*, *Moritz 136*b) clearly represent *Campyloneurum amphostenon*, and the Ruiz's specimen appears to be the one on which the description was based. Only one specimen (*Schomburgk 1145*) appears to belong to the taxon here called *Campyloneurum asplundii*.

4B. *Campyloneurum amphostenon* var. *irregulare* (Lellinger) B. León, *stat. nov.* Fieldiana Bot. n.s. 1993: in press.

Campyloneurum irregulare Lellinger, Amer. Fern J. 78: 24. 1988. Type. Ecuador: Pichincha, *Holdridge 1580* (holotype US!).

Polypodium crassifolium f. *angustissimum* Rosenst. Mém. Soc. Sci. Nat. Neuchâtel 5: 45. 1912. Type. Colombia: Cundinamarca, Sabana de Bogotá, *Mayor 40* (holotype not found; isotypes S!, US!).

Stem scales ovate, 4-6 mm long, 2-2.5 mm wide; cells oblong irregularly arranged. Figs. 6 b; 17 a; 27.

It is known from Mexico, Guatemala, Costa Rica, Panama, and from Ecuador to Bolivia, where it grows above 2500 m elevation. It is usually found as a terrestrial in open habitats.

REPRESENTATIVE SPECIMENS: MEXICO. VERACRUZ: Mun. Atzalan, vicinity Puente de Rieles, 4 km NE of Altotonga, 28 Jun. 1980, *Nee & Hansen 18701* (F).
GUATEMALA. HUEHUETENANGO: between San Mateo Ixtatán, at Cruz de Limón, 31 Jul. 1942, *Steyermark 49793* (F).
COSTA RICA. SAN JOSE-CARTAGO: NW of La Asunción, 5 Feb. 1982, *Burger & Barringer 11506* (AAU, F); ca. 15-20 km SE from El Empalme, 15 Jul. 1970, *Lellinger & White 1177* (F).
PANAMA. CHIRIQUI: Volcán de Chiriquí, 7.3 mi from Boquete, 24 Jul. 1970, *Armond 533* (F).
ECUADOR. CARCHI: Cunquer-Cuesaca, 17 Jul. 1945, *Acosta-Solís 10456* (F). PICHINCHA: around Quito, 28 Mar. 1942, *Paredes s.n.* (F). COTOPAXI: Latacunga,

Humbles 6289 (MO); road Pilaló-Zumbagua, 10 km above Pilaló, 28 Jul. 1980, *Holm-Nielsen & Quintana 24650* (AAU, QCA). TUNGURAHUA: Pasa-San Fernando, 27 Oct. 1944, *Acosta-Solís 8709* (F). CHIMBORAZO: Riobamba, Schimpff 831 (F). CAÑAR: Partidero El Corte-San Miguel de Porotos-Parcialidad Jatumpamba, 26 May 1979, *Jaramillo 936* (AAU, QCA); between Cañar and Biblian, 29 Aug. 1984, *Laegaard 52747* (QCA). LOJA: Parque Nacional Podocarpus, above Nudo de Cajanuma, 14-15 May 1988, *Øllgaard et al. 74138* (QCA); *Øllgaard et al. 74145* (QCA).
PERU. PIURA: Huancabamba, above Canchaque, 10 Oct. 1957, *Hutchison 1646* (UC). CAJAMARCA: Huancabamba, trail from Las Huaringas to Huancabamba, 23 Feb. 1981, *Davis & Turner 717* (GH); Celendín, canyon of the Río Marañón, above Balsas, 23 May 1964, *Hutchison & Wright 5282* (F, GH, UC, USM); Contumazá, Las Tres Cruces, Guzmango-Contumazá, 7 May 1965, *Sagástegui & Fukushima 5122* (GH); Guzmango, 31 Jul. 1961, *Sagástegui 3381* (GH); Trinidad, Juque, 19 Jun. 1962, *Sagástegui 3787* (GH); Cajamarca, above La Encañada, Celendín, 18 May 1976, *Sagástegui et al. 8394* (MO, NY, US); Contumazá, Las Quinuas-El Mojón, 14 Jun. 1981, *Sagástegui et al. 10102* (MO, UC); Cerro Cu*mbe Mayo, 13 Jun. 1966, Sánchez Vega 36* (GH, US); Lluscapampa, 12 Sep. 1965, *Sánchez Vega 109* (GH); Hualgayoc, pass above Hualgayoc, 17 Feb. 1983, *D.N. Smith & R. Vásquez 3519* (F, MO, UC); Hualgayoc, 28 Jun. 1968, *Soukup & Carmona 5010* (US). LA LIBERTAD: Otuzco, Chilte, Hacienda Lalguen, 2 Jun. 1951, *Lopez-Miranda 661* (BM, US); near km 214 from Trujillo, between Huamachuco and Cajabamba, 27 Mar. 1960, *Correll & Smith 916* (GH); about 3 km W of Huamachuco, *Correl & Smith 937* (GH); Santiago de Chuco, Huacás, Cachicadán, 15 Jun. 1984, *Sagástegui et al. 11917* (MO, NY); Santiago de Chuco, Cahicadán, 25 Nov. 1973, *Stork & Horton 9969* (F, UC, US). ANCASH: Carhuaz, Parque Nacional Huascarán, Quebrada Ishinca, 13 Feb. 1985, *D.N. Smith et al. 9516* (F); Yungay, Parque Nacional Huascarán, Quebrada Ranincuray, 18 Apr. 1985, *D.N. Smith et al. 10407* (F, MO); Huari, P. N. Huascarán, 6 May 1986, *D.N. Smith et al. 12243* (F). LIMA: Río Blanco, 8-19 Mar. 1922, *Macbride & Featherstone 716* (F, S, US). JUNIN: near turn off to Huasahuasi, 17 Mar. 1960, *Correll & Smith 779* (GH, US); Huancayo, Mar. 1947, *Soukup 3143* (BM, F, GH, US); Quebrada Ocopilla, Feb. 1948, *Soukup 3646* (BM, F, US); Acopalca, 16 Jan. 1969, *Soukup 6099* (US); Palián, 2 May 1961, *Tovar 3351* (GH). APURIMAC: Quebrada of Juccuchic-chupan, on trail Andahuaylas-Chincheros, 3 Nov. 1935, *West 3723* (UC). HUANCAVELICA: North of Mejorada, km 362 on the Carretera Central, 28 Oct. 1957, *Hutchison 1673* (UC). CUSCO: Cusco, Saxaihuaman, 28 Feb. 1954, *Coronado 156* (GH, UC); Urubamba, Maranqaqa, 12 Jan. 1982, *Davis et al. 1384* (F); Saxaihuaman, Dec. 1928, *Herrera 204* (F, GH, US); Saxaihuaman, Mar. 1929, *Herrera 2371* (F); Cusco, *Herrera 2585* (F); Urubamba, Chincheros, 26 Jan. 1982, *King et al. 112* (F); Huayoccari to Yanacocha, 14 Feb. 1987, *Nuñez et al. 7035* (MO); Cusco, near Sacsaihuaman, 23 Sep. 1956, *R. Tryon & A. Tryon 5345* (BM, F, GH, US, USM); Lauca, Espinar, 10 Jan. 1957, *Vargas 11506* (F). PUNO: Baja Isla in Lago Titicaca, 26 Nov. 1935, *Mexia 7787* (BM, F, GB, GH, MO, S, UC); Huancané, Moho, 20 Dec. 1919, *Shepard 54* (GH); Granja Salcedo, near Puno, Oct. 1935, *Soukup 10* (F); *Soukup 82* (F).
BOLIVIA. La Paz: Sud Yungas, Calacoto, 69 km E, pasando nevado Illimani, 31 Dec. 1980, *Beck 3899* (F); Franz Tamayo, Pelechuco, 5 Mar. 1980, *Krach & Feuerer 9143a* (F). COCHABAMBA: Chapare, Llantas-Aduana, 9 Mar. 1929, *Steinbach 9557* (F, S, UC).

Campyloneurum amphostenon var. *irregulare* is characterized by the irregular arrangement of the cells in most of the stem scales. Some studied material show stem scales with both regular and irregular arrangement of cells (*e. g. Armond 533*, *Herrera 204*, *Smith & Vasquez 3519* and *Smith et al. 12243*), for this reason recognition of this taxon as a variety instead of a species is preferred.

5. *Campyloneurum anetioides* (Christ) R. Tryon & A. F. Tryon, Rhodora 84: 125. 1982.
Polypodium anetioides Christ, Bull. Soc. Bot. Genève 2: 219. 1909. Type. Costa Rica: Alajuela, Candelaria, 4 Aug. 1908, *A. C. Brade 177* (holotype S!; isotypes BM!, K!, S!, US!).
Hyalotricha anetioides (Christ) Copeland, Amer. Fern J. 42: 12. 1953.
Hyalotrichopteris anetioides (Christ) W. Wagner, Taxon 27: 548. 1978.

Stem creeping, not pruinose, 1-2 mm wide. Stem scales brownish in mass, 3-6 mm long, 1.5-2 mm wide, narrowly ovate, clathrate, the cells oblong, cell walls 6-8 µm thick. Phyllopodia rarely present, 1-5 mm apart. Leaves 3-10 cm long; petiole 0.5-1.5 cm long, usually not articulate, greenish-stramineous; lamina simple, entire, spathulate, bases decurrent, apices obtuse, 0.6-2 cm wide, herbaceous, repand margins, indument of multicellular furcate hairs, 1.5 mm long, the basal branch usually unicellular, short, sometimes apical and basal branches multicellular; stomata polocytic or copolocytic; costa inconspicuous on the adaxial side, slightly

prominulous abaxially, slightly flexuous, primary and secondary veins inconspicuous, 3 areoles between the costa and margin, tertiary excurrent veinlet one per areole. Sori subterminal or terminal, paraphyses present, filamentosous, spores slightly verrucate, 80-100 µm de long, 50-60 µm wide. 2*n*= 148. Figs. 13 c; 14 i; 28.

Central American species known from Nicaragua, Costa Rica and Panama, between 1000 m and 1450 m elevation. It grows with hanging leaves among mosses on rocks, in shady and humid sites in tropical forest.

EXAMINED SPECIMENS: NICARAGUA. MATAGALPA: 6-10 km NE of Matagalpa, road to El Tuma, 14-16 Jan. 1963, *Williams et al. 23835* (F). COSTA RICA. CARTAGO: Tapantí, Río Grande de Orosí, 19 Jan. 1964, *Jimenez 1601* (F); Orosí, Dec. 1923, *Lankester 702* (BM). SAN JOSE: vicinity of El General, Jul. 1936, *Skutch 2753* (GH, K, MO, S). Without locality: Apr. 1987, *Stevens 15350* (MO). PANAMA. CHIRIQUI: valley of Río Caldera, from El Boquete to the Cordillera, 5-19 Feb. 1918, *Killip 5013* (BM); Chiriquí Viejo, vicinity of Monte Lirio, *Seibert 310* (K).

Campyloneurum anetioides is characterized by its spathulate leaves with inconspicuous venation and multicellular hairs.

This species was considered by Lellinger (1988) within the "satellite genus" *Hyalotrichopteris* based on size, habit, and indument features, which he considered rare in *Campyloneurum*. However, leaf size is not an important taxonomic character for these species. Small leaves, as in *C. anetioides*, also occur in *C. falcoideum* and *C. chrysopodum*. The hairs of *C. anetioides* are branched and multicellular. They are thought to be derived from the hair type found in *C. aphanophlebium* and *C. repens* (see Chapter IV). The venation of *C. anetioides* is the typical *Campyloneurum* venation. It is similar to that found in *C. aphanophlebium* and *C. falcoideum*, where non-costal areoles bears one excurrent free veinlet. In addition, the presence of excurrent free veinlets along the margin in *C. anetioides* occurs in mature plants of other species, such as *C. brevifolium* and *C. falcoideum*, and it is also present in juvenile leaves of such species as *C. angustifolium* and *C. phyllitidis* (Mitsuda 1981, 1983).

The closest affinities of *Campyloneurum anetioides* are with *C. aphanophlebium*, and they both in turn might be related to the open areolate species.

6. *Campyloneurum angustifolium* (Sw.) Fée, Gen. Fil. 257. 1852.
Polypodium angustifolium Sw., Prodr. Veg. Ind. Occ. 130. 1788. Type Jamaica, *Swartz s.n.* (holotype not found, isotypes BM!, LD!, S!).
Marginaria angustifolia (Sw.) C. Presl, Tent. Pterid. 188. 1836.
Grammitis angustifolia (Sw.) Heward, Mag. Nat. Hist. 458. 1838.
Cyrtophlebium angustifolium (Sw.) J. Sm. Bot. Mag. 72: 12. 1846.
Goniophlebium angustifolium (Sw.) Brack. *in* Wilkes, U.S. Explor. Exped. 16: 33. 1854.
Polypodium taeniosum Willd. Sp. 5. 155. 1810. Type. Venezuela: Caripe, *Humboldt (Herb. Willdenow 19631)* B!; photos BM!, USM!.
Campyloneurum taeniosum (Willd.) Fée, Gen. Fil. 257. 1852.
Cyrtophlebium difforme Loddiges, Cat. Pl. 1849. Type. Cultivated. *Nom. nudum*
Polypodium difforme (Loddiges) Kunze, Linnaea 23: 69. 1850.
Campyloneurum difforme T. Moore, Index Fil. 224. 1861. *Nom. nov.* for Polypodium difforme (Loddiges) Kunze. *Non Polypodium difforme* Blume 1828.
Polypodium angustifolium var. *gramineum* Sodiro, Crypt. Vasc. Quit. 366. 1893. Type. Ecuador, Napo, bosque de Los Colorados, Río Zuma, 1892, *Sodiro s.n.* (holotype not found, photo of P, BM!).

Stem creeping, usually pruinose, (2-) 3-4 (-5) mm wide. Stem scales dark brown or brown in mass, spreading, 3-6 mm long, 0.8-1 (-1.5) mm wide, narrowly ovate, scale bases auriculate, apices long acuminate, clathrate, the cells narrowly oblong, regularly arranged, cell walls 10 µm thick, cell lumen transparent. Phyllopodia 1-2 mm long, 1.5-2 mm wide, 1-4 mm apart. Leaves 30-100 cm long; petiole stramineous or dark stramineous, 0.5-5 (-7) cm long, slightly ranurate adaxially, convex abaxially, glabrate;

laminae linear or narrowly lanceolate, bases and apices attenuate, (0.5-) 1-2 (-3) cm wide, herbaceous-chartaceous, lamina margins cartilaginous, plane or slightly revolute, slightly sinuate, indument of inconspicuous hairs, scattered abaxially, stomata polocytic; costa prominent, sometimes with scales similar to those on the stem, primary veins inconspicuos, 1-2 (-3) areoles between the costa and margin, marginal areoles usually smaller than costal ones, excurrent veinlet one per areole. Sori medial, paraphyses inconspicuous, scarce, simple, shorter than the sporangia; spores (40-) 50-70
(-80) µm long, 40-45 µm wide. Chromosome number 2n=74. Figs. 9 b; 10 a; 12 a, b; 14 c; 16; 30.

This species grows from southern U.S.A. to Bolivia, central Brazil and the Antilles; it is found between sea level and 2400 m elevation, mostly as an epiphyte.

REPRESENTATIVE SPECIMENS: USA. FLORIDA: near Brown's, 10 Dec. 1903, *Eaton s.n.* (F). MEXICO. SAN LUIS POTOSI: km 338 on route 85, 25 Mar. 1961, *Hewitson 67* (MU); barranca Las Canoas, 8 Aug. 1891, *Pringle 3821* (MU); Jamazunchale, 2 Aug. 1937, *Taylor 923* (F). COLIMA: rancho El Jabali, NNW of Colima, in the SW foothills of the volcán de Colima, 28 Oct. 1990, *Lott et al. 2953* (F). QUERETARO: 74 mi NE of Zimapan, 22 Aug. 1957, *Waterfall & Wallis 14271* (F). HIDALGO: Mun. Xochicoatlán, 3 km S de Jalamelco, 21 Nov. 1982, *Acosta & Barrios 306* (MO); Jacala, 15 Nov. 1937, *Kenoyer 650* (F); Mun. Tenango de Doria, 3 km SW de Tenango de Doria, 17 Mar. 1979, *Koch 798* (F, NY); below Trinidad Iron Works, 1904, *Pringle 8972* (F, MO); 12 mi SW of Chapulhuacán, 4 May 1983, *Yatskievych & Wollenweber 83-125* (F). MICHOACAN: Montes de Oca, Pasión, 7 Oct. 1937, *Hinton 10775* (F, NY). PUEBLA: Huauchinango, 9 Feb. 1932, *Fröderström & Hulten 704* (S); deroute to Atotocoyan, Teteles-Mazatepec, 24 Mar. 1976, *Marquez et al. 718* (F). VERACRUZ: Veracruz, 2 Aug. 1979, *Avendaño & Calzada 429* (F); Mun. Teocelo, La Cuetería, 2 Apr. 1980, *Avendaño 703* (F); Jalapa, 13 Sep. 1906, *Barnes et al. 93* (F), *Barnes et al. 94* (F); 19 Sep. 1906, *Barnes et al 95* (F); along the Mexican railway, above Fortín, 15 Nov. 1908, *Barnes & Land 644* (F); Pedregal Las Vigas, 22 km NW of Jalapa, 3 Jan. 1982, *Bohs et al. 1770* (F); hill de la Cima, La Sombra-Tierra Blanca, 10 Apr. 1981, *Castillo & Vazquez 1534* (F); along Mexican hwy. 140, 26.5 km NW of Jalapa, 1.7 km of La Jolla, 19 Jul. 1978, *Caughlan et al. 320* (F, NY); near Fortín, 27 Jun. 1977, *Croat 39459* (MO); 3 km WNW of Cuichapa on road to Coetzala, 3 Jul. 1982, *Diggs t al. 2720* (F); road Plan de Arroyos-Alvaro Obregón, Hidalgotitlán, 13 Apr. 1974, *Dorantes et al. 2766* (F); road Cedillo-Río Alegre, 18 Jan. 1975, *Dorantes et al. 3916* (F); Agaltepec Island, lake Catemaco, 5 Aug. 1976, *Faden et al. 134* (F); Cuahutlalpan, Ixtaczoquitlán, Jul. 1976, *Faden et al. 168* (AAU, F, US); road Huayacocotla-Viborillas, 14 Jul. 1977, *Fay & Calzada 898* (F); Orizaba, 9 Aug. 1924, *Fischer s.n.* (F, MO); Mun. Huatusco, Puente Adolfo Ruiz Cortines, 7 km NE of Huatusco, 28 Mar. 1979, *García & Delgado 950* (F, MO, NY); near Catemaco, 22 Jan. 1972, *Hernandez 1386* (F); Montepio, Estación Biológica Los Tuxtlas, 29 Jul. 1976, *Kennedey & Horvitz 3676* (F); Cordoba, 5 mi E of Cordoba, 26 Oct. 1957, *Knobloch 710* (F); San Andrés Tuxtla, between Montepio and Sontecomapan, 12 Jun. 1981, *Lorence 3477* (MO); 2 km NE of La Joya, Acajete, 25 Nov. 1975, *Marquez et al. 447* (F); La Joya, 28 Sep. 1940, *Moore 59* (MO); 10 km N of Altotonga, on road to Tlapacoyan, 28 Jun. 1980, *Nee & Hansen 18668* (F); 7 km NW of Coscomatepec, on road to Escola, 12 Jan. 1981, *Nee & Schatz 19828* (F); Mun. Pajapan, 3 Nov. 1981, *Nee & Calzada 22768* (F); Mun. Chocaman, 8.5 km W of Chocomán, on road to Xocotla, 18 Nov. 1981, *Nee 23226* (F); Sanborn, 10 Mar. 1910, *Orcutt 2994* (BM, MO); 1 mi W of Fortín, 4 Aug. 1947, *Paxson et al. 17M680* (F); Córdoba, May 1927, *Reko 5129* (F); Region de los Tuxtlas, Salto de Eyipantla, 16 Mar. 1974, *Riba & Perez 836* (MO); Mun. Xalapa, Salto del Gato, 29 Feb. 1976, *Ronzon 6* (F); road from Catemaco to Sontecomapan, around lake Catemaco, 14 Jan. 1981, *Schatz & Nee 227* (F); Jalapa, 21 Dec. 1894, *C. Smith 2001* (F, MO, UC); Veracruz-Coattacoalcos highway, Cerro Cimtepec, 13 Jul. 1974, *Sohmer 9465* (F); 3 km N of Catmaco, 15 Jun. 1982, *Solheim & Powers 848* (F); Mun. Huayacocotla, 17 km NNE of Huayacocotla, NE of Agua de Calabaza, 27 Jan. 1984, *Taylor & Nee 256* (F); Mun. Altotonga, Nahualaco, 24 Nov. 1969, *Ventura 110* (F, MO); Mun. Acatlán, El Balneario, 14 Nov. 1981, *Ventura 19134* (MO); Mun. Jesús Carranza, 14 Jul. 1984, *Wendt & Villalobos 4454* (MO). OAXACA: Teotitlán del Camino-Chilchotla, 23 Feb. 1979, *Croat 48406* (MO); near Arroyo Sangre, ca. 2 km E of Santa María, *Hernández 369* (MO); dist. Ixtlán, 3 km E of Ixtlán, 24 Jul. 1971, *Mickel 5542* (UC); Mun. Valle Nacional, 21 km N of Vista Hermosa, SW of Vista Hermosa, 15 Dec. 1985, *Nee 32158* (UC); dist. Tuxtepec, Mun. Valle Nacional, 4 km SW of Valle Nacional, 15 Dec. 1985, *Nee 32158* (UC). CHIAPAS: boundary between Zinacantán and Chamula, 20 Jan. 1965, *Breedlove & Raven 8129* (F); Mun. La Trinitaria, along the Comitán river, Lagos de Montebello, NE of La Trinitaria, 13 Nov. 1971, *Breedlove & Smith 22360* (F, NY); Mun.

Ocozocoautla de Espinosa, 26-28 km N of Ocozocoautla, 15 Nov. 1971, *Breedlove & Smith 22445* (F); Mun. Cintalapa, 4 km W of La Cienaga, 10 May 1972, *Breedlove 25134* (F); Mun. Tenejapa, Paraje of Mahosik, 5 Jun. 1972, *Breedlove 25526* (F, NY); Mun. Ocosingo, 10 km SW of Ocosingo , road to San Cristóbal, 23 Sep. 1972, *Breedlove 27855* (F); Mun. San Andres Larrainzar, summit of Chuchil Ton, NE of Bochil, 17 Oct. 1972, *Breedlove 29245* (F); Mun. San Cristobal de las Casas, 17.5 km SE of San Cristóbal, 14 Jan. 1973, *Breedlove & Smith 31511* (F); Ocozocoautla, above 2 mi N Roblada, 23 Mar. 1949, *Carlson 1558* (F); between Tapachula and Unión Juárez, 1-3 mi N of Trinitaria, 10 Feb. 1979, *Croat 47205* (MO); Honduras, ca. Siltepec, 9 Jul. 1941, *Matuda 4371* (MO); Mun. Ocozocoautla, Reserva Ecológica El Ocote, 17 Feb. 1986, *Palacios-Ríos 2884* (UC). Without locality: Temascaltepec, Cucha, 19 Nov. 1934, *Hinton 6833* (MO); Orizaba, 1905, *Lemmon 325* (UC); Ruina Palenque, 10-12 Jul. 1939, *Matuda 3705* (F); 10 Mar. 1910, *Orcutt 2994* (BM, MO); Oxtacihuat, Feb. 1905, *Purpus 1841* (F); Orizaba, 17 Feb. 1982, *J. G. Smith 78* (MO); Orizaba, 29 Mar. 1890, *Stone 104* (MO); *Stone 107* (MO).

GUATEMALA. PETEN: La Cumbre, km 139-139 Cadenas road, 27 Jul. 1969, *Contreras 8861* (F, MO). HUEHUETENANGO: Huehuetenango, 25 Sep. 1944, *Melhus & Goodman 3569* (F); vic. of Maxbal, ca. 17 mi N of Barillas, Sierra de los Cuchumatanes, 15-16 Jul. 1942, *Steyermark 48763* (F); Huehuetenango, 22 Jul. 1942, *Steyermark 49153* (F); above La Libertad, on Cerro Pueblo Viejo, 20 Aug. 1942, *Steyermark 51004* (F). QUICHE: W of Chichicastenango, 12-23 Jan. 1966, *Molina et al. 16309* (F). ALTA VERAPAZ: between San Pedro Carcha and Campur, 20 Mar. 1970, *Harmon & Fuentes 2166* (MO); Alta Verapaz, 10 May 1963, *Molina & Molina 12019* (F); Chamal, 13 May 1963, *Molina & Molina 12152* (F); Alta Verapaz, 26 Mar.-15 Apr. 1939, *Standley 69268* (F), *Standley 69431* (F); region of Chicoj, NE of Carchá, 2 Apr. 1939, *Standley 70059* (F); Alta Verapaz, 5 Apr. 1939, *Standley 70744* (F), *Standley 70940* (F); Alta Verapaz, 26-27 Mar. 1941, *Standley 89854* (F); along Río Carchá, between Cobán and San Pedro Carchá, 26-27 Mar. 1941, *Standley 89906* (F); near Tactic, above bridge Río Frío, 30 Mar. 1941, *Standley 90488* (F); Alta Verapaz, 10 Apr. 1941, *Standley 92030a* (F); Alta Verapaz, 27 Jan. 1969, *L.O. Williams et al. 40193* (F); Alta Verapaz, 4 Jan. 1973, *L.O. Williams et al. 42022* (F); N of Cobán, 4 Jan. 1973, *L.O. Williams et al. 42111* (F); 6 km NE of Cobán, 3 Jan. 1974, *L.O. Williams et al. 42225* (F, GH); near San Cristóbal Verapaz, 6 Jan. 1973, *L.O. Willliams et al. 42207* (AAU, F); 21 Jan. 1974, *L.O. Williams et al. 43627* (F); along Río Cobán, 4 km E of Cobán, 21 Jan. 1974, *L.O. Williams et al. 43627* (F); cerro Sielab, 23 Feb. 1939, *Wilson 244* (F). BAJA VERAPAZ: N of Santa Rosa, 30 Mar. 1939, *Standley 69774* (F); below Patal, 4 Apr. 1941, *Standley 91156* (F, UC), *Standley 91244* (F); Baja Verapaz, 7 Feb. 1969, *L.O. Williams et al. 40678* (F). IZABAL: along Río Frío and tributaries, 18 Dec. 1941, *Steyermark 39992* (F). SAN MARCOS: Volcán Tajumulco, NW of San Marcos, 15 Feb. 1940, *Steyermark 35678* (F); between San Rafael Pie de la Cuesta and Palo Gordo, 10-18 Dec. 1963, *L.O. Williams et al. 25745* (F); Sierra Madre Mountains, N of San Marcos, 13 Dec. 1963, *L.O. Williams et al. 25867* (F, NY). QUEZALTENANGO: 17 Feb. 1939, *Standley 65432* (F); Quezaltenango, 11 Mar. 1939, *Standley 68419* (F); above Los Vahos, Cerro Quemado, 5 Feb. 1941, *Standley 86087* (UC); along old road between Finca Pirineos and Patzulín, 9 Feb. 1941, *Standley 86975* (F, UC), *Standley 87028* (F). TOTONICAPAN: Totonicapán, 8 Dec. 1962, *L.O. Williams et al. 22582* (F); Sierra Madre Mountains, S of Totonicapán, 13 Dec. 1962, *L.O. Williams 22922* (F). SOLOLA: Sierra Madre mountains, near Nahuala, 17 Dec. 1962, *L.O. Williams et al. 23173* (F). SACATEPEQUEZ: 2.3 mi SW Alotenango, from Antigua to Escuintla, 26 Jul. 1977, *Croat 41956* (MO); above Barranco Hondo, 11 Mar. 1941, *Standley 88933* (F). EL PROGRESO: hills SE of Finca Piamonte, 4 Feb. 1942, *Steyermark 43402* (F). JALAPA: Jalapa, 1 Dec. 1939, *Steyermark 32355* (F). ZACAPA: Sierra Las Minas, between Río Hondo and waterfall, 10 Oct. 1939, *Steyermark 29428* (F), *Steyermark 29429* (F). RETALHULEU: Retalhuleu, along Río Coyote, W of Retalhuleu, 24 Feb. 1941, *Standley 88398* (F, UC). ESCUINTLA: between Río Jute and Río Pantaleón, on road between Escuintla and Santa Lucía, 24 Jan. 1939, *Standley 13479* (F). SANTA ROSA: Santa Rosa, near Cuilapilla, 23 Nov. 1940, *Standley 78056* (F, UC).

EL SALVADOR: Volcán San Vicente, Dec. 1930, *Iglesias 9* (F). CHAL: Cerro El Pital, 10 Jun. 1978, *Seiler 394* (F). AHUACHAPAN: vic. of Ahuachapán, 9-27 Jan. 1922, *Standley 19932* (F, NY, US).

HONDURAS. Olancho, Los Zapotes, 8 Oct. 1979, *Andino 86* (MO). FRANCISCO MORAZAN: Valle de Angeles, 15 km NE of Tegucigalpa, 17 Sep. 1983, *Clotter 71* (UC); Quebrada de Zambrano, Zambrano-La Pirámide, 26 Jun. 1964, *Molina 14249* (F); road Cerro Uyuca, 8 km of El Zamorano, 10 Sep. 1982, *Montoya 64* (MO); 14 km NE Tegucigalpa, 6 Aug. 1983, *Morales 34* (MO); Cerro Uyuca, 15 km SE of Tegucigalpa, 30 Oct. 1987; *Moreno 185* (F); Cerro El Picacho, 13 Nov. 1982, *Ochoa 64* (MO); 20 km NE of Tegucigalpa, 14 Nov. 1982, *Padilla 76* (MO); along and near Río Agua Amarilla, above El Zamorano, Oct.-Nov. 1948, *Standley 13956* (F); between Peña Blanca and Ponce, 5 Feb. 1950, *L.O. Williams & Molina 17143* (F). COMAYAGUA: Río San Marcos, Intibucá, 24 May 1970, *Barkley & Hernández 40420* (MO); Montaña Comayagua, 29 Jan. 1975, *Hazlett 2448* (F); Intibucá, between Siguatepeque and Jesús de Otoro, 2 Nov. 1974, *Horwath 135* (F);

Coyocute, 23 May 1956, *Molina 7151* (US); Intibucá, La Esperanza, 12 Sep. 1981, *Segovia 118* (MO); Siguatepeque, 5 Apr. 1947, *Standley & Chacón 6706* (F); vic. Siguatepeque, 14-27 Feb. 1928, *Standley 56335* (F); vic. Siguatepeque, Jun.-Aug. 1936, *Yuncker et al. 5607* (MO), *Yuncker et al. 5650* (F, MO); vic. Siguatepeque, 8 Jul. 1936, *Yuncker et al. 5728* (F, S) . EL PARAISO: Güinope, El Paraíso, Dec. 1943, *Valerio 1868* (F); El Paraíso, 28 Dec. 1962, *Molina & Williams 11199* (F). SANTA BARBARA: Trinidad, 25 Jun. 1982, *Salguero 33* (MO). CORTES: Puerto Cortés, 23 Aug. 1984, *Gómez 49* (F); Montaña de la Nieve, caserío El Tapiquilar, 20 km S San Antonio Cortes, 23 Feb. 1982, *Nelson et al. 7897* (MO). Without locality: 1852, *Hjalmarson s.n.* (S). NICARAGUA. MATAGALPA: between Jinotega and Matgalapa, 1 Apr. 1964, *Bunting & Licht 1004* (F); Finca Tepeuac, 18 km N de Matagalpa, 25 Feb. 1982, *Castro 2488* (UC); Santa María de Ostuma, N of Matagalpa, 25 Aug. 1976, *Hall & Bockus 7897* (BM, NY); Santa María de Ostuma, Cordillera Central de Nicaragua, 1960-1961, *Heller 6* (F); Matagalpa, 1963, *Heller s.n.* (F); Fuente Pura, 26 Aug. 1982, *Moreno 17001* (MO); Cerro Matapalo, 9 km of Matagalpa, 23 Feb. 1983, *Moreno & Robleto 20498* (MO); Matagalpa, along route 5 toward TUMA, 28 Feb. 1971, *Seymour 4037* (MO); Matagalpa, 8-15 Jan. 1963, *L.O. Williams et al. 23313* (F), *L.O. Williams et al. 23516* (F), *L.O. Williams et al. 23596* (F); road to El Tuma, NE of Matagalpa, 14-16 Jan. 1963, *L.O. Williams et al. 24053* (F, NY, US); Matagalpa, 19-21 Feb. 1963, *L.O. Williams et al. 24790* (F), *L.O. Williams et al. 24794* (F); near Santa María de Osuma, 20, 24 Feb. 1963, *L.O. Williams et al.25055* (F); Matagalpa, 15 Jan. 1965, *L.O. Williams et al. 27659* (F); Matagalpa, 16 Jan. 1965, *L.O. Williams et al. 27715* (F); Matagalpa, 18 Jan. 1965, *L.O. Williams et al. 27911* (F); Hacienda Santa María de Ostuma, 11 Feb. 1965, *L.O. Williams et al. 29151* (F); Cordillera Central de Nicaragua, near Xelaju, 12 Feb. 1965, *L.O. Williams et al. 29243* (F); Finca Santa María de Ostuma, 30 Nov-4 Dec. 1973, *L.O. Williams & Molina 42615* (F). JINOTEGA: Laguna Miraflores, ca. 26.1 km NE of hwy 1 at Estelí, 10-11 Jun. 1981, *Henrich & Stevens 339* (MO); Jinotega, 23 Jun. 1947, *Standley 9905* (F); Jinotega, Finca Aventina, E of Jinotega, 23 Jun. 1947, *Standley 9956* (F); region of La Montañita, W of Jinotega, 29 Jun. 1947, *Standley 10360* (F); vic. of Finca San Roque, E of Jinotega, 5 Jul. 1947, *Standley 10843* (F); between La Danta and La Luna, E of Esquipulas, 25 Jan. 1979, *Stevens 11863* (MO); Ocotillo near Santa Lastenia, Cordillera Central de Nicaragua, 17 Jan. 1965, *L.O. Williamas et al. 27801* (F), *L.O. Williams et al. 27864* (F, NY). ESTELI: Cerro Quiabú, 2 Jul. 1982, *Moreno 16775* (MO); 0.6 km from hwy. 3 on road to Aranjuez, 9 Apr. 1978, *Stevens 7543* (MO); Peñas Blancas, above Río El Gusaneras, 13-18 Jan. 1979, *Stevens 11692* (MO). Nueva Segovia, ca. 5.2 km N of San Fernando, NE to Portillo los Coyotes, 10-13 Aug. 1977, *Stevens 3227* (MO).

COSTA RICA. GUANACASTE: Parque Nacional Rincón de Vieja, SE slopes Volcán Santa María, 27-28 Jan. 1983, *Davidse et al. 23326* (MO); Parque Rincón de la Vieja, Herrera 662 (F), *Herrera 728* (MO); 4.5 km W of Tilarán, 26 Jul. 1967, *Mickel 2905* (NY, UC); Rincón de la Vieja National Park, slopes of Volcán Santa María, 26 Jan. 1986, *A.R. Smith et al. 1963* (UC). ALAJUELA: Fila volcán Muerte, above headwaters Río San Lorenzo, 15-17 Apr. 1982, *Barringer & Gomez-Laurito 2545* (F); La Palma de San Ramón, 2 Nov. 1924, *Brenes 4133* (F); San Pedro-San Ramón, 22 Jun. 1926, *Brenes 4880* (F); Santiago de San Ramón, El Piñón, 5 Dec. 1928, *Brenes 6459* (F); La Balsa, 4 Mar. 1983, *Carvajal 476* (MO); 14 km NE Ciudad Quesada, San Carlos, 22 Jul. 1963, *Jiménez 950* (F); La Marina-Aguas Zarcas, 24 Jun. 1966, *Jiménez 4084* (F); S of San Ramón, ca. 3 km above San Rafael, 26 Jul. 1970, *Lellinger & White 1350* (F); above Angel falls, Río La Paz Grande, 23 Mar. 1969, *Lent 1501* (F); above Río Toro, 3 Sep. 1972, *Lent 2813* (F); lower slopes of Volcán Arenal, 17 Sep. 1972, *Lent 2945* (F); Cordillera Central, about 2 km E of Zarcero, 15 Feb. 1966, *Molina et al. 17098* (F, NY); Zarcero, Jun. 1983, *A. Smith H25* (F); region of Zarcero, 16 Jan. 1938, *A. Smith H134* (F); region of Zarcero, 9 Feb. 1938, *A. Smith 301* (F); region of Zarcero, 13 Mar. 1938, *A. Smith 305* (F); Alajuela, 10 Jan. 1939, *A. Smith 1429* (F); slopes of Volcán Poas, 1 May 1949, *L.O. Williams 16591* (F); N of Zarcero, ca. Tapesco river, 6 Feb. 1965, *L.O. Williams et al. 28926* (F). HEREDIA: Sarapiquí Cantón, between Cariblanco and San Miguel, 12 Jul. 1983, *Barringer et al. 3738* (F); El Gallito, 19 Dec. 1933, *Brenes 21711* (F); between Bajo La Hondura and Alto La Palma, 19 Jul. 1983, *Barringer et al. 4002* (F); Río Puerto Viejo, near 2 km confluence Río Sarapiquí, 14-17 Jun. 1968, *Burger & Stolze 5810* (F); near Porrosati on the southern slopes of volcán Barba, 22 Jun. 1968, *Burger & Stolze 6009* (F), *Burger & Stolze 6027* (F); Volcán Barba, 13 Jul. 1967, *Evans & Bowers 2698* (MO); forest of Río Vueltas, 23 May 1969, *Gómez 2287* (F); Monte de la Cruz, 19 Mar. 1963, *Jimenez 474* (F); between San Miguel and Cariblanca, 11 Jul. 1983, *Moran 3155* (F). HEREDIA-SAN JOSE: slopes along Río Para Blanca, Cerros de Zurqui, 13 Sep. 1978, *Burger & Antonio 11034* (F). SAN JOSE: Tablazo, above San Lorenzo de Tres Ríos, 25 Jun. 1985, *Barringer & Christenson 3313* (F); Parque Nacional Braulio Castillo, 19 Feb. 1983, *Chacón 384* (MO); Las Tablas, Río Cotoncito, 10 Dec. 1983, *Chacón et al. 1783* (MO); San Isidro del General, 29 Jul. 1940, *Chrysler 5309* (MO); San José, Cedrus plantation, 15 Aug. 1982, *Moran 2393* (MO); ca. 8 km San José at La Carpintera, 24 Jun. 1983, *Moran 3030* (F), *Moran 3045* (F, MO); Parque Nacional Braulio Carrillo, 19 Jul. 1983, *Moran 3294* (F); vic. of El General, Jan. 1936, *Skutch 2351* (MO, NY, S); about 0.7 km N of Tarbaca on road to Aserrí, 26 Aug. 1979,

Stevens 13676 (F, MO); S slopes of Cerro Zurquí, 5 km N of San Luis Norte, 28 Mar.-4 Apr. 1973, *Stolze 1532* (AAU, F); El Copey, 6 mi E of Santa María de Dota, 19 Apr. 1928, *Stork 1599* (UC). CARTAGO: Río Grande de Orosí, between Orosí and Tapantí, 14 Apr. 1973, *Burger & Gentry 9216* (F); Agua Caliente, 6 Aug. 1940, *Chrysler 5396* (MO); Cartago, Apr. 1888, *Cooper 6053* (F); between Motavia and Quebrada Platanillo, 30 Jun. 1976, *Croat 36614* (MO); lower slopes of La Carpintera, 14 Aug. 1925, *Dodge 3446* (S); vic. Quebrada Casa Blanca, 30 Sep. 1984, *Grayum 3958* (MO); crossing Río Tuis-Río Perlas, near Humo village, 25 Nov. 1986, *Hennipman et al. 7172* (MO); Valley of Río Reventazón, in back of Turrialba hospital, 18 Jul. 1949, *Holm & Iltis 435* (BM, F, NY); Tapantí, Río Grande de Orosí, 19 Jan. 1964, *Jiménez 1603* (F); Cartago, 7 Oct. 1964, J*iménez 2437a* (F); NW of Turrialba, near Pastora, ca. 0.3 km from the highway on the road to Finca Central, 5 Aug. 1970, *Lellinger & White 1455* (F, MO, US); 20 mi S of Cartago, 10 May 1928, *Stork 1906* (UC); Orosí, 23 Jun. 1928, *Stork 2744* (UC); between Puente Negro (Río Agua Caliente) and Río Sombrero, 25 Aug. 1975, *Utley & Utley 2979* (F); near Tuis, 3 May 1956, *L.O. Williams 19547* (F). PUNTARENAS: road to Talamanca, Río Cotón, 2 Sep. 1983, *Davidse 24498* (MO); foothills of Cordillera de Talamanca, Sitio Cotón, 3-4 Sep. 1983, *Davidse 24552* (AAU, MO); upper Río Burú, 19 Aug. 1983, *Gómez et al. 21431* (MO); Monteverde, 13 Nov. 1979, *Koptur 223* (UC). ALAJUELA-PUNTARENAS-GUANACASTE: Cordillera de Tilarán, cerca de Reserva, 22 Jun. 1976, *Dryer 351* (F). LIMON: along road between Limón and Shiroles, along Río Sixaola, 9 mi SW of Bambu, 12 Aug. 1977, *Croat 43304a* (MO); Cordillera de Talamanca, Atlantic slope, Valle del Silencio, N of Cerro Hoffman, 8 Sep. 1984, *Davidse et al. 28649* (MO).

PANAMA. CHIRIQUI: vic. of "New Switzerland", central valley of Río Chiriquí Viejo, 6-14 Jan. 1939, *Allen 1357* (F); *Allen 1358* (F, NY); La Fortuna dam site, 20.9 mi from bridge over Río Estí, 27 Nov. 1979, *Antonio 2821* (MO); vic. of El Boquete, 24 Jul. 1966, Blum & *Dwyer 2572* (MO); vic. of El Boquete, 9 Feb. 1918, *Cornman 902* (US); 2 mi N of El Hato del Volcán, 30 May 1970, *Croat 10649* (MO); El Boquete, pastures on Cerro Azul, near Quebrada Jaramillo, 11 Aug. 1974, *Croat 26868* (MO); slopes of Cerro Horqueta, 13 Aug. 1974, *Croat 26943* (MO); ca. 9 km WNW of El Boquete, 21 Nov. 1975, *Davidse & D'Arcy 10319* (AAU); Nueva California, 31 May 1986, Lara & Chavarria 5 (F). COLON: hills just N of the Río Guanche, 16 Nov. 1975, *Davidse & D'Arcy 10063* (MO). COCLE: road from La Pintada to Coclesito, 7 Feb. 1983, *Hamilton & Davidse 2851* (MO); El Valle de Antón, along Río Indio trail, 30 Jan. 1935, *Hunter & Allen 315* (F, MO, S); El Valle de Antón, 2-3 Dec. 1967, *Lewis et al. 2660* (MO); La Mesa del Valle de Antón, 12 Jun. 1977, *Moreno & Vasquez 9* (F). DARIEN: Punta Guayabo Grande, 20 Apr. 1980, *Antonio & Hahn 4219* (MO); Parque Nacional del Darien, ridge between Río Topalisa and Río Pucuro, ca. 17 km E of Pucuro,, 15 Oct. 1987, *Hammel et al. 16222* (F); Cruce del Mono Field Station, ca. 20 km SSW of Boca de Cupe, 29 Apr. 1990, *Moran 4176* (F).

PUERTO RICO. Alto de la Bandera, near Adjuntas, 14 Mar. 1913, *Britton & Schafer 2081* (F); Reserva Forestal Maricao, 22 mi SE of Maricao, 9 Nov. 1983, *Sauleda et al. 8551* (F). Without Locality: 28 Apr. 1886, *Sintenis 4276* (F).

CUBA. LAS VILLAS: Cienfuegos, Cumanayagua, Las Vegas, 29 Oct. 1985, *Berazaín et al. 57973* (HAJB); Sancti Spiritus, Fomento, road from Pedreras to Gavilán, 10 Nov. 1982, *Bisse & Diaz 48477* (HAJB); Trinidad mountains, San Blas-Buenos Aires, trail to Naranjal, Aug. 1941, *Howard 6419* (MO); hill behind Gavinas, Aug. 1941, *Howard 6504* (F, MO); San Blas, Trinidad mountains, 29 Jul. 1936, *L.B. Smith et al. 3255* (F, MO); Mina Carlota, in Trinidad hills, SE of Cumanayagua, 24 Jul. 1947, *Wood & Atchison 7467* (GH). SANTIAGO: El Yunque, 30 Jan. 1902, *Pollard & Palmer 178* (F, MO, NY). EL ORIENTE: La Prenda, Jul 1919, *Hioram 2452* (MO); Sierra del Nipe, Río Piedra, ad Loma de Estrella, 3 Jul. 1914, *Ekman 1754* (S); Sierra Maestra, N spur of Pico Turquino, 16 Apr. 1915, *Ekman 5412* (S); Baconas, María Pilar, 5 Nov. 1916, *Ekman 8222* (LD, S); Sierra Maestra, between Río Yara and Río Palmamocha, 18 Jul. 1922, *Ekman 14425* (S); N spur of Sierra Maestra, W of Río Yao, 24-30 Oct. 1941, *Morton & Acuña 3390* (F, GH, NY); on top of El Yunque, 19-20 Dec. 1910, *Shafer 7985* (F); camp La Gloria, S of Sierra Moa, N of Río Jaguani, 24 Dec. 1910, *Shafer 8049* (F); Monte Verde, 13 Feb. 1911, *Shafer 8691* (F); Firmeza to Gran Piedra, 3 Mar. 1911, *Shafer 8983* (F); Monte Verde, Jun.-Jul. 1859, *Wright 797* (BM, NY, S), *Wright 800* (BM, S, UC, US). Without locality: Aug. 1923, *Clement 956* (F); *Eggers 4820* (F).

JAMAICA. ST. ANN: Cedar valley, 13 Feb. 1900, *Clute 165* (F); 1.1. mi E of Clarksonville, St. Ann, 3 Aug. 1977, *Goodfriend s.n.* (F); 8.5 mi W by road of Albion, 10 Aug. 1965, *Hespenheide et al. 1032* (GH); Mt. Diabolo, 6 Aug. 1957, *Walker & Walker 1263* (BM). Between Claremont and Moneague, 7 Nov. 1902, *Fawcett 8404* (BM, F). MANCHESTER: hill at Banana Ground, 14 Jul. 1963, *Crosby et al. 704* (F, NY). CLARENDON: S of Aenon town, 16 Jul. 1963, *Crosby et al. 739* (F, GH, NY, UC). PORTLAND: vic. of Mill Bank, 16-17 Feb. 1920, *Maxon & Killip 206* (F); near Green River, on trail from Cinchona, 22 Mar. 1920, *Maxon & Killip 1354* (F); gorge of the Stony river above junction of the Macungo river, 25 Jul. 1967, *Proctor 28337* (F). Blue Mountains, 12 Dec. 1890, *Rothrock 411* (F); Trelawny, Cockpit county, ca. 3 mi W of Troy, 20 Jun. 1959, *Webster et al. 8390* (S).

HAITI. Massif de la Selle, Morne Trauchant, 6 Sep. 1914, *Ekman 1791* (S); Petionville, Tête de l'Eau, 27

Nov. 1927, *Ekman 9369* (S, US). Massif du Nord, Marmelade, Morme Belle-Terre, 22 May 1927, *Ekman 8200* (F, S); vic. Marmelade, 18 Dec. 1925, *Leonard 8088* (F). Massif de la Holle, Jérémie, between Mafrand and Maron, 11 Jul. 1928, *Ekman 10292* (S). Mt. Vincent, 14 Dec. 1944, *Holdridge 2058* (F, NY). L'Artibonite, vic. of Ennery, 20 Jan. 1926, *Leonard 9047* (F, GH). Vicinity of Furcy, 26 May-15 Jun. 1920, *Leonard 4493* (F, UC).
DOMINICAN REPUBLIC. AZUA: Santo Domingo, Cordillera Central, top of La Pelona, 3 Oct. 1929, *Ekman 13646* (C, S). LA VEGA: Santo Domingo, Pico del Valle Nuevo, 15 Oct. 1929, *Ekman 13774* (F, S). PACIFICADOR: vic. of San Francisco de Macorís, La Bracita, 5-17 Apr. 1922, *Abbott 2086* (F). Peravia, Dieciseis, 6.1 km SW of San Juan Aldian on Piedra Blanca to Rancho Arriba road, 10 Jun. 1980, *Mejía & Zanoni 6838* (MO). SANTIAGO: Cordillera Central, SW spur of Monte Gallos, 19 Jun. 1929, *Ekman 12915* (S); San José de las Matas, Arroyo Jicomé, 21 Dec. 1929, *Valeur 302* (F).
GUADELOUPE. Matorba, 1868, *Husnot 297* (F).
COLOMBIA. ANTIOQUIA: San Luis, 12.4 km from San Luis, 15 Sep. 1988, *Betancur et al. 611* (MO); Mun. Tarazá, 201 km NE de Medellín, road to Barroblanco, 19 Aug. 1986, *Callejas et al. 2449* (F); banks of the Río Cauca, at Puerto Valdivia, 1942, *Metcalf & Cuatrecasas 30052* (F). SANTANDER: vic. Puerto Berrio, between Carare and Magdalena rivres, 2 May 1935, *Haught 1691* (F). BOYACA: road to Casanare, Pajarito, *Uribe 6354* (US). CUNDINAMARCA: Suba, Sep. 1941, *Uribe 211* (F).
VENEZUELA. FALCON: Sierra de San Luis, arriba de La Chapa, 24 Mar. 1979, *Werff 3405* (UC). MONAGAS: Caripe, N of El Guácharo cave, 5 Jan. 1987, *Hahn & Grifo 3387* (F, MO). YARACUY: Sierra de Aroa, Cerro Tigre, ridge W of Río Carabobo, 3 Apr. 1980, *Liesner & Gonzalez 9961* (UC).
ECUADOR. CARCHI: Maldonado, 1 Jun. 1978, *Madison et al. 4844* (F). IMBABURA: between El Pajón and Cachaco, 2 Jun. 1949, *Acosta-Solís 12706* (F) Cantón Ibarra, SW of Ibarra, 30 Jun. 1935, *Mexia 7402* (F). PICHINCHA: 35 km S of Santo Domingo, at Puerto Isla farmland, 3 Jun. 1980, *Balslev & Quintana 24163* (AAU, QCA); Santo Domingo de los Colorados, *Fagerlind & Wibom 1652* (S); road Nanegalito-Pacto, archaelogical site at Tulipe, 21 Jul. 1980, *Holm-Nielsen et al. 24498* (AAU, USM). MANABI: Jul. 1893, *Eggers 14899* (F, LD). COTOPAXI: 3 km E of El Empalme, on road Quevedo-Latacunga, 5 Apr. 1980, *Dodson & Gentry 10200* (MO); trail from El Corazón to Facundo Vela, 1-3 km from El Corazón, 17 May 1980, *Harling & Andersson 19194* (F); Quevedo-Latacunga road, 6 Apr. 1973, *Holm-Nielsen et al. 3099* (AAU, F). BOLIVAR: Charquiyacu, 3 Oct. 1943, *Acosta-Solís 6090* (F). NAPO: Reserva Biológica Jatun Sacha, *Cerón 1461* (QCA) Misahuallí, at junction Río Misahuallí-Rio Napo, 13-14 Aug. 1979, *Holm-Nielsen 19337* (AAU, QCA); Napo creek, 3.5 km NW of Borja, 20 Sep. 1980, *Holm-Nielsen et al. 26334* (QCA); Añangu, 30 Jun. 1983, *Lawesson et al. 39660* (QCA); Zatzayacu, 22-28 Mar. 1935, *Mexia 7063* (F, GH, US); Añangu, in the Parque Nacional Yasuní, 30 May-21 Jun. 1982, *Øllgaard et al. 39209* (AAU, QCA), *Øllgaard et al. 38853* (AAU, QCA). CAÑAR: between Suscal and Chontamarca, 25 Apr. 1945, *Camp E-2883* (F). AZUAY: between Paute-Guarumales road, sector Amaluisa, 9 Aug. 1983, *Jaramillo & Winnerskjold 5633* (QCA). LOJA: Alamor-Celica, 2-3 km S of Río Alamor, 5 Apr. 1980, *Harling & Andersson 17939* (QCA); Celica-Zapotilla, ca. 4 km below Pozul, 22 Feb. 1985, *Harling & Andersson 22428* (QCA). ZAMORA-CHINCHIPE: new road Loja-Zamora, km 12.5 E of the pass, 14 Feb. 1991, *Øllgaard et al. 98795* (QCA). Without locality: 12 Aug. 1893, *Eggers 14899* (F).
PERU. CAJAMARCA: Río Aacra, 30 Jun. 1975, *Espinoza 305* (USM); Jaen, Chontalí, 28 Jun. 1979, *Llanos & Chimoy s.n.* (USM). AMAZONAS: Bagua, ca. 1 km NE of Quebrada Chinganza, 11 Jun. 1986, *Knapp & Alcorn 7732* (F, NY); between Aramango and Montenegro, 26 May 1963, *Lopez et al. 4220* (GH); mountains E of Balsas, 22 May 1912, *Osgood & Anderson 85b* (F). SAN MARTIN: Mariscal Cáceres, 6 km NE of Tingo María, Cerro Azul, 4 Sep. 1956, *Tryon & Tryon 5273* (GH, US). LORETO: between Yurimaguas and Balsapuerto, 26-31 Aug. 1929, *Killip & Smith 28349* (NY, US); Santa Rosa, lower río Huallaga, below Yurimaguas, 1-5 Sep. 1929, *Killip & Smith 28862* (GH, NY, US); Maynas, Indiana, Yanayacu, 30 Dec. 1982, *McDaniel & Rimachi 26564* (MO, NY); above Pongo de Manseriche, left bank of Río Santiago, 3 Jan. 1932, *Mexia 6369a* (BM, GH, NY, UC, US); Maynas, Lupuna cocha, 10 Aug. 1956, *Tryon & Tryon 5187* (BM, F, GH, US, USM); Maynas, Río Manití, NE of Iquitos, 22 Dec. 1980, *Vásquez & Jaramillo 1119* (F, MO). LAMBAYEQUE: Ferreñafe, Tute, 25 Jun. 1989, *Llatas-Quiroz 2514* (F). HUANUCO: Muña, 23 May-4 Jun. 1923, *Bryan 547* (F); Pachitea, Honoria, Bosque Nacional Iparia, Miel de Abeja, 18 Jan. 1967, *Schunke V. 1526* (F); Río Pachitea, near Miel de Abeja camp, 11 Apr. 1967, *Schunke V. 1847* (F); Isla del Pacanasi, 5 km above Iparía camp, 14 Nov. 1967, *Schunke V. 2322* (F, GH, NY); Panguana, 11 Jun. 1983, *Seidenschwarz 447* (US); Tingo María, at confluence of Huallaga and Monzón rivers, 25 Oct. 1938, *Stork & Horton 9493* (UC, US). PASCO: Oxapampa, Ulcumanu, SW of Oxapampa, 31 Dec. 1983, *Foster et al. 7695* (F); Oxapampa, forest S of city , 31 Jan. 1983, *León 494* (USM); Oxapampa, 1944, *Soukup 2343* (F, GH). JUNIN: Chanchamayo valley, above La Merced, at cumbre Yacunay, 15 Aug. 1957, *Hutchison 1889* (F, GH, NY, UC); Río Pinedo, N of La Merced, 30 May 1929, *Killip & Smith 23647* (F, GH, NY, US); colonia Perené, 14-22

Jun. 1929, *Killip & Smith 25089* (F, NY, US); Chanchamayo, Jun. 1908, *Schunke s.n.* (BM, US); La Merced-Chanchamayo, Feb. 1939, *Soukup 1013* (F), *Soukup 1016* (F). AYACUCHO: between Huanta and Río Apurimac, 7,17 May 1929, *Killip & Smith 22588* (F, NY). CUSCO: ntre Mistiana y Keros, valle de Cosñipata, 23-31 Jul. 1948, *Scolnik 882* (US). BOLIVIA. LA PAZ: Milluguaya, Dec. 1917, *Buchtien 4229* (BM, F, US); along road between Unduavi and Caranavi, 27 Nov. 1980, *Croat 51553* (LPB, UC); Canamina, 19 Jul. 1921, *White 525* (F); Río Tipuani, Okara, Apr. 1926, Tate 925 (LPB). BENI: Ballivian, Serranía Pilón Lajas, 13-15 km de Yucumo, 20 May 1989, *D.N. Smith et al. 13290* (F). SANTA CRUZ: Cerro Tres Cruces, 9 Oct. 1928, *Steinbach 8205* (F). BRAZIL. ACRE: vic. of Tarauacá, 18 Sep. 1968, *Prance et al. 7384* (F, NY, S). PARA: Lageira, airstrip on Río Maicuru, 18 Jul. 1981, *Strudwick et al. 3133* (F, NY); Lageira, airstrip on Río Maicuru, 19 Jul. 1981, *Strudwick et al. 3222* (F); Macau airstrip on Río Maicuru, 25 Jul. 1981, *Strudwick et al. 3555* (F); west bank of Río Maicuru, ca. 23 km upstream from Lageira airstrip, 29 Jul. 1981, *Strudwick et al. 3744* (F, NY).

Campyloneurum angustifolium is distinctive in having narrowly lanceolate leaves and closely spaced phyllopodia. The stem scales are mostly caducous, persisting only at the growing points of the short creeping stem; the scales are characterized by having narrowly oblong cells and transparent cell lumina. It can be differentiated from *C. aglaolepis*, *C. angustipaleatum*, *C. austrobrasilianum*, *C. centrobrasilianum*, and *C. ensifolium* by the characters of the stem scales used in the key.

Some populations of *Campyloneurum. angustifolium*, growing mainly at middle elevations, have leaves that resemble those of *C. amphostenon*. However, they can be distinguished by the number of areoles between the costa and margin, which in the former species are 1-2 (-3), while in the latter they are 2-4 (-5); further more the stem scales in the latter species are wider, as mentioned in the key.

7. *Campyloneurum angustipaleatum* (Alston) Meyer ex Lellinger, Amer. Fern J. 74: 56. 1984.
Polypodium angustipaleatum Alston, J. Bot. 77: 346. 1939. Type. Bolivia: near Cochabamba, 1891, *Bang 1288* (holotype BM!; isotypes B!, F!, MO!, US)

Stem short creeping, sometimes branched, 1-2 (-4) mm wide, pruinose. Stem scales dark or red brown in mass, 3-5 (-6) mm long, 0.4-0.8 mm wide, subulate or linear from a round base, scale bases shortly auriculate, apex long acuminate, clathrate, without differentiated margins, the cells with walls 10-12 µm thick, sometimes with marginal trichomes. Phyllopodia 1-2 mm wide, 2-3 mm long, less than 5 mm apart. Leaves 12-77 cm long; petiole 1.5-2 cm long, stramineous; lamina linear, bases decurrent, apices acuminate, 0.3-0.8 (-1.5) cm wide, herbaceous-chartaceous, margins cartilaginous, sometimes slightly revolute, indument of simple, inconspicuous hairs, scattered abaxially, stomata polocytic; costa prominent, primary veins inconspicuous, 60-65^{o} divergent from the costa, 1-2 areoles between the costa and margin. Sori medial or subterminal, paraphyses not seen; spores 50-55 (-70) µm long, 40-45 µm wide. Figs. 4; 14 a; 31.

This species is found from Costa Rica, Colombia to Bolivia, where it grows between 800 m and 3000 m elevation, mostly as an epiphyte.

REPRESENTATIVE SPECIMENS:
COSTA RICA. CARTAGO: San Herrano, 11 Aug. 1982. *Moran 2358* (MO).
COLOMBIA. EL VALLE: along hwy. Cali-Buenaventura, 20 km W of village Borrero Ayerbe, 28 Aug. 1976, *Croat 38620* (MO).
VENEZUELA. ZULIA: dist. Mara, 10-15 Nov. 1982, *Bunting et al. 12135* (MO).
ECUADOR. CARCHI: ascent of Río Gualpi Chico, *Hoover et al. 3564* (MO). NAPO: Río Napo, Huiririma, *Harling et al. 7516* (GB, MO). ZAMORA-CHINCHIPE: road Loja-Zamora, km 24-25, *Holm-Nielsen et al. 3526* (AAU, F, MO, UC).
PERU. CAJAMARCA: Colasay, *Woytkowski 6941* (GH, MO, US). AMAZONAS: Bagua, 12 km E of La Peca, *Barbour 2565* (F, MO, NY, UC); Chachapoyas, Ingenio-Pomacocha, 28 May 1963, *López et al. 4310* (GH); NW of Jumbilla, laguna Pomacocha, 23 Jan. 1965, *Soukup 5258* (GH); Bongará, hills WNW of Pomacocha, 19 Jun. 1962, *Wurdack 946* (US, USM); Chachapoyas, along Río Ventilla, 1-2 km W of Molinopampa, *Wurdack 1503* (F, GH, NY, UC, US, USM); Mendoza, *Woytkowski 8167* (GH, MO, US). SAN MARTIN: Rioja, Pedro Ruiz, Moyobamba road, km 390 Venceremos, D.N. Smith 4358 (MO), *D.N. Smith & Vásquez 4630* (MO, NY). HUANUCO: Muña, 23 May-4 Jun. 1923, *Bryan 516* (F); Monzón, "Cuevas de las Lechuzas", 11 Jul. 1958, *Ferreyra 13217* (USM); 32 km from Huánuco, road Huánuco-La Unión, 25 Jul. 1982, *D.N. Smith 2191* (USM). PASCO: Ulcumanu, SW of Oxapampa, road to

María Teresa and Llaupi, 31 Dec. 1983, *Foster et al. 7695* (MO); aprox. 3 km del puente sobre el Río Paucartambo, camino a Oxapampa, *León 473* (USM); Oxapampa, Fundo La Esperanza, 11 Aug. 1985, *León 624* (F, USM); 8 km N of Huancabamba, on the Oxapampa-Pozuzo road, 26 May 1978, *Skog et al. 5075* (US); 5 km SE of Oxapampa, *D.N. Smith & W. Brack 2796* (F, MO); *D.N. Smith 3653* (F, MO, NY, USM). JUNIN: Huacapistana, 5-8 Jun. 1929, *Killip & Smith 24222* (NY, US); Chanchamayo valley, C. Schunke 29 (F); Yaupe, *Woytkowski 6468* (MO), *Woytkowski 6480* (GH, MO, US), *Woytkowski 6481* (MO); Yunguy, *Woytkowski 6603* (MO); Tarma, Utcuyacu, *Woytkowski 37006* (MO, S, UC). CUSCO: Convención, Tupitari, *Bües 5447* (MO, US); San Miguel, Urubamba valley, 10 Jul. 1915, *Cook & Gilbert 17599* GH, NY, US), *Cook & Gilbert 1760* (US); Urubamba, Machu Picchu, *Doppelbaur & Doppelbaur s.n.* (MO); Machu Picchu, 25 Jan. 1983, *León 454* (USM); Río Marcapata, 60 km above Quincemil, 17 Jan. 1973, *Madison 999* (GH); La Convención, Maranura, Chaullay, *Nuñez 8150* (MO, NY); valle de Santa Ana, above Quillabamba, *Plowman & Davis 4800* (F, GH); Potrero, 8 km W of Quillabamba, *Tryon & Tryon 5385* (GH, US, USM); Quispicanchis, Inambari, 2 Sep. 1965, *Vargas 16427* (GH); La Convención, Itma, 28 Jun. 1967, *Vargas 19831* (GH); Apr. 1976, *Vargas 22746* (GH). PUNO: Carabaya, Ollachea-San Gabán road, 25 Aug. 1980, *Boeke & Boeke 3208* (MO, NY).
BOLIVIA. LA PAZ: Nordyungas, Polo Polo bei Coroico, *Buchtien 3529* (F, S, US); *Buchtien 3530* (F, S). COCHABAMBA: Chapare, Paractí, 83 km from Cochabamba, on road to villa Tunan, *M. Foster 79-174* (MO); Sacaba, Incachaca, 11 Oct. 1921, *Steinbach 5848* (F, GH); Chapare, *Steinbach 9073* (GH); Llanta-Aduana, *Steinbach 9599* (F, MO, S). SANTA CRUZ: Ichilo, Parque Nacional Amboro, along Río Saguayo, 20 Dec. 1988, *Nee & Saldias 37289* (MO). Without locality: *Rusby 2461* (F).

Campyloneurum angustipaleatum is closely related to *C. angustifolium*. These species have similar leaf morphologies and patterns of venation. They differ in the characteristics of the stem scales, which in the former are less than 1 mm wide and are linear from a wide base, while in the latter they are lanceolate, with the base more than 1 mm wide.

8. *Campyloneurum aphanophlebium* (Kunze) T. Moore, Index Fil. 223. 1861.
Polypodium aphanophlebium Kunze, Bot. Zeitung (Berlin) 288. 1845. Type. Venezuela: Caracas, *Moritz 17* (B!).
Campyloneurum occultum (Christ) L. D. Gómez, Brenesia 8: 46. 1976.
Polypodium occultum Christ, Bull. Herb. Boissier 2: 7. 1905. Type. Costa Rica: Cartago, Río de las Vueltas, Tucurrique, Nov. 1898, *Tonduz 12752* (holotype, P!; isotypes B!, BM!). Christ in the protologue of the species mentioned *Tonduz 12756*, as the type collection, but this may represent a typographic error.
Polypodium trichiatum Rosenst., Repert. Spec. Nov. Regni Veg. 7: 148. 1909. Type. Ecuador: Riobamba, Cordillera Occidental, *Rimbach 87* (holotype, not found; isotypes, S!, US!, photo of S, BM!).
Campyloneurum trichiatum (Rosenst.) Ching, Sunyatsenia 5: 263. 1940.

Stem creeping, black, dark stramineous, 1-3 (-4) mm wide. Stem scales dark brown in mass, 2-4 (-5) mm long, 0.75-1 (-1.2) mm wide, narrowly ovate, bases auriculate, apices acuminate, clathrate, slightly differentiated margins, cells oblong, except the rondish cells at the base of the scale, central cell walls 16-20 µm wide, marginal cell walls 8-12 µm wide. Phyllopodia 1-1.5 mm long, 2-2.5 mm wide, 2-4 (-6) mm apart. Leaves (10-) 20-40 (-55) cm long; petiole stramineous or dark stramineous, (0.3-) 0.7-3 (-0.6) cm long, slightly ranurate adaxially, puberulent, rarely with scattered scales similar to those on the stem; laminae oblanceolate, rarely narrow lanceolate, bases attenuate, apices acuminate or caudate, (1.2-) 2-4 (-4.7) cm wide, herbaceous-chartaceous, margins cartilaginous, plane or slightly revolute, sinuate, indument of pluricellular hairs, with one small basal branch, glandular and the other long; , stomata polocytic; costa prominent on both surfaces of the lamina, primary veins slightly prominulous or inconspicuous, same color as the leaf tissue or different adaxially, slightly flexuosous, (-50^{o}) 60-65^{o} divergent from the costa, (3-) 4-7 (-9) mm apart, secondary veins inconspicuous, transverse veins sometimes darker than the leaf tissue, forming 3-6 primary areoles between the costa and margin, primary areoles usually undivided, 2 (-3) excurrent veinlets in each primary non-costal areole; sori medial or subterminal, paraphyses dendritics, spores 50-60 (-65) µm long, 30-40 µm wide. Figs.

9; 13 b; 18 a; 28.

This species is distributed from Belize to Brazil and Bolivia. It grows in forests, from sea level to 1500 m, usually as an epiphyte.

REPRESENTATIVE SPECIMENS: BELIZE. Edwards road, beyond Columbia, 13 May 1951, *Gentle 7327* (US).
NICARAGUA. ZELAYA: between cerro La Pimienta and El Hormiguero, 15 Mar. 1980, *Pipoly 5971* (MO, UC); Caño El Hormiguero, 17 Mar. 1980, *Pipoly 6106* (MO). CHONTALES: Chontales, Jun. 1868, *Tate s.n.* (BM). Without locality: Jun. 1868, *Tate 57* (K).
COSTA RICA. GUANACASTE-ALAJUELA: slopes of Miravalles, above Bijagua, Nov. 1982, *Gómez et al. 19050* (AAU, UC). ALAJUELA: NW of Volcán Arenal, ca. 2 km NE of Tabacón, 16 Aug. 1970, *Lellinger & White 1650* (F, US). CARTAGO: behind main building of CATIE, Turrialba, 30 Jul. 1985, *Grayum & Hammel 5748* (MO, USM); near Turrialba, slope of Río Reventazón, behind the Instituto Interamericano de Ciencias Agrícolas, 20 Aug. 1967, *Mickel 3362* (NY, US); bords du Río Colorado, Golfo Dulce, Mar. 1896, *Pittier 9993* (US); Turrialba, near Interamerican Institute, 30-31 Mar. 1953, *Scamman 7244* (GH). HEREDIA: La Selva, along Río Viejo, 1 Feb. 1988, *Hennipman et al. 7156* (MO); Puerto Viejo, Finca La Selva, 18 Jun. 1967, *Sota 5120* (US). PUNTARENAS: about 5 km W of Rincón de Osa, Osa Península, 24-30 Mar. 1973, *Burger & Gentry 8875* (F).
PANAMA. COLON: E Santa Rita ridge, 23 Feb. 1968, *Correa & Dressler 754* (MO). COCLE: El Valle de Antón, 4 Jun. 1939, *Alston 8712* (BM). CANAL ZONE: Barro Colorado Island, Shannon trail 100, 17 Jun. 1970, *Croat 10906* (F, NY); Armour trail 1040, 29 Jul. 1970, *Croat 11634* (F, NY); Isthmo de Panama, 1859-61, *Hayes 54* (B); trail along Río Petitpie, from road to Ft. Sherman from Gatun Locks, 22 Oct. 1974, *Mori & Kallunckí 2676* (US); 6 mi N of Gamboa, on ridge S of Río Frijol, 6 Oct. 1965, *Tyson 1514* (GH). DARIEN: Río Morti, drill site 7, 15 Sep. 1967, *Duke 14138* (F); vic. of Caná, 24 Jun. 1959, *Stern et al. 687* (US). GOLFO DE PANAMA: San José Island, Perlas Archipielago, about 55 mi SSE of Balboa, 25 Oct. 1944, *Johsnton 285* (BM, GH, K).
COLOMBIA. ANTIOQUIA: around Villa Arteaga, 10 Oct. 1947, *Gutierrez & Barcley 17C101* (BM); Villa Arteaga, 4-8 Aug. 1947, *Hodge 6988* (GH); Mun. Zaragoza, Corregimiento de Providencia, vicinity of Tirana, 12 Feb. 1971, *Soejarto & Villa 2817* (GH). CHOCO: W of Puerto Mutis, Bahía Solano, 25 Jan. 1971, *Lellinger & Sota 12* (US); Chocó, *Schott s.n.* (MO). INTENDENCIA DEL META: Sierra de la Macarena, Caño Estrada, 3 Jan. 1950, *Philipson & Idrobo 2017* (BM). EL VALLE: Río Digüa valley, La Margarita, 4-5 Apr. 1939, *Killip 34889* (GH, US). SUR DE SANTANDER: vic. of Puerto Berrío, between Carare and Magdalena river, 14 Jun. 1935, *Haught 1777* (US). CAUCA: valle del Cauca, *Duque-Jaramillo 1985* (F).
VENEZUELA. Colonia Tovar, 1856-1857, *Fendler 409* (K). Encanto, 1929, *Vogl s.n.* (S).
FRENCH GUIANA: Without locality, Jan. 1836, *Leprieur s.n.* (B).
ECUADOR. NAPO: San Pablo de los Secoyas, Río Wai-si-aya, northern tributary to Río Aguarico, 7 Aug. 1980, *Brandbyge et al. 32635* (AAU, QCA); 6 km upriver from San Pablo, 10 Aug. 1980, *Brandbyge & Asanza 32734* (AAU, QCA); W of confluence with Río Napo, at Bimbino, 21 Oct. 1960, *Whitmore 787* (BM). PICHINCHA: San José de Toachi, 100 km W of Quito, 3 Apr. 1951, *Bell 217* (S); forest of the Cooperativa Santa Marta No. 2, at km 3 of bypass, around Santo Domingo, 22 Jul. 1979, *Dodson et al. 8505* (US); road Aloag-Santo Domingo, Alluriquin, 14 Mar. 1967, *Sparre 14819* (S); Quito, *Spruce 5738* (BM, K). PASTAZA: Ceilán, Pica, from Ceilán to Río Cononaco, N side of the Río Curaray, 6 Jun. 1980, *Brandbyge & Asanza 31659* (AAU, QCA); oil exploration camp Chirirota, on the Río Bobonaza, 26 Jul. 1980, *Øllgaard et al. 35298* (AAU, QCA). GUAYAS: Teresita, 3 km W of Bucay, 5-7 Jul. 1923, *Hitchcock 20410* (GH, US). MORONA-SANTIAGO: Tukupi, near the military camp, 25 Jun. 1980, *Brandbyge & Asanza 32276* (AAU, QCA); 35 km NE of Montalvo, 2-12 Jul. 1989, *Zak & Espinoza 4646* (MO). SANTIAGO-ZAMORA: valley of Río Negro and río Chupianza, 2-3 km W of Méndez, 13 Dec. 1944, *Camp E-1495* (US). Without locality, Sep. 1884, *Sodiro s.n.* (UC).
PERU. AMAZONAS: Bagua, ca. 1 km NE of Quebrada Chinganza, 10 km NE of Mayo, 11 Jun. 1986, *Knapp & Alcorn 7733* (F, NY); Bagua, Montenegro-Chiriaco, 16 Oct. 1965, *Sagástegui 5924* (HUT). SAN MARTIN: Mariscal Cáceres, dist. Campanilla, Cajón Pericote, 21 Aug. 1970, *Schunke V. 4288* (F, UC, US, USM); Río Marañón, Apr. 1855, *Spruce 3912* (K); Tarapoto, 1855-1856, *Spruce 3912* (K). LORETO: Balsapuerto, lower Río Huallaga basin, 28-30 Aug. 1929, *Killip & Smith 28642* (NY, US); San José de Parinari (Río Marañón) , 10 Aug. 1981, *Vásquez et al. 2274* (NY) San Martín de Tipishca (Río Samiria), 13 May 1985, *Vásquez & Jaramillo 6511* (F, MO); Maynas, Indiana, Explorama reserve, 10 Nov. 1989, *Vásquez & Jaramillo 13167* (MO). HUANUCO: Tingo María, 30 Oct. 1949-19 Feb. 1950, *Allard 21520* (US), *Allard 21982* (US); Fundo Chela, Sinchono, 3 Aug. 1948, *Aguilar 946* (USM); above Río Huallaga, at Tingo María, 4 Oct. 1972, *Croat 21034* (USM); Pachitea, dist. Puerto Inca, Agua Dulce, Bosque Nacional Iparía, 6 Dec. 1968, *Schunke V. 2818* (F, GH, US); Tingo María, by Río Huallaga, 16 Sep. 1956, *Tryon & Tryon 5335* (GH, US,

USM); Cachicoto, 5 Apr. 1963, *Woytkowski 7868* (UC). PASCO: Puerto Bermudez, 14-17 Jul. 1929, *Killip & Smith 26647* (US). JUNIN: La Merced, 29 May-4 Jun. 1929, *Killip & Smith 25268* (S); *Killip & Smith 23781* (GH, NY, US). MADRE DE DIOS: Parque Nacional Manu, Cocha Cashu, 8 Nov. 1984, *M. Foster 84-64* (F); Manu, Cocha Cashu Station, 15 Aug. 1978, *Foster & Terborgh 6630* (F).
BOLIVIA. Yumupasa, 10 Jun. 1902, *Williams 1064* (US).
BRAZIL. ACRE: Cruzeiro do Sul, Rio Juruá and Rio Moa, vic. of Porangaba, Rio Juruá-Mirim, 21 May 1971, *Maas et al. P131381* (S, US); Mun. Tarauacá, vic. of Tarauacá, 14 Sep. 1968, *Prance et al. 7267* (GH, K, S, US). PARA: W bank of Rio Maicuru, ca. 23 km upstream from Lageira airstrip,29 Jul. 1981, *Strudwick et al. 3709* (F).

Campyloneurum aphanophlebium is characterized by its dense puberulent leaves and inconspicuous secondary veins. *Campyloneurum aphanophlebium* and *C. anetioides* belong to the same group, sharing morphological features, such as stem scales characters, closely spaced leaves on the stem, and the presence of foliar indument on both sides of the lamina.

9. *Campyloneurum asplundii* (C. Chr.) Ching, Sunyatsenia 5: 263. 1940.
Polypodium asplundii C. Chr., Ark. Bot. 20A (7): 24. 1926. TYPE: Bolivia, Prov. Sur Yungas, La Sirena, ca. 2300 m, 1920, *Asplund 282* (holotype S!, isotype BM!).

Stem creeping, (2-)3-4 (-4.5) mm wide, sometimes pruinose, black. Stem scales narrowly ovate, non-clathrate, shining dark brown in mass, 3-5 mm long, 1-1.5 mm wide; with cell lumen yellow brownish, scale base short biauriculate. Phyllopodia 1.5-3 mm long, 1.5-2 mm wide, 4-7 mm apart. Leaves 35-60 cm long; petiole stramineous, (1-) 4-12 cm long, indument of hairs; lamina linear to narrowly lanceolate, bases and apices attenuate, (0.6-) 1.5-3.5 (-5.8) cm wide, chartaceous, lamina margins cartilaginous, slightly revolute, indument of bicellular hairs, scattered abaxially; stomata polocytic; costa prominent on both surfaces, with indument of often persistent scales, primary veins obscure or slightly prominulous to different degrees on either side of the lamina, sometimes to the same degree, slightly flexuous, 4-5 mm apart, diverging 50-60º from the costa, with 2-4 areoles between costa and margin, one, rarely two, veinlet in each areole. Sori subterminal, paraphyses not seen, spores 60-65 µm long, 40-42 µm wide. Fig. 32.

This species is distributed from Venezuela, Ecuador, Peru to Bolivia, where it grows between 1000 m and 3500 m elevation, among rocks and sometimes as an epiphyte.

REPRESENTATIVE SPECIMENS: VENEZUELA. MERIDA: Andrés Bello, Zerpa, La Carbonara, bosque San Eusebio, 14 Nov. 1981, *Marin et al. 115* (F).
ECUADOR. PICHINCHA: Chaparro de Sebritana, 9 Jul. 1944, *Acosta-Solis 8364* (F). CHIMBORAZO: Cerro Chiguazo, ca. 15 km from Penipe, 24 Sep. 1968, *Lugo 474* (F).
PERU. SAN MARTIN: Mariscal Cáceres, Parque Nacional Río Abiseo, trail between La Playa and Papayas, 25 Jul. 1987, *Young & León 4995* (F, USM); Huallaga, valley of Río Apisoncho, 30 km above Jucusbamba, 9 Sep. 1965, *Hamilton & Holligan 903* (US), *Hamilton 905* (US). HUANUCO: Carpish, 12 Dec. 1953, *Coronado 62* (GH, UC, US), Coronado 67 (US); 6 mi S of Mito, 1-5 Aug. 1922, *Macbride & Featherstone 1835* (US); Yanano, 13-16 May 1923, *Macbride 3818* (F, GH, US); Muña, 23 May-4 Jun. 1923, *Macbride 3911* (F, US); Muña, 10 Mar. 1959, *Woytkowski 5181* (GH, US). PASCO: Oxapampa, 31 Jan. 1983, *León 491* (F, USM); 1 Feb. 1983, *León 506* (F, USM); canyon of Huancabamba, Fundo La Esperanza, 11 Aug. 1985, *León 617* (F, GH, USM); border of Parque Nacional Yanachaga, 21 Jun. 1986, *León et al. 946* (F, USM); Río El Tunqui, 2 Jan. 1984, *D.N. Smith & Alban 5526* (F, MO, NY); Santa Bárbara, 3 Aug. 1984, *D.N. Smith 8160* (F); border Prov. Oxapampa and Pasco, below San Gotardo, 7 Mar. 1986, *Werff et al. 8521* (MO, NY, UC). JUNIN: Carpapata, above Huacapistana, 7 Jun. 1929, *Killip & Smith 24429* (NY, US); Chanchamayo, Jun. 1908, *C. Schunke s.n.* (BM, F); Chanchamayo, Río Rondayacu, 45 km from San Ramón, 2 Jun. 1982, *D.N. Smith 2117* (USM); La Merced, Aug. 1947, *Soukup 3400* (F); Yaupe, 9 Jul. 1961, *Woytkowski 6497* (US). LIMA: Chancay, Huaccaña, E of Supe, 4 Jan. 1952, *Cerrate 1062* (USM). AYACUCHO: Huanta-La Mar, Tambo, 37 km from Ayna, 23 Mar. 1977, *Ellenberg 7021* (LPB). CUSCO: Cerro Huacontoy, Hacienda Muy Muy, valle de Lares, Mar. 1932, *Bues 1868* (US); La Convención, Vilcabamba, trail from Yupanqui to Apurimac, 4 Jul. 1981, *Davis et al. 1231* (GH); Machu Picchu, 18 Nov. 1947, *Ferreyra 2707* (BM, USM); along Inca trail, above Machu Picchu, 13 Apr. 1977, *Gentry et al. 19422* (F), near Cusco, Apr. 1923, *Herrera 5* (US); Río Urubamba,

22 May 1958, Humbert 30662 (GH); Urubamba, Winay Wayna, 26 Oct. 1986, Nuñez et al. 8422 (F, MO, NY, UC); Kosñipata, between Yanamayo and Santa Isabel, 23-31 Jul. 1948, *Scolnik 847* (US); Urubamba, Machu Picchu, Tancarpata, 20 Jul. 1961, *Vargas 13591* (GH); La Convención, Potrero, Sapansayoc, 23 Sep. 1961, *Vargas 13645* (GH). PUNO: Sandia, bajando a Valle Grande, 7 Aug. 1957, *Vargas 11864* (GH); Sandia, Limbani a Chacani, 13 Oct. 1963, *Vargas 14936* (GH). BOLIVIA. LA PAZ: Murillo, Zongo valley, above Jarca, Río Chuchulluni, 31 May 1980, *Beck 3590* (F); Zongo valley, Cambaya, 14 Dec. 1982, *Liberman 490* (F).

Campyloneurum asplundii is characterized by having linear-lanceolate, non-clathrate, shining dark brown stem scales, with an almost occluded lumina.

One syntype of *Polypodium leucorhizon* Kunze ex Klotzsch, *Schomburgk 1145* from British Guiana, has scales of the stem similar to *Campyloneurum asplundii*. However, it seems uncertain that this specimen from lowland areas belong in this taxa.

This species belongs to the *C. amphostenon* group. *Campyloneurum asplundii* is closely related to *C. solutum*; these species are similar in shape and color of the scales. The former, however, has non-clathrate scales with yellow brown cell lumina, almost occluded.

10. *Campyloneurum austrobrasilianum* (Alston) Sota, Op. Lilloana 5: 99. 1960.
Polypodium austrobrasilianum Alston, J. Bot. 77: 347. 1939. Type. Brazil: Paraná, Curitiba, *Hoehne 24365* (holotype, BM!, isotype GH!).

Stem short-creeping, not pruinose, 1-3 mm wide. Stem scales red brown or brown in mass, 2.5-4.5 mm long, 0.3-0.8 (-1) mm wide, narrowly ovate, bases auriculate with open or superposed auricles, margins sometimes with hairs 12 µm long, scales clathrate, with nondifferentiated margins, the cells oblong, cell walls 12-16 µm wide. Phyllopodia 0.5 mm long, 1 mm wide, 2-4 mm apart. Leaves 15-50 cm long, petiole greenish or stramineous, 0.3-0.8 (-3.5) cm long; laminae linear, bases and apices attenuate, 0.3-0.6 cm wide, herbaceous-chartaceous, margins cartilaginous, sometimes revolute, indument not seen, stomata polocytic; costa prominent on both surfaces, without indument, primary veins inconspicuous, 1-2 areoles between costa and margin, one veinlet in each areole; sori medial, paraphyses not seen, spores 60-65 µm long, 40-42 µm wide. Fig. 26.

This species is restricted to central east and southeast Brazil, where it occurs below 1500 m elevation, mostly as an epiphyte in forests.

REPRESENTATIVE SPECIMENS: BRAZIL. MINAS GERAIS: Mun. Jabaticatubas, Serra do Cipó, *Hatschbach 30048* (UC); Serra do Espinhaço, lower slopes of Serra do Caraça, ca. 12 km W of Barão de Cocais, 27 Jan. 1971, *Irwin et al. 29288* (F, NY); Mun. Ouro Preto, *Macedo 3046* (S); Caldas, *Mosen 2218* (S); Caldas, Pedra Branca, *Regnell 317* (S). MATO GROSSO: Palmeiras, *Lindman A2527* (S). GOIAS: ca. 30 km N of Alto Paraíso, Chapada dos Veadeiros, 23 Mar. 1971, *Irwin et al. 33063* (F, NY). PARANA: Mun. Lapa. Fundo São Sebastião, *Kummrow 1396* (MU, UC); Mun. Bocaiuva do Sul, Bacaetava, *Kummrow 1423* (UC); Mun. Quatro Barras, Borda do Campo, *Kummrow 1959* (UC). RIO GRANDE DO SUL: Sep. 1940, *Eugenio & Leopoldo 1773* (F); Paso da Mangueira, Santa Cruz, *Jürgens s.n. (Rosenstock 96)* (BM, F, S, UC); Cachoeira, *Lindman 1169* (S); Silveira Martins, *Lindman 1169b* (LD, S); Porto Alegre, Cañoas, *Lindman 1169c* (S); Esmeralda, Est. Ecol. Aracauri, 8 Oct. 1980, *Waechter 1726* (F). SANTA CATARINA: Lages, *Spannagre 7* (UC); Joinville, *Schmalz 175* (F, MO); Mun. Cacador, Pinheiral, *Smith & Reitz 8965* (US). SÃO PAULO: Campos de Jordão, 20 Feb. 1937, *Campos Porto 3211* (F, US). RIO DE JANEIRO: Itatiaya, Maromba-Macieiras, *Zerny s.n.* (W). Without exact locality: *Sehnem 6321* (US).

Campyloneurum austrobrasilianum is characterized by brown, linear stem scales, with cell walls clearly defined. This species belongs to the *C. angustifolium* group.

11. *Campyloneurum brevifolium* (Lodd. ex Link) Link, Fil. Spec. 124. 1841.
Polypodium brevifolium Lodd. ex Link, Hort. Berol. 90. 1833. Type. *Habitatio ignota*. Cultivated. (holotype B!; photo BM!).
Campyloneurum latum T. Moore, Index Fil. 225. 1861. Type. Windward Islands. St. Vincent: s.d. *Guilding s.n.* (Lectotype chosen by Proctor in R. Howard 2: 342, 1977, K!).
Polypodium phyllitidis Linn. var. *lata* (T. Moore) Hook. Sp. Fil. 5: 38. 1864.

Polypodium latum (T. Moore) T. Moore *ex* Sodiro, Crypt. Vasc. Quit. 371. 1893.
Campyloneurum phyllitidis var.*latum* (T. Moore) Farwell, Amer. Midl. Naturalist 12: 297. 1931.
Polypodium phyllitidis f. *latum* (T. Moore) Proctor, Bull. Inst. Jamaica Sci. Ser. 5: 49. 1953.

Stem creeping, not pruinose, (4-) 6-17 (-24) mm wide. Stem scales light brown in mass, 4-6 mm long, 2-3 mm wide, broadly ovate, pseudopeltate, auriculate, apices acuminate, clathrate, with differentiated margins, the cells oblong, central cells along the main axis of the scale, marginal cells transverse, these usually smaller than the central ones, central cell walls 16-20 µm wide, marginal cell walls 6-8 µm wide. Phyllopodia 2-5 mm long, 3-6 mm wide, 2-4 (-10) mm apart. Leaves (35-) 40-120 cm long; petiole stramineous or brownish, (2-) 5-28 cm long, ranurate adaxially, convex abaxially, glabrate, indument of broadly ovate scattered scales similar to those in the stem; lamina elliptic-lanceolate, bases attenuate or subcuneate then short or long decurrent, apices acuminate or caudate, 5-13.5 cm wide, chartaceous or coriaceous, margins cartilaginous, sinuate or undulate, indument of inconspicous simple hairs, scattered abaxially, stomata polocytic; costa prominent on both surfaces, slightly ranurate abaxially, convex or slightly angulate adaxially, sometimes with oval-lanceolate scattered scales, primary veins prominent on both surfaces, stramineous, straight or slightly flexuosous at the margin, 70-75º divergent from the costa, (4-) 6-9 (-13) mm apart, secondary veins inconspicuous or slightly prominulous abaxially, rarely adaxially, transverse veinlets forming 8-18 primary areoles between the costa and margin, excurrent veinlets 2-5, entires or furcate, free or forming 2-5 secondary areoles; decurrent veinlets 1-2 in each primary areole; sori medial, subterminal or at the junction of the secondary veins, 2-4 series between the secondary veins; paraphyses not seen, spores 50-60 (-70) µm long, 35-40 µm wide, verrucate surface. 2n= 74. Figs. 14 j; 33.

Campyloneurum brevifolium is distributed from Mexico, Central America, the Antilles Venezuela to Bolivia, rarely in southern U.S.A. (Florida). It occurs from sea level to 2000 m elevation. It grows on abundant organic matter on the ground or as a hemiepiphyte in tropical forest.

REPRESENTATIVE SPECIMENS: U.S.A. FLORIDA: Dade County, 13 Dec. 1903, *Eaton 562* (GH, US). MEXICO. JALISCO: Los Chorritos, La Rinconada, Purificación, 450 m, 5 Feb. 1979, *Alcocer 11111* (UC). PUEBLA: between Pahuatlan and Honey, 16 Dec. 1942, *Martinez 101* (F). OAXACA: Tuxtepec, hills 9 km S of Tuxtepec and 4 km W of route 175, 30 Jul. 1971, *Mickel 5782* (UC); 4-9 km S of Valle Nacional, 31 Jul. 1971, *Mickel 5867* (UC); 1-3 km S of Usila, 27 Sep. 1973, *Mickel 7375* (UC).
BELIZE. TOLEDO: 1.5 mi S of Mayan village of San José, 12 Jun. 1973, *Croat 24351* (F, US); near Jacinto Creek, 17 Nov. 1944, *Gentle 4982* (F, S); on hilltop beyond Carmelita camp, Edwards road beyond Columbia, 27 Jun. 1951, *Gentle 7385* (F, S, US); Salamanca camp, 26 May 1979, *Whitefoord 1887* (BM). EL CAYO: Valentin, Jun.-Jul. 1936, *Lundell 6231* (US). Middlesex, 16 Sep. 1929, *Schipp 8-46* (F).
GUATEMALA. PETEN: Vaxactum, 20 Mar. 1931, *Bartlett 12148* (F, UC, US). IZABAL: S shore of Lake Isabel, between Izabal and Mariscos, 28 May 1966, J*ones & Facey 3498* (F). Quirigua, lawn at United Fruit Co. Hotel, 8 Feb. 1945, *Weatherwax 228* (UC).
HONDURAS. CORTES: N of Lago de Yojoa, SW of Santa Cruz de Yojoa, 4 Aug 1977, *Croat 42737* (UC); Isla de La Guamita, N shore of Lake Yojoa, 29 May 1974, *Horwath 44* (F). COMAYAGUA: 10 km N of Talube, 28 May 1974, *Horwath 18* (F). ATLANTIDA: Lancetilla, Tela, 17 Jun. 1964, *Lent 7* (F, US); near Tela, Lancetilla valley, 6 Dec 1927-20 Mar. 1928, *Standley 53540* (US); Tela river, above Lancetilla, 1 Aug. 1951, *Steeves & Ray 413* (GH, UC, US); above Lancetilla, 12 Jul. 1934, *Yuncker 4548* (F). GRACIAS A DIOS: La Mosquita, alrededores del Río Plátano, 17-23 May 1973, *Clewell & Cruz 4138* (US). OLANCHO: vicinity of Juticalpa, 5-16 Mar. 1949, *Standley 18043* (F).
EL SALVADOR. SAN SALVADOR: Botanical Garden La Laguna, 2 Mar. 1979, *Seiler 971* (F).
NICARAGUA. CHONTALES: between Santo Tomas and Villa Somozo, 7 Apr. 1961, *Bunting & Licht 1098* (F, GH); vic. La Libertad, 29 May-1 Jun. 1947, *Standley 9002* (F). MATAGALPA: summit of Matagalpa-Tuma road, 24 May 1981, *Stevens & Henrich 20316* (UC). ZELAYA: Sector Mina Nueva America, 22 Sep. 1984, *Ortiz 2129* (MO). BLUEFIELDS: SE slopes of Cerro San Isidro, 3.6 km SE Cerro San Isidro, 25 Mar. 1966, *Proctor et al. 27254* (F, NY). MANAGUA: vic. Casa Colorada, near El Crucero, summit of Sierra de Managua, 14-25 May 1947, *Standley 8425* (F). Without exact locality: Cabo Gracias a Dios, 1 May 1923, *Schramm s.n.* (US); Castillo, Mar. 1893, *Shimek s.n.* (F); s.l. 1853-1856, *Wright s.n.* (US).

COSTA RICA. GUANACASTE: Rincón de la Vieja National park, ridge SE of Quebrada Zopilote, lower SE slope of Volcán Santa María, 24 Jan. 1986, *Smith et al. 1925* (UC). ALAJUELA: ca. 7 km E of Ciudad Quesada, 17-18 May 1968, *Burger & Stolze 4934* (F); wooded area above Río Aguas Zarcas, S of Aguas Zarcas, 20 May 1968, *Burger & Stolze 5111* (F); near Artezalea, ca. 8 km NE of Villa Quesada, 16 Feb. 1966, *Molina et al. 17220* (F, US); Florencia, 14 Jul. 1963, *Rickson 208* (GH). HEREDIA: forest near Río Puerto Viejo, 14-17 Jun. 1968, *Burger & Stolze 5819* (GH); *Burger & Stolze 5914* (F, NY); Finca of Dr. Holdridge, on the Río Puerto Viejo, 18-28 Feb. 1955, *Scamman 7511* (GH); Cerros Sardinal, ca. 2-2.5 km N of Chilamate de Sarapiquí, 21 Jan. 1986, *Smith et al. 1800* (UC); Finca La Selva, Sarapiquí region, 30 Aug. 1961, *Weber 6121* (GH, US). PUNTARENAS: about 5 km W of the Rincón de Osa, Osa Peninsula, 24-30 Mar. 1973, *Burger & Gentry 8889* (F); foothills of the Cordillera de Talamanca, vic. of Helechales, 29 Mar. 1984, *Davidse & Herrera 26275* (MO); Rincón de Osa, ridge between Quebrada Aparicio and Quebrada Aguabuena, 7 Oct. 1984, *Grayum et al. 3989* (UC); Monteverde, Turrialba, 26 Apr. 1980, *Koptur 322* (UC); Osa Peninsula, ca. 20 km S of Rincón de Osa, 18 Jul. 1967, *Mickel 2784* (NY, UC); Turrialba, near Interamerican Inst. *Scamman 6166.5* (GH). SAN JOSE: Bajo La Hondura, 4 Jul. 1972, *Mc Alpin et al. 1186* (F); valley La Palma, above the La Hondura, ca. 9 km NE of San Jerónimo, 23 Mar. 1973, *Stolze 1434* (F); *Stolze 1446* (F). CARTAGO: ravine of Río Reventazón, Interamerican Institute Turrialba, 1 Aug. 1961, *Brown 211* (US); Cartago, May 1954, *Carpenter 639* (F, US). LIMON: banana and cacao plantations between Siquerres and the Río Pacuaré, 20-22 Dec. 1969, *Burger & Liesner 6942* (F). ISLA DEL COCO: Chatham Bay, 13 Apr. 1965, *Jimenez 3165* (F, NY). Without exact locality: Carrillo, 400 m, 18 Jun. 1909, *Brade & Brade 715* (S). Bois de Tremedal, San Ramón, Apr. 1913, *Tonduz 17575* (F, GH, S, US).
PANAMA. BOCAS DEL TORO: Laguna Chiriquí, Bocas del Toro, Nov-Dec. 1885, *Hart 49* (US); along road to Chiriquí Grande, 24 Jun. 1986, *McPherson & Allen 9620* (UC). CHIRIQUI: vic. of El Boquete, 5 Feb. 1918, *Cornman 813* (US); district Boquete, Bajo Chorro, 11 Jan. 1938, *Davidson 106* (F, S). PANAMA: Cerro Campana, on road to Sun Lin, 3 Jan. 1973, *Kennedy et al. 2039* (MO); 12-16 km above Pan-Am hwy. from El Llano to Carti-Tupile, 5 May 1973, *Kennedy et al. 3114* (MO); on trail to Cerro Campana, 23 Aug. 1967, *Kirkbride & Hayden 284* (MO). CANAL ZONE: W of Río Chagres, opposite Bohio, 12 Feb. 1911, *Maxon 4780* (S, US); Barro Colorado Island, Pearson trail, 20 Nov. 1931, *Shattuck 541* (F). COLON: bridge over Río Guanche, 0-15 m, 27 May 1980, *Antonio 4814* (MO); Santa Rita ridge, 26 May 1987, *McPherson 10989* (MO, USM); Santa Rita ridge, 25 Sep. 1980, *Sytsma 1315* (MO). DARIEN: Serranía del Darién, trail from Cerro Mali to Río Pocuro, 20 Jul. 1976, *Gentry, A. et al. 16827* (US); trail NW of Caná, 28 Jul. 1976, *Sullivan 687* (MO).
ISLA COLON: 16 May 1940, *Wedel 131* (MO).
CUBA. SANTA CLARA: SE of Cuamanayagua, Sierra de San Juan, 21-23 Mar. 1938, *Senn 189* (GH); *Senn 367* (GH). CIENFUEGOS: around Topes de Collantes, 16 Jul. 1974, *Areces & Berazain s.n.* (HAJB 25095). ORIENTE: Santiago de Cuba, loma del Gato, Sierra Maestra, Jul. 1923, *Clement 917* (BM); Sierra Maestra, Florida above Daiquiri, 28-29 Jun. 1914, *Ekman 1593* (S); Bayate, 5 Jun. 1915, *Ekman 5911* (S). GUANTANAMO: s.l., *Hioram 6491* (F). Without locality: Apr. 1881, *Herb. Small s.n.* (F); *Eggers 4953* (F).
JAMAICA. Dollwood, 6 Aug. 1898, *Harris 7273* (BM, F); near Mocho, above Catadupa, 3 Apr. 1920, *Maxon & Killip 1558a* (US); along the trail from Bath to Cuna Cuna Pass, 1 May 1903, *Maxon 1713* (US); near Bath, 2 Jun. 1904, *Maxon 2438* (US). Gorge of the Stony River below junction of the Macungo River, 24 Jul. 1967, *Proctor 28322* (F).
REPUBLICA DOMINICANA. SAMANA: Samana Peninsula, vic. Sanchez, 29 Nov.-12 Dec. 1920, *Abbott 141* (US); Península de Samana, slope of Pan de Azúcar, 4 May 1930, *Ekman 14861* (S). LA VEGA: Cotuy, 28 Jan.-7 Feb. 1921, *Abbott 762* (US). Sánchez Ramirez, 1 km from Hernando Alonso on road to Palmarito, on side of Loma El Diviso, 28 Jan. 1981, *Mejía et al. 10460* (MO).
PUERTO RICO. N of Bayamón, 26 Apr. 1944, *Wagner s.n.* (US); slopes of El Yunque, 28 May 1944, *Wagner s.n.* (US).
VIRGIN ISLANDS. St. THOMAS: Charlotte Amalia, 17-18 Jan. 1899, *Millspaugh 546* (F).
LESSER ANTILLES. LEEWARD ISLANDS: Antigua, 4-16 Feb. 1913, *Rose et al. 3336* (F, GH, US). Guadeloupe, s.f, *Blanchard s.n.* (F); 1893, *Duss 4104* (F). WINDWARD ISLANDS: Montserrat, 18 Feb. 1907, *Shaffer 752* (F, US). Saint Lucia, 21 Jun. 1945, *Beard 1109* (F, US).
COLOMBIA. MAGDALENA: Sierra Nevada de Santa Marta, 28 Aug. 1972, *Kirbride 1957* (UC). GUAJIRA: Serrania de Macuira, Arroyo Chichimahu, 2 Aug. 1975, *Sugden 13* (UC). NORTE DE SANTANDER: camp 84 on pipeline, 16 Sep. 1946, *Foster & Foster 1714* (GH); road from Pamplona de Toledo, crossing divide between Río La Teja and Río Mesme, 27-28 Feb. 1927, *Killip & Smith 19989* (US). CHOCO: 0.5-2.5 km N of the Inderena camp, 3 Mar. 1971, *Lellinger & Sota 547* (US). ANTIOQUIA: Mun. Caramanta, 9.8 km from Caramanta to Supia, Cerro Viringa, 15 Oct. 1988, *Betancur et al. 1051* (MO); road tol Villa Arteaga, 4-8 Apr. 1947, *Hodge 7050* (F, GH); Anori, Providence hydroelectrical station, 6 Jun. 1971, *Soejarto 2901* (F). SANTANDER: upper Río Lebrija valley, NW of Bucaramanga, 29 Dec. 1926, *Killip & Smith 16284* (GH,

US). CALDAS: Mun. Salamina, Río San Lorenzo, 12 Aug. 1975, *Acosta-Arteaga 981* (AAU). CUNDINAMARCA: Cordillera Oriental, Sebastopol, 3 Sep. 1944, *Little & Little 8603* (F, GH, US); Cordillera Oriental, at railroad station Tablanca, 31 Dec. 1944, *Little & Little 9151* (F, US); Santandercito, near Río Bogotá, Sep. 1941, *Uribe 202* (F). EL VALLE: Cisneros, 5 May 1939, *Killip 35570* (US). CAUCA: Cordillera Occidental, Cerro Munchique, Hoya del Río Tambito, 16 Jul. 1939, *Pérez Arbelaez & Cuatrecasas 6244* (F, US). Without exact locality: 9 Aug. 1910, *Mayor 119* (US); Santa Marta, 1898-1901, *H. Smith 1013* (F, S).
VENEZUELA. ZULIA: Dist. Mara, NW side of Cerro Negro, 28 May 1980, *Steyermark et al. 122672* (UC). FALCON: Cerro Santa Ana, S de Santa Ana, 24 Jan. 1966, *Steyermark & Braun 94264* (US). LARA: Dist. Moran, Quebrada El Guairon, 2 km Guarico, 1 Apr. 1983, *Rivero & Ortega 283* (UC). YARACUY: Sierra de Aroa, 15 km NW of Cocorote and 1 km SW of Los Cruceros, 4 Apr. 1980, *Liesner & Gonzalez 10052* (UC). SUCRE: Dist. Sucre, El Guayabito, along Río Guayabo, 20-22 Nov. 1981, *Davidse & Gonzalez 19111* (MO, UC). MIRANDA: Colonia Tovar, 1854-1857, *Fendler 230* (BM, F); between Panaquire and El Peñón, 20 Sep. 1977, *Fernández 3281* (F); Distrito Paez, fila La Tigra, 18 km SW of Cupira, 2-7 Sep. 1977, *Ortega & Gonzalez 413* (MO); Ortega & Gonzalez 424 (UC). BOLIVAR: Río Caura from foot of gorge below Salto Para, 250 m, 14 Aug. 1985, *Horner et al. 237* (MO).
TRINIDAD. Lalaja, Blanchisseus road, 28 Sep. 1969, *Fay 364* (BM). Mararas bay, 1903, Othmer 423 (S); Aripo, 2 Oct. 1953, *Pickering s.n.* (BM). Without locality: 1877-1880, *Fendler 117* (BM, UC, US).
TOBAGO. Near Memma forests, 9 Nov. 1932, *Broadway 9062* (BM).
GUYANA: Kamakusa, 19 Dec. 1922, *Lang & Persaud 398* (F).
ECUADOR. ESMERALDAS: Río Onzolé, 3 Sep. 1980, *Holm-Nielsen et al. 25741* (AAU); Río Santiago, at Concepción, 4 Sep. 1980, *Holm-Nielsen et al. 25980* (AAU). IMBABURA: Lita, 4 Oct. 1980, *Maas & Cobb 4681* (QCA). PICHINCHA: road Aloag-Santo Domingo, Chitoa, 28 Oct. 1980, *Holm-Nielsen et al. 28001* (QCA). NAPO: Cantón Aguarico, Parque Nacional Yasuní, laguna Garza Cocha, 22 Sep. 1988, *Cerón & Gallo 4934* (MO); 1.1 km of Río Conejo, on road to Lago Agrio, 31 Mar. 1972, *Dwyer & Mac Bryde 9769* (QCA); creek 3 km NW of Borja, 20 Sep. 1980, *Holm-Nielsen 26280* (QCA). COTOPAXI: Quevedo-Latacunga hwy., 17 Dec. 1976, *Boeke 510* (QCA, UC). PASTAZA: from Ceilan to Río Cononaco, 6 Jun. 1980, *Brandbyge & Asanza 31633* (AAU); Puyo-Arajuno road, 1-5 km SW Diez de Agosto, 4 Mar. 1980, *Harling & Andersson 16896* (GB); Hacienda San Antonio, 2 km N de Mera, 5-19 Mar. 1985, *Baker et al. 5613* (MO). MORONA-SANTIAGO: Pachicutza, km 140 rd. Loja-Gualaquiza, 26-27 Apr. 1973, *Holm-Nielsen et al. 4620* (AAU, USM). AZUAY: between Cruzpamba and Loma de Canela, in region of Río Sadacray, s.f., *Steyermark 52959* (F, US). SANTIAGO-ZAMORA: Región Oriental, between Río Sordo and La Esperanza, 13 Feb. 1944, *Acosta-Solis 7318* (F). GALAPAGOS ISLANDS: Indefatigable Island, 6 mi N of Academy Bay, 6 Apr. 1930, *Svenson 114* (UC). Without locality: slope of western Cordillera, *Rimbach 79* (F); Río Cristal, 26 Oct. 1933, *Schimpff 301* (F, MO); 1857-1859, *Spruce 5249* (BM).
PERU. SAN MARTIN: Mariscal Cáceres, Campanilla, Mashuyacu, 12 Aug. 1970, *Schunke V. 4225* (GH, US); Rioja, Río Negro, 20 Jan. 1965, *Soukup 5146* (GH). LORETO: 12 km SW of Iquitos, 18 Jul. 1972, *Croat 18257* (F, UC); Río Ampiyacu, Brillo Nuevo-Río Yaguasyacu, 13 Mar. 1981, *Davis et al. 900* (F); Yurimaguas, lower Río Huallaga, 23 Aug.-7 Sep. 1929, *Killip & Smith 27668* (F, S, US); Mishuyacu, near Iquitos, Oct.-Nov. 1929, *Klug 238* (F, NY, US). HUANUCO: Sinchono, Fundo Chela, 3 Aug. 1948, *Aguilar 943* (USM); Pozuzo, 20-22 Jun. 1923, *Macbride 4581* (F); Huánuco, near confluence of Río Cayumba with Río Huallaga, 10 Oct. 1936, *Mexia 8272* (BM, F, S, UC). PASCO: Oxapampa, 5 km SE of Oxapampa, 9-11 Dec. 1982, *D.N. Smith 2917* (MO); Palcazú valley, near the confluence of Río Palcazú and Río Iscozacin, 23 Apr. 1983, *D.N. Smith 3874* (MO, UC). JUNIN: Puente Perené, 31 Oct. 1954, *Coronado 253* (GH, UC, US); E of Quimiri bridge, 1-3 Jun. 1929, *Killip & Smith 23896* (F, GH); Colonia Perené, 14-22 Jun. 1929, *Killip & Smith 24917* (F); Pichis trail, between Meriatiriani and Yessup, 28 Jun.-8 Jul. 1929, *Killip & Smith 26221* (US); La Merced, 28 Jun. 1982, *León 242a* (USM); Chanchamayo, Feb. 1939, *Soukup 1100* (F); La Merced, Aug. 1947, *Soukup 3403* (BM). CUSCO: Prov. Convención, Río Apurimac, 20 minutes below Puerto Capiro, 9 Jul. 1981, *Davis et al. 1302* (F, GH); Potrero, 8 km W of Quillabamba, 7 Oct. 1956, *Tryon & Tryon 5393b* (BM, F, GH, US). PUNO: Carabaya, Hacienda Palmera, Inambari, 4 Mar. 1965, *Vargas 16149* (GH). MADRE DE DIOS: Tambopata, SSW of Puerto Maldonado at effluence of Río La Torre, 25 Apr. 1980, *Barbour 4967* (F, MO); Prov. Manu, Río Palotoa, tributary of Alto Madre de Dios, NW of Shintuya, 26-28 Aug. 1978, *Foster & Terborgh 6759* (F); Cocha Cashu Camp, Río Manu, Parque Nacional del Manu, 16 Oct. 1979, *Gentry et al. 26784* (F).
BOLIVIA. PANDO: SW of Cobija on the Río Naraueda, 1 Aug. 1982, *Sperling & King 6456* (F, UC). LA PAZ: Prov. Sur Yungas, Chungamayo, La Sirena, 31 Aug. 1920, *Asplund 283* (S); Uchimachi, 22 Aug. 1894, *Bang 2395* (F); Murillo, valle de Zongo, Cahua, 7 Apr. 1979, *Beck 1219* (F); Polo Polo bei Coroico, 1912, *Buchtien 3532* (F, S, UC); Hacienda Casana, sobre el camino a Tipuani, 6 Oct. 1922, *Buchtien 7078* (NY, S,

UC); Sur Yungas, basin of Río Bopi, near Calisaya, 1-22 Jul. 1939, *Krukoff 10203* (F, GH, MO); Bopi river valley, 6 Aug. 1921, *Rusby 721* (F, US); Larecaja, 6 km N of Consata, 15 Dec. 1981, *Solomon et al. 6579* (UC). BRAZIL. RONDONIA: Rodovia 399, a 13 km de Vilhena, 4 Nov. 1979, *Vieira et al. 897* (F). AMAZONAS: near Livramento, 12 Oct.-6 Nov. 1934, *Krukoff 6756* (MO, S).

Campyloneurum brevifolium is characterized by its pattern of venation of irregularly divided areoles, and by the presence of costal scales. *Campyloneurum brevifolium* is the correct basyonym for the taxon here defined. It replaces *C. latum*, a name which has been used commonly in the literature.

Some problems arose in distinguishing this species from *Campyloneurum phyllytidis*, mainly because of the presence of similar venation, and similar shape and size of leaves. Lellinger (1988) suggested that the pattern of venation of *C. phyllitidis* is an intermediate state of the "loosely organized" pattern of venation found in *C. brevifolium*. Here, the pattern of venation in *C. brevifolium* is interpreted as specialized, because it is more complex than that of *C. phyllitidis*. These species probably belong to different lineages in the genus. Pattern of venation appears is a good character to define *Campyloneurum brevifolium* as a distinct species. Although, still in some cases symmetrical and asymmetrical divided primary areoles occur within an individual.

In the Caribbean region, leaf shape can be used to differentiate *C. brevifolium* from *C. phyllitidis*, as was shown by Proctor (1977, 1985). *Campyloneurum brevifolium* has broader leaves than *C. phyllitidis*, although this character seems restricted to specimens from the Antilles.

Campyloneurum brevifolium is closely related to *C. nitidissimum*, *C. pascoense*, and *C. tucumanense*.

12. *Campylonerum centrobrasilianum* Lellinger, Amer. Fern J. 78: 16-17. 1988. Type. Brazil, Minas Gerais, Viçosa, *Kuhlmann 1898* (holotype, US!).

Stem creeping, not pruinose, 2-3 (-4) mm wide. Stem scales dark brown in mass, 3-4 mm long, 0.5-1 mm wide, narrowly ovate, bases broadly auriculate, apices acuminate, clathrate with differentiated margins mainly at the base of the scale, cells narrowly oblong along the main axes of the scale, cells at the base of the scale irregularly arranged, cell lumen translucent, central cell walls 12-18 µm thick, marginal cell walls 9-12 µm thick. Phyllopodia 1 mm long, 1-1.5 mm wide, tightly closed less than 2 mm apart. Leaves 15–50 cm long; petiole stramineous, 0.5-3 cm long; lamina linear, rarely narrow lanceolate, bases and apices attenuate, 0.3-1 cm wide, herbaceous-chartaceous, margins slightly revolute, sinuate, cartilaginous, indument of inconspicuous, simple and bicellular hairs, spreading abaxially, along the costa; stomata polocytic; costa prominent, usually castaneous abaxially, primary veins inconspicuous, with 1-2 primary areoles between the costa and margin, with one excurrent veinlet; sori subterminal, paraphyses not seen, spores 60-65 µm long, 35-40 µm wide. Fig. 26.

This species is found in central eastern Brazil, where it grows between 800 and 1500 m elevation. The species occurs in campo rupestre vegetation of the Brazilian Planalto.

EXAMINED SPECIMENS: BRAZIL. GOIAS: SW of Brasília D.F. 20 Feb. 1966, *Irwin et al. 13057* (F); Serra dos Pirineus, 50 km N of Corumbá de Goiás on road to Niquelândia, valley of Rio Maranhão, 25 Jan. 1968, *Irwin et al. 19184* (F); ca. 30 km N of Alto do Paraíso, Chapada dos Veadeiros, 23 Mar. 1971, I*rwin et al. 33063* (F, NY); Serra dos Pirineus, ca. 20 km E de Pirenópolis, 16 Jan. 1972, *Irwin et al. 34302* (F, NY). MINAS GERAIS: Serra do Espinhaço, rocky hillside ca. 7 km N of São João da Chapada, road to Inhaí, 29 Mar. 1970, *Irwin et al. 28607* (F); Serra do Espinhaço ca. 12 km W of Barão de Cocais, 27 Jan. 1971, *Irwin et al. 29288* (F, NY).

Campyloneurum centrobrasilianum is characterized by having stem scales with a broad base and the cells irregularly arranged at the base of the scale, but regularly arranged along the main axis. This species belongs to the *Campyloneurum angustifolium* group.

13. *Campyloneurum chlorolepis* Alston, Bull. Jard. Bot. Etat 27: 56. 1957. Type. Colombia:

Caldas, Chinchina, Pereira-Manizales, 1400 m, s. f., *Køie 5208* (holotype C, photo BM!).

Polypodium angustifolium Sw. var. *heterolepis* Rosenst., Mem.Soc. Sci. Nat. Neuchâtel 5: 54. 1914. Type. Colombia:Antioquia, near Angelopolis, ca. 1800 m, *Mayor 140* (holotype, P!; isotypes S!, UC!, US!, photo of P, BM!).

Campyloneurum heterolepis (Rosenst.) Lellinger, Amer. Fern J. 67: 58. 1977.

Stem creeping, rarely pruinose, 3-4 (-5) mm wide. Stem scales whitish, 5-7 mm long, 0.75-1 mm wide, narrowly ovate, bases auriculate, apices acuminate, non-clathrate, the cells narrowly oblong along the main axes of the scale, cell walls usually well defined, but without pigmentation, 8 µm wide, lumen translucent. Phyllopodia 1 mm long, 2-3 mm wide, tightly closed less than 2 mm apart. Leaves 40-85 cm long; petiole stramineous or brownish, 4-8 (-10) cm long; laminae narrowly lanceolate or linear-lanceolate, bases narrowly cuneate or attenuate, apices acuminate, 1-3 (-5) cm wide, coriaceous, margins slightly revolute, cartilaginous, apices acute to acuminate, indument of inconspicuous, simple and multicellular hairs, scattered abaxially; stomata polocytic; costa prominent, usually castaneous abaxially, primary veins inconspicuous, however when dry the color of the veins are darker than the leaf tissue, 5-8 mm apart, 50-60^{o} divergent from the costa, transverse secondary veins forming 2-4 primary areoles between the costa and margin, excurrent veinlets 3-4 free or anastomosed to the transverse veins forming secondary areoles, sometimes asymmetrically; sori subterminal, paraphyses not seen, spores 60 µm long, 30-35 µm wide. Fig. 25.

This species is found from Colombia, Venezuela to Bolivia and central Brazil, where it grows between 260 m and 3000 m elevation. It is mainly distributed along the eastern side of the Andes.

REPRESENTATIVE SPECIMENS: COLOMBIA. ANTIOQUIA: Mun. Amalfi, 1-4 km from Amalfi to Rumezón, 27 Sep. 1988, *Betancur et al. 738* (MO); Río Verde, 12 Jul. 1880, *Kalbreyer 1770* (B, S). SANTANDER: vic. of Las Vegas, 21-23 Dec. 1926, *Killip & Smith 15994* (BM, F). CALDAS: Cannan, S of Salento, 31 Jul. 1922, *Pennel 9079* (US). CUNDINAMARCA: Mun. San Cayetano, road to Hondura, 10 May 1977, *Acosta 1198* (B); Salto de Tequendama, 1-3 Oct. 1938, *Cuatrecasas 73* (F); Santardecito, Sep. 1941, *Uribe 201* (F); Bogotá, at railroad station Tablanca, 21 Dec. 1944, *Little & Little 9143* (F). VALLE: Hoya del Río Sanquininí, 10-20 Dec. 1943, *Cuatrecasas 15428* (F); Hoya el Río Cali, Pichinde, Morro Pelado, 17 Oct. 1944, *Cuatrecasas 18147* (F, S, US); Mun. Sevilla, vía Sevilla-Barragán, 26 Sep. 1981, *Silverstone 697* (MO). WIithout locality: *Lindig 358* (B). VENEZUELA. BARINAS: road Barinitos-La Soledad, *Stergios 1631* (UC). MIRANDA: Tumerito a Ocumare del Tuy, 15 Oct. 1939, *Williams 12410* (F, UC). PORTUGUESA: Guanare, San José de la Montaña, 27 Sep. 1981, *Ortega & Stergios 1290* (F, UC); Ortega & Stergios 1320 (UC); Sucre-La Divisoria de la Concepción, 23-26 Oct. 1985, *Ortega et al. 2798* (MO, UC); Sucre, Palo Alzao-Guayabital, 3 Nov. 1981, *Ortega & Aymard 1437* (UC); San José de la Montaña, 8 Nov. 1982, *A.R. Smith et al. 1075* (MO, UC); dist. Ospino, 20 km W of La Estación, 10 Nov. 1982, *A.R. Smith et al. 1159* (MO, UC); 17.8 km de la Estación, N de Ospino, 1 Nov. 1982, *Steyermark et al. 126976* (AAU, MO, UC). LARA: dist. Iribarren, vía Guamasire, 16 Jul. 1983, *Rivero & Ortega 346* (UC); dist. Jiménez, Parque Nacional Yacambú, Quebrada El Blanco, 24 Oct. 1982, *Davidse & González 21076* (MO). Colonia Tovar, 1854-1855, *Fendler 225* (MO). ECUADOR. CARCHI: Chical, Colombian side of Río San Juan, along trail leading to Altaquer, 26 Feb. 1983, *Barfod & Blicher-Mathisen 41574* (QCA). PICHINCHA: road Nanegalito-Pacto, Tulipe, 21 Jul. 1980, *Holm-Nielsen et al. 24498* (AAU, QCA, USM). NAPO: Ceilán, path from Ceilán to Río Cononaco, 6 Jun. 1980, *Brandbyge & Asanza 31695* (AAU, USM); Río Wai si ayá, a northern tributary of Río Aguarico, about 6 km upriver from San Pablo, 10 Aug. 1980, *Brandbyge & Asanza 32757* (AAU, USM); Añangu, Río Napo, 30 Jun. 1983, *Lawesson et al. 39660* (AAU); *Lawesson et al. 39662* (AAU); Cantón Napo, Zatzayacu, 22 Mar. 1935, *Mexia 7059* (F, US). LOS RIOS: Río Palenque Biological Station, km 56 road Quevedo-Santo Domingo, 30 Mar. 1980, *Dodson & Gentry 10045* (MO). PASTAZA: Cantón Pastaza, 50 km SSE de Curaray, 1-19 Oct. 1990, *Rubio & Coba 878* (MO); Río Bobonaza, between Cachitama and the outleet of Río Bufeo, 19 Jul. 1980, *Øllgaard et al. 34678* (AAU, USM); Destacamento Chiriboga and Apachi Entza, 24 Jul. 1980, *Øllgaard et al. 35177* (AAU, USM); Río Bobonaza, Destacamento Cabo Pozo, 20 Jul.1980, *Øllgaard et al. 34878* (AAU, USM), *Øllgaard et al. 34883* (AAU, USM). EL ORO: 11 km W of Pinas on new road to Santa Rosa, 8 Oct. 1979, *Dodson et al. 9148* (MO). MORONA-SANTIAGO: Bomboiza, 17 km SE Gualaquiza, 25 Jul. 1985, *Palacios 562* (MO); 35 km NE of Montalvo, 2-12 Jul. 1989, *Zak & Espinoza 4474* (MO).

PERU. AMAZONAS: Huampaní, 18 Jul. 1974, *Kayap 1206* (MO). SAN MARTIN: Tingo María, along Huallaga about 20 km from Tingo María on road to Huánuco, 30 Oct-19 Feb. 1950, *Allard 21974* (US); km 21-22 of Tarapoto-Yurimaguas road, 7 Aug. 1986, *Knapp et al. 7883* (MO, NY, USM); San Martín, km 28 of Tarapoto-Yurimaguas road, 17 Aug. 1986, *Knapp 8037* (MO); Prov. Mariscal Cáceres, dist. Uchiza, NW of caserío Nuevo Progreso, 25 Jun. 1969, *Schunke V. 3241* (F, GH, NY, US, USM); dist. Tocache Nuevo, Quebrada de Almendras, 2 Sep. 1970, *Schunke V. 4453* (F, GH, US); Lamas, Alonso de Alvarado, fundo Las Flores, E of San Juan de Pacayzapa, 11 May 1973, *Schunke V. 6243* (NY). LORETO: Río Corrientes at the Ecuador border, between Teniente López and Puesto Avanzado, 4 Apr. 1977, *Gentry et al. 19057* (F, MO, USM). HUANUCO: Tingo María, W side of Río Huallaga, 1 Jul. 1977, *Solomon 3389* (MO). PASCO: Colonia Perené, 14-22 Jun. 1929, *Killip & Smith 25089* (F). JUNIN: Tarma, *Ruiz 11* (B); Chanchamayo valley, *Schunke 124* (US); s.l., *Soukup 1102* (F). AYACUCHO: Río Apurímac valley, near Kimpitiriki, 10-11 May 1929, *Killip & Smith 22890* (NY, US). CUSCO: Pilcopata, Atalaya, Paucartambo, 15 Jan. 1987, *Núñez 6866* (MO). MADRE DE DIOS: Manu, Atalaya, Hacienda Amazonía, *Foster & Wachter 7417* (USM). BOLIVIA. LA PAZ: Yumpasa, 10 Jan. 1902, *Williams 1067* (GH, US). BENI: Ballivian, Serranía del Pilón Lajas, 13-15 km de Yucumo, 20 May 1989, *D.N. Smith et al. 13294* (F).
BRAZIL. MATO GROSSO: Santa Anna da Chapada, 14 Oct. 1902, *Malme s.n.* (S).

Campyloneurum chlorolepis is a very distinctive species characterized by the whitish non-clathrate stem scales. The width of leaves in *C. chlorolepis* varies markedly within and between individuals.

This species belongs to the *Campyloneurum amphostenon* group.

14. *Campyloneurum chrysopodum* (Klotzsch) Fée, Gen. Filic. 258. 1852.

Polypodium chrysopodum Klotzsch, Linnaea 20: 401-402. 1847. Type. Venezuela: Monagas, Cumanacoa, *Moritz 134* (holotype B!; isotypes BM!, K!, photo BM!).

Campyloneurum fendleri T. Moore, Index Fil. 224. 1861. Type.. Venezuela: Colonia Tovar, 1854-1855, *Fendler 228* (holotype, not found; isotypes B!, BM!, K!, MO!).

Stem 1-2 mm wide, stramineous or greenish, not pruinose. Stem scales dark brown in mass, (1-) 1.2-2 (-3) mm long, 0.5-0.7 mm wide, narrowly ovate, bases peltate or slightly auriculate, apices acuminate, clathrate, with differentiated margins, cells oblong, marginal cells with transparent lumen, central cells with brownish lumen, cell walls 10-13 µm thick. Phyllopodia 1-2 mm long, 1.5-2 mm wide, 2.5-3 cm apart. Leaves 17-25 cm long; petiole stramineous, 1.5-4 cm long, slightly ranurate adaxially, convex abaxially, glabrous; lamina narrowly lanceolate, bases and apices attenuate, 1-3 cm wide, herbaceous-chartaceous, margins cartilaginous, slightly sinuate, indument of inconspicuous simple hairs; stomata polocytic; costa prominent on both sides of the lamina, indument of scarce scales, similar to those on the stem, primary veins slightly prominulous on both surfaces, 65-70º divergent from the costa, flexuous, secondary transverse veins forming 3-4 primary areoles between the costa and margin, 1-3 excurrent veinlets, primary areoles sometimes symmetrically divided; sori subterminal or terminal, paraphyses not seen, spores 45-50 µm long, 30-35 µm wide. Fig. 34.

This species is found only in Venezuela, between 1200-1800 m elevation, where it grows as an epiphyte.

REPRESENTATIVE SPECIMENS: VENEZUELA. TACHIRA: Córdoba, fila de Paramito, N of Mesa de Tigre, 16 Nov. 1982, *Davidse & Gonzalez 22407* (MO, UC). PORTUGUESA: Sucre, La Divisoria de la Concepción, 23-26 Oct. 1985, *Ortega et al. 2749* (MO, UC). FALCON: arriba en La Chapa, Sierra de San Luis, 18 Jan. 1979, *Werff van der et al. 189* (UC). TRUJILLO: en las cercanías de Vitú, Cerro El Zamuro, Quebrada El Limón, 23 Nov. 1984, *Ortega & Werff van der 2292* (UC).

Campyloneurum chrysopodum is characterized by long creeping stems less than 3 mm wide, by stem scales less than 3 mm long, and by well-spaced leaves. It belongs to the *C. repens* group.

15. *Campyloneurum coarctatum* (Kunze) Fée, Gen. Filic. 258. 1852.

Polypodium coarctatum Kunze, Linnaea 9: 39. 1834. Type.. Peru: Huánuco, Cucheros, Jul.

1829, *Poeppig s. n.* (holotype, LZ, probably destroyed; isotypes P!, W!; photo of W, BM!).

Stem long-creeping, greenish, black or dark stramineous, 2-3 mm wide. Stem scales dark brown or brown in mass, 1.5-4 mm long, 0.3-0.7 (-1) mm wide, linear or narrowly ovate, pseudopeltate, clathrate, cells oblong-elongate, cell walls (8-) 10-15 µm wide. Phyllopodia 2 mm long, 2-3 mm wide, 1-1.5 cm apart. Leaves 45-85 cm long; petiole stramineous or dark stramineous, (10-) 13-28 cm long, ranurate abaxially, indument of caducous scales similar to those on the stem; lamina broadly elliptic to ovate elliptic, bases narrowly cuneate or acuminate, sometimes shortly decurrent, apices acuminate or subcaudate, (6-) 8-13 cm wide, herbaceous-chartaceous, margins slightly sinuate, cartilaginous, indument of inconspicuous hairs abaxially, hairs 50-70 µm long; hydatodes sometimes present adaxially; stomata polocytic; costa prominent on both surfaces, primary veins prominulous to prominent at same degree on both surfaces, straight, (60°-) 65-70° divergent from the costa, 5-6 mm apart, transversal veins forming 9-19 primary areoles between the costa and margin, primary areoles undivided, (1-) 2 excurrent veinlets in each areole; sori subterminal, paraphyses not seen, spores not seen. Fig. 34.

This species is found from Costa Rica to Bolivia, and Amazonian Brazil, where it is usually found between 100 m and 2000 m elevation, in forested areas.

REPRESENTATIVE SPECIMENS: COSTA RICA. PUNTARENAS: San Vito de Coto Brus to Ciudad Neily, 11 Jul. 1985, *Hammel 14163* (UC). CARTAGO: Navarro, 6-8 mi SW of Cartago, 24 Jul. 1924, *Stork 4263* (UC). W de lago Dabagri, 4 Nov. 1984, *Gómez et al. 23178* (UC). Tucurrique, Torres de las Vueltas, Dec. 1898, T*onduz 12914* (B).
PANAMA. PANAMA: 16 km above Pan-am hwy. from El Llano to Carti Tupile, *Kennedy & Dressler 2921* (MO); 6-7 mi from Pan-am. hwy. on El Llano-Carti road, 26 Feb. 1982, *Knapp & Mallet 3859* (MO, UC); El Llano-Carti road, 21 Mar. 1975, *Mori & Kalluncki 5131* (MO). CHIRIQUI: shoulder of El Barú, above Bajo Grande, *Folsom et al. 2138* (MO); along Río Colorado, 11 Jul. 1983, *Hamilton & Krager 3818* (MO); along Río Colorado, 17 Mar. 1983, *Hamilton & Stockwell 3534* (MO, UC); valley of Río Piarnasta, about 5 mi E of El Boquete, 9-22 Feb. 1918, *Killip 5142* (GH, MO, S). DARIEN: N Punta Guayabo, 21 Apr. 1980, *Antonio & Hahn 4319* (MO); Serranía del Darien, trail from Cerro Mali to Río Pucuro, 20 Jul. 1976, *Gentry et al. 16827* (MO); Rancho Frío, 9 Aug. 1986, *Mc Donagh et al. 594* (MO).
COLOMBIA. CHOCO: Mun. San José del Palmar, basin of Río Torito, 7 Mar. 1980, *Forero et al. 6861* (MO); W slope S ridge of Cerro Mecana, 7 Jan. 1984, *Juncosa 1762* (MO, UC). Llanos de San Martín, Villavicencio, *Stübel 639* (B).
GUYANE. Haut Tapoc: Crique Alice, 4 Apr. 1977, *Cremers 4625* (CAY); Monts Atachi Bacca, *Granville 745* (CAY); Tumuc Humac, SE of Toukouchipann', 21 Aug. 1972, *Granville 1323* (CAY); sources de la Mana, Monts Galbao, 11 May 1973, *Granville 1614* (CAY); Grand Tamouri river, affluent of Camopi, 15 Mar. 1974, *Granville 2124* (CAY); Petit Tamouri river, 19 Mar. 1974, *Granville 2174* (CAY); Haut Oyapock, crique Takululi, 17 Jul. 1975, *Granville 2470* (CAY).
ECUADOR. PICHINCHA: Santo Domingo de los Colorados, *Dodson & Duke 7713* (MO). PASTAZA: Montalvo, on the Río Bobonaza, 28 Jul. 1980, *Øllgaard et al. 35411* (AAU, QCA, UC). MORONA-SANTIAGO: Pachicutza, km 140 on road Loja-Gualaquiza, 26-27 Apr. 1973, *Holm-Nielsen et al. 4620* (AAU, F, MO). NAPO: Nuevo Rocafuerte, al SW de la población, 2 Mar. 1981, *Jaramillo & Coello 4629* (AAU); Añangu, Río Napo, 6 Jul. 1983, *Lawesson et al. 39775* (AAU, QCA); Añangu, Parque Nacional Yasuní, 30 May-21 Jun. 1982, *Øllgaard et al. 38827* (AAU, UC). ZAMORA-CHINCHIPE: road La Saquea Yacuambi, 9 Apr. 1985, *Harling & Andersson 23859* (QCA); 4 km W of Panguintza, 14 Apr. 1985, *Harling & Andersson 24156* (QCA). Without locality: Andes Quitenses, *Spruce 5644* (BM, W).
PERU. CAJAMARCA: Santa Cruz, Catache, upper Río Zaña valley, ca. 5 km above Monteseco on path to Chorro Blanco, 16-18 Mar. 1986, *Dillon et al. 4355* (F, GH); Santa Cruz, ENE of Monteseco, 7 May 1987, *Santisteban & Guevara 31* (F). SAN MARTIN: Tarapoto, 1855-1856, *Spruce 4646* (BM, NY, W). LORETO: Río Marañón, above Saramuro, 22 Jan. 1979, *Diaz & Ruiz 875* (MO); Yurimaguas, 23 Aug.-7 Sep. 1929, *Killip & Smith 27668* (F, MO, NY, S, US); Balsa Puerto, 28-30 Aug. 1929, *Killip & Smith 28427* (F, US), *Killip & Smith 28472* (NY, US); Santa Rosa, lower Río Huallaga, below Yurimaguas, 1-5 Sep. 1929, *Killip & Smith 28854* (F); above Pongo de Manseriche, left bank of Río Santiago, 23 Nov. 1931, *Mexia 6141a* (F, MO, UC); from Marañon valley to Iquitos, crossingis Santiago-Morona, at Pongo de Manseriche, 7 Dec. 1924, *Tessmann 4885* (B). HUANUCO: Sinchono, 3 Aug. 1948, *Aguilar 943* (F, USM); Tingo María, at Las cuevas de los Pavos, 30 Oct. 1949-19 Feb. 1950, *Allard 20527*

(US); Tingo María-Pucallpa, 1971, *Ellenberg 3886* (GH); Huánuco, gorge of Río Chinchao, 11 Sep. 1956, *Tryon & Tryon 5302* (F, GH, NY, UC, US). JUNIN: E of Quimiri bridge, near La Merced, *Killip & Smith 23896* (F, GH); La Merced, 28 Jun. 1982, *León 242a* (USM); Chanchamayo, Aug.-Oct. 1923, *C. Schunke 167* (US); Chanchamayo, 24-27 Sep., *C. Schunke 512* (F); Chanchamayo, Jul. 1929, *C. Schunke 978* (F); La Merced, Chanchamayo, Feb. 1939, *Soukup 1100* (F); Tarma, Agua Dulce, 16 Apr. 1948, *Woytkowski 37025* (MO, UC). UCAYALI: Coronel Portillo, Bosque von Humboldt, *Young & Salazar 1015* (F, MO). MADRE DE DIOS: Parque Nacional Manu, Cocha Cashu, 7 Sep. 1984, *Foster 84-16* (F).
BOLIVIA. COCHABAMBA: Antahuacana, Jun. 1909, *Buchtien 2153* (UC).
BRAZIL. ACRE: Mun. Canamari Amazonas, Rio Jurúa, N of Cruzeiro do Sul, lake Cigana, S of Porto Alvaro Mestrinho, 22 Aug. 1986, *Croat 62525* (MO); Mun. Canamari Amazonas, vic. of Floresta, 23 Aug. 1986, *Croat 62550* (MO). AMAZONAS: Juruá Mury, Jun. 1901, *Ule 5607* (B).

Campyloneurum coarctatum is recognized by its linear and clathrate stem scales. The leaf is elliptical, with undivided primary areoles. It belongs to the *C. sphenodes* group.

16. *Campyloneurum cochense* (Hieron.) Ching, Sunyatsenia 5: 263. 1940.
Polypodium cochense Hieron., Hedwigia 48: 269. 1909. Type. Colombia: Pasto, lake Cocha, *Stübel 250* (holotype B!, photo BM!).
Polypodium angustifolium Sw. var. *monstruosum* Mett., Ann. Sci. Nat. (Paris) V, 2: 258. 1864. Type. Colombia: Cundinamarca, Cipacón, *Lindig 241* (B!, photo F!).

Stem creeping, dark stramineous, black, usually pruinose, (5-) 6-8 mm wide. Stem scales grey brown in mass, adpressed, ovate, 2-3 (-4) mm long, (1-) 1.5-2 mm wide, bases auriculate, apices acuminate, scales clathrate, the cells oblong, along the main axes of the scale, central cell walls 9-12 µm thick, margins differentiated, marginal cell walls 6-9 µm thick. Phyllopodia 4-6 mm long, (4-) 5-7 mm wide, (6-) 10-15 (-30) mm apart. Leaves (35-) 70-92 (117) cm long; petiole dark stramineous, 4-12 (-24) cm long, ranurate adaxially, concave abaxially; lamina narrowly lanceolate, bases and apices attenuate, (1.5-) 2.5-4.5 (-7) cm wide, chartaceous-subcoriaceous, margins cartilaginous, sometimes slightly revolute; costa prominent, indument of scales similar to those on the stem, primary veins prominulous, usually stramineous, (50°-) 55-60° divergent from the costa, 5-7 mm apart, secondary veins sometimes slightly prominulous, same color as the leaf tissue, forming 5-6 primary areoles between costa and margin, regularly or irregularly divided, excurrent veinlets 1-2 in each secondary areole, sometimes free veinlets along the margin; sori subterminal or medial, paraphyses not seen, spores 45-50 µm long, 28-30 µm wide. Figs. 1 a; 14 e; 29.

This Andean species is known from Colombia and Ecuador, where it grows above 2400 m altitude. It is found in the paramo and in montane forest vegetation types, in crevices of rocks or rarely as an epiphyte.

REPRESENTATIVE SPECIMENS: COLOMBIA. TOLIMA: Boquerón de Quindiu, 27 Mar. 1939, *Alston 7747* (MO). CALDAS: carretera entre Manizales y hotel "Termales del Ruiz", 8 Jun. 1966, *Forero et al. 552* (F). CUNDINAMARCA: Páramo de Guasca, 15 Dec. 1938, *Balls 5726* (UC, US). CAUCA: southern slope above Carpintería, 24 Apr. 1939, *Alston 8250* (MO); Río Palo, Quebrada de Santo Domingo, 13 Dec. 1944, *Cuatrecasas 19266* (F). NARIÑO: vicinity of Cordoba, 28 Sep. 1944, *Ewan 16236* (BM, S, UC). PUTUMAYO: Sibundoy, 4 May 1939, *Alston 8395* (MO); S of la Cocha lake, 8 Jan. 1941, *Cuatrecasas 11805* (F, US); Laguna de la Cocha, 29 Oct. 1944, *Ewan 16373* (BM, GH, S, UC).
ECUADOR. CARCHI: road Julio Andrade-El Carmelo, km 7-10, 16 May 1982, *Balslev et al. 2558* (AAU, B, NY, QCA). *Balslev et al. 2628* (AAU, B, NY, QCA); Paramo El Angel, on road El Angel-Tulcán, 14 May 1973, *Holm-Nielsen et al. 5336* (AAU, MO, UC); Tulcan-El Angel, 24 Feb. 1984, *Juncosa 2395* (MO). IMBABURA: Shanshipamba, Macnoloma, 14 Nov. 1949, *Acosta-Solís 14295* (F); *Acosta-Solís 14317* (F); Lake Cuicocha, Islote Chica, 23 Jun. 1939, *Asplund 7128* (S, US); Otavalo-Hacienda Perugachi, NW of Peñas Blancas, 5 Jan. 1980, *Jaramillo et al. 1891* (AAU, QCA). PICHINCHA: Quito-Santo Domingom de los Colorados road, 11 Jun. 1977, *Ayala 1* (QCA); carretera Chillogallo-Chiriboga, km 36, 18 Oct. 1981, *Balslev 2107* (QCA); Concepción, 28 Mar. 1951, *Bell 18* (S); Parroquia Calacali, Reserva Geobotánica Pululahua, 16 Nov. 1987, *Cerón & Cerón 2756* (QCA); Cantón Ruminiahui, Parroquia Amaguaña, Pasochoa, *Cerón &*

Alarcón 3544 (MO); Lloa valley, 18 May 1980, *Holm-Nielsen 23536* (AAU); Chillogallo-San Juan, 23 Jun. 1980, *Jaramillo & Lascano 2552* (AAU, QCA); road between Calacali and San José de Niebli, *Zogg & Gassner 13045* (QCA). NAPO: upper slopes of Guagra Urcu, 26 Sep. 1980, *Holm-Nielsen et al. 27124* (AAU); road Tena-Baeza, 12 Jan. 1981, *Jaramillo 4085* (AAU, QCA); SE slopes of Cordillera Huacamayos, 12 Jan. 1981, *Proctor 38725* (QCA); Quebrada Violetas, about 4 km W of Aloag, on road Aloag-Santo Domingo, 25 Mar. 1967, *Sparre 14967* (S); road betwen Quito and Baeza, Río Chalpi, 18 Sep. 1989, *Zogg & Gassner 13007* (QCA). BOLIVAR. Urcu corral, Chillanes, 3 Nov. 1943, *Acosta-Solís 6609* (F) TUNGURAHUA: Chaupi, 4 Jan. 1962, *Dodson & Thien 1847* (MO, US), *Dodson & Thien 2054* (MO); road Patate-El Triunfo, 4 Mar. 1989, *Buitrion 475* (QCA). CHIMBORAZO: sector Las Chorreras, Hacienda La Carmela, Cord. Occidental Sibambe, 20 Aug. 1943, *Acosta-Solís 5466* (F). AZUAY: 1-8 km N of Sevilla de Oro, 27 Jul.-12 Aug. 1945, *Camp E-4571* (MO, S, US); road Sigsig-Ludo, 16 Nov. 1983, *Eriksen & Boysen-Larsen 45676* (QCA). MORONA-SANTIAGO: trail Alao-Huamboya, 8 May 1982, *Øllgaard et al. 38449* (AAU, QCA). LOJA: Parque Nacional Podocarpus, Cerro Toledo, E of Yangana, 4 May 1987, *Werff & Palacios 9323* (MO); along road between Loja and Zamora, 2 Aug. 1978, Zarucchi & Andrade 2301 (MO, S, US). ZAMORA-CHINCHIPE: Loja-Zamora road, at the pass, 12 Feb. 1985, *Harling & Andersson 21990* (QCA); road Loja-Zamora, 16 Apr. 1973, *Holm-Nielsen et al. 3628* (AAU, F, GB, UC).

Campyloneurum cochense is characterized by its linear-lanceolate leaves, which resembles those from *C. amphostenon* and *C. densifolium*. It also has more than 5 areoles on each side of the costa. In addition, *C. cochense* has adpressed stem scales, usually with obtuse apices, and margins clearly differentiated from the center of the scale. It belongs to the *Campyloneurum xalapense* group.

17. *Campyloneurum costatum* (Kunze) C. Presl, Tent. Pterid. 190. 1836.

Polypodium costatum Kunze, Linnaea 9: 38. 1834. Type. Cuba: Limonar, *Poeppig s.n.* (holotype LZ, probably destroyed; isotypes B, BM!, C!, K!, P!, photo BM! from B).

Cyrtophlebium costatum (Kunze) J. Sm., London J. Bot. 1: 196. 1842.

Campyloneurum immersum J. Sm., Bot. Voy. Herald 231. 1854. Type. Panama: Darién, Bay of Utria, Apr. 1848, *Seeman s.n.* (holotype K!).

Polypodium costale Jenm., Bull. Bot. Dep. 4: 140. 1897. (*err. script.* for *P. costatum*).

Campyloneurum phyllitidis var. *costatum* (Kunze) Farwell, Amer. Midl. Nat. 12: 297. 1931.

Stem short-creeping, not pruinose, 4-6 mm wide. Stem scales brown in mass, 3-5 mm long, 0.8-1 (-1.5) mm wide, narrowly ovate, bases auriculate, apices acuminate, clathrate, the cells oblong, along the main axes of the scale, cell walls 10-15 µm thick, sometimes hairs at the margin. Phyllopodia 1 mm long, 2 mm wide, 1-4 mm apart. Leaves 30-55 (-75) cm long; petiole stramineous or brownish, (4-) 7-13 cm long, ranurate adaxially, convex abaxially; lamina lanceolate or narrowly obovate-lanceolate, bases assymetrically narrowly cuneate or attenuate, apices subcaudate, rarely attenuate, 3-7 cm wide, herbaceous-chartaceous, chartaceous, margins cartilaginous, slightly sinuate, indument of inconspicuous simple hairs, scattered abaxially; stomata polocytic; costa prominent, primary veins inconspicuous or slightly prominulous adaxially, 60-65^{o} divergent from the costa, 4-6 mm apart, secondary transversal veins forming 8-10 primary areoles between the costa and margin, primary areoles usually symmetrically divided, excurrent veinlets 1-2 in each secondary areole; sori medial, paraphyses and spores not seen. Figs. 17 b; 35.

This species is known from southern United States (Florida) to Panama, Greater Antilles, Trinidad, Venezuela and Ecuador, where it is found below 1000 m elevation. It grows as terrestrial or as low trunk epiphyte.

REPRESENTATIVE SPECIMENS: UNITED STATES. FLORIDA: Collier County, Fahkahatchie Cypress, about 7 mi NW of Copeland, Nov. 1958, *Darling, s.n.* (US); near Everglade, 11 Jul. 1904, *Eaton 1135* (GH). MEXICO. VERACRUZ: near the summit of Ejecatepetl, Zongolica, 6 Jun. 1944, *Vera-Santos 3010* (US). CHIAPAS: Mun. Ocozocoautla, Reserva Ecológica El Ocote, 14 Feb. 1986, *Palacios-Ríos 2802* (UC).
BELIZE. TOLEDO: Punta Gorda and Joe Taylor Creek, 2 Jul. 1949, *Gentle 6792* (US).
GUATEMALA. Chamá, 26 Feb. 1920, *Johnson 358* (US).
HONDURAS. ATLANTIDA: Lancetilla, ca. 10 mi SE of Tela, 3 Aug. 1977, *Croat 42663* (MO).

NICARAGUA. ZELAYA: Bahía de Bluefields, Río Escondido, 30 Mar. 1949, *Molina 2024* (US), 3.6 km SE Cerro San Isidro, Río Kama, Río Escondido, 6 Mar. 1966, *Proctor 27004* (NY); SE Cerro San Isidro, 9 Mar. 1966, *Proctor et al. 27063* (NY). MATAGALPA: Jinotega, between Las Camelias and La Salvadora, along small tributary od Río Jigüina, 31 Oct. 1979, *Stevens & Grijalva 15323* (MO, UC).
COSTA RICA. ALAJUELA: Upala, Dos Ríos, Río Cucaracha, 4 Nov. 1987, *Herrera 1114* (MO). PUNTARENAS: Parque Nacional Corcovado, Monkey Woods, 9 Jun. 1988, *Kernan 575* (MO).
PANAMA. BOCAS DEL TORO: Herrera, 10 km W of Las Minas on road to El Toro, 24 Jan. 1981, *Sytsma & D'Arcy 3254* (MO). CANAL ZONE: pipeline road, 4-6 mi N of Gamboa, 24 Sep. 1981, *Knapp 1272* (MO); over Río Masambi Grande, 1 km NW of Summit Garden, 20 Oct. 1973, *Nee 7497* (US); along Río Mendosa, 8 km NW of Gamboa, 16 Apr. 1974, *Nee & Smith 11364* (US). DARIEN: Isthmus, *Seemann s.n.* (US). Near upper Juan Díaz river, *Killip 2851* (US).
CUBA. PINAR DEL RIO: La Plata, Sierra del Rosario, Jan. 1957, *Bro. Alain 6100* (US); Bahía Honda, N of Pan de Guajaibón, Aug. 1968, *Bisse 9637* (HAJB); mountains N of San Diego de los Baños, 11 Apr. 1900, *Palmer & Riley 511* (BM). ORIENTE: Florida Blanca, Apr. 1947, Bro. *Clement 5230* (US); Sierra de Nipe, on Río Piloto, 20 Jul. 1914, *Ekman 2063* (S); Bayate, Cayo del Rey, 6 Sep. 1914, *Ekman 2757* (S); Sierra de Nipe, ad Río Piloto, 9 Jun. 1915, *Ekman 5979* (S); Farallones of La Perla, N of Jaguey, Yateras, 2 May 1907, *Maxon 4377* (US). El Palenque, Mar. 1889, *Eggers 4854* (F, S). Without locality: 1849, *Rugel 22* (BM); 19 Aug. 1889, *Eggers 4854* (B, F); 1859-1860, *Wright 802* (MO, S).
JAMAICA. PORTLAND: Seamen's valley, 14 Feb. 1920, *Maxon & Killip 5* (F); Mansfield, near Bath, 2 May 1903, *Maxon 1820* (US); Hartford, near Priestman's river, 9 Jun. 1904, *Maxon 2554* (US); Ginger river, May 1884, *Syme s.n.* (BM). ST. THOMAS: Corn Puss Gap, 27 Jun. 1954, *Wilson & Webster 466* (GH).
DOMINICAN REPUBLIC. Pacificador: Villa Riva, 11-19 Jan. 1912, *Abbott 570* (US). Samaná: Santo Domingo, Cordillera Central, 27 Jun. 1930, *Ekman 15450* (S).
TRINIDAD. Without locality, *Jenman 205* (NY).
VENEZUELA. PORTUGUESA: dist. Araure, Ríos Bocoy and Riecito, *Ortega & Aymard 1801* (UC).
ECUADOR. LOS RIOS: surroundings of Montalvo, ca. 40 km E of Babahoyo, 30 Mar.-2 Apr. 1973, *Holm-Nielsen et al. 2827* (AAU). Without exact locality: *Eggers 14373* (F); 6 Sep. 1896, *Eggers 15306* (F).

Campyloneurum costatum is characterized by lanceolate or elliptical-lanceolate leaves, with inconspicuous or slightly prominulous veins.

It is closely related to *C. xalapense*, and they can differentiated by the characteristics used in the key.

18. *Campyloneurum cubense* Fée, Gen. Filic. 259. 1852. Type. Cuba, 1843-1844, *Linden 1912* (holotype RB, isotypes BM!, K, L, photo BM!).

Polypodium vexatum D. C. Eaton, Mem. Amer. Acad. Arts n.s. 8: 199. 1860. *Nomen Novum* for *Campyloneurum cubense*.

Polypodium cubense (Fée) Christ, Bot. Jahrb. Syst. 24: 131. 1897. Nom. Illeg. *Non Polypodium cubense* Fée 1852.

Campyloneurum fasciale var. *gracile* T Moore, Index Filic. 224. 1861.

Stem creeping, not pruinose, 1-4 (-5) mm wide. Stem scales brown in mass, 4 mm long, (1.5-) 2-2.5 mm wide, ovate, clathrate, apices short acuminate, central cells usually oblong, cell walls 12.5-15 (-20) µm thick, along the major axes of the scale, marginal cells usually isodiametric, cell walls 5-7.5 (-10) µm wide, transversal to the major axes of the scale. Phyllopodia 0.5-1 mm long, 1.5-2 (-3) mm wide, 2-3 mm apart. Leaves 23-60 (-90) cm long; petiole stramineous, (1-) 3-15 (-20) cm long, ranurate adaxially, indument sometimes of scattered caducous scales less than 1 mm long; lamina narrowly obovate, bases attenuate, apex acuminate, (0.6-) 1-2 (-3.5) cm wide, herbaceous-chartaceous, margin sinuate, plane, indument of simple bicellular hairs, disperse and caducous abaxially, stomata polocytic; costa prominent, primary veins inconspicuous or slightly prominulous adaxially, prominulous abaxially, flexuosous, 50-65º divergent from the costa, 3-5 (-6) mm apart, secondary transversal veins forming 2-4 (-6) areoles between the costa and margin, areoles entire or divided, 1-2 excurrent veinlets in each secondary areole; sori subterminal, paraphyses not seen; sporangia 14-17 cells of the bow, spores (45-)50-60 µm long, 30-40 µm wide. Figs. 10 c; 36.

This species is known from Cuba, Jamaica, and Haiti, where it grows between 100 m and 600 m elevation.

REPRESENTATIVE SPECIMENS: CUBA. GUANTANAMO: Las Ninfas, Dec. 1917, *Hioram 1443*

(S). LA HABANA: Lomas de Tapaste, 4 Feb. 1973, *León 3528* (S). CIENFUEGOS: Cumanayagua, Las Vegas, Cafetal de Buenos Aires, 29 Oct. 1985, *Berazaín et al. 57968* (HAJB). LAS VILLAS: Valley of the Río Los Negros, 10-14 km beyond Siguanea, around El Junco, Jul. 1950, *Hawkes 2082* (UC); Trinidad Mountains, Loma Ventana, Aug. 1941, *Howard 6482* (GH); above San Blas, 4 Dec. 1928, *Jack 6769* (US); San Blas, La Sierra, 4 Mar. 1929, *Jack 6966* (F); Sierra Gavilán, 9-10 Nov. 1941, *Morton 4002* (GH, MO). ORIENTE: Sierra Maestra, Loma del Gato, 1923, *Clement 779* (S); Loma del Gato, El Cobre, Aug. 1924, *Clement 1387* (BM); Jaguey, *Eggers 4921* (F); Loma del Jaguey, Mar. 1889, *Eggers 4942* (B, S); Bayate, 13 Jul. 1914, *Ekman 1969* (S); Cayo del Rey, in the Cañón de Canapu, 6 Nov. 1914, *Ekman 2756* (S); S of Jaguey, Yateras, Apr. 1907, *Maxon 4161* (BM, S); summit of El Yunque, near Baracoa, 30-31 Jan. 1902, *Pollard & Palmer 176* (F); gorge Río Yamuri, 7-9 Dec. 1910, *Shafer 7862* (GH); Monte Verde, 13 Feb. 1911, *Shafer 8704* (MO); Monte Verde, Jan.-Jul. 1859, *Wright 801* (BM, MO, S); *Wright 1020* (B, MO, S, US). PINAR DEL RIO: Baños San Vicente, 12-16 Sep. 1910, *Britton et al. 7354* (F). Mountains near El Guama, 11 Mar. 1900, *Palmer & Riley 254* (BM, US); San Diego de los Baños, 1 Feb. 1917, *Palmer s.n.* (US). Without exact locality: w.d., *Eggers 4740* (B, F); Finca Las Prendas, 30 Dec. 1920, *Hioram & Maurel 4124* (US); 1860-1864, *Wright 1829* (MO).
JAMAICA. Gordontown, 11 Sep. 1906, *Moore s.n.* (BM); Mansfield, near Bath, 2 May 1903, *Maxon 1832* (US). Saint Thomas: Cuna Cuna Pass, Mar. 1895, *Gilbert s.n.* (MO); vic. of House Hill, 15 Jun. 1926, *Maxon 9226* (S, UC); Cuna Cuna Gap and vicinity, 19 Jun. 1926, *Maxon 9390* (F, GH, US); Arntully, 19 Mar. 1963, *Proctor 23346* (BM); along track between House Hill and Cuna Cuna, 26 Dec. 1969, *Proctor 31145* (F). Venegas Hill, 12-13 Apr. 1909, *Watt 130* (S, US). Without exact locality, w.d., *Swartz s.n.* (BM).
HAITI. Gorge Crete-a-Piquants, Port au Prince, 14 Feb. 1927, *Ekman 7604* (S); Massif de la Holle, Jeremie, between Maffrand and Maron, 11 Jul. 1928, *Ekman 10292* (S); Massif de la Holle, Dame Marie, 14 Aug. 1928, *Ekman 10519* (S); Riviere Glace, 4 Aug. 1945, *Holdridge 2090* (US); vicinity of Mission Fonds Varettes, 17 Apr.-4 May 1920, *Leonard 3762* (US), *Leonard 4031* (US); vicinity of Furcy, 26 May-15 Jun. 1920, *Leonard 4616* (GH).

Campyloneurum cubense is characterized by its lamina narrowly obovate, primary veins with a 50-65º divergence angle from the costa, and by ovate-lanceolate stem scales. Christ (1897) mentioned the intermediate characters of this species compared with those of *C. angustifolium* and *Polypodium laevigatum* Cav. (a name that he used probably for *P. lapathifolium* Poiret, a synonym of *C. repens*), suggesting a probable hybrid origin for *C. cubense*.

During this study, the pattern of venation of *Campyloneurum cubense* were compared with those of *C. angustifolium* and *C. repens*. In *C. cubense*, primary veins form narrow angles with the costa and divided primary areoles, as in *C. angustifolium*, although undivided areoles, as in *C. repens* are more common. Other characters, such as pattern of stomata, spore number and morphology were also examined in *C. cubense*. Specimens of *C. cubense* showed the epidermis with some irregular or abortive stomata. Spores in herbarium specimens of *C. cubense* are very scarce, and usually collapsed; the number of spores in each sporangia, however, were 64, as in normal meiosis.

This information collectively may suggest hybridization. A hybrid origin cannot be discarded, especially considering one of the parental species to be *C. angustifolium*, but at the same time there is not still cytological evidence for solving the origin of this species.

19. *Campyloneurum decurrens* (Raddi) C. Presl, Tent. Pterid. 190. 1836.
Polypodium decurrens Raddi, Syn. Fil. Bras. 287. 1819. Type. Brazil, *Raddi s.n.* (holotype not seen).
Aspidium pentaphyllum Willd., Sp. Pl. 5: 216-217. 1810. Type: *Plumier, Fil. tab. 114*. *Non Polypodium pentaphyllum* Baker, 1891.
Cyrtophlebium decurrens (Raddi) J. Sm., J. Bot. 4: 58. 1841.

Stem short-creeping, not pruinose, stramineous, 8-10 (-15) mm wide. Stem scales adpressed, light brown in mass, 3-4 mm long, 2.5-3 mm wide, ovate, bases auriculate, apices acute, clathrate, the cells broadly oblong. Phyllopodia 5-6 mm long, 5-7 mm wide, 8-10 mm apart. Leaves 1-pinnate, 75-100 cm long; petiole brown stramineous, usually more than half the lenght of the lamina, ranurate adaxially, convex abaxially; 5-10 pinnae on each side of the rachis, pinnae narrowly lanceolate, bases assymmetrically attenuate, apices acuminate, upper pinna decurrent on the rachis, basal

pinnae sessile or very shortly petiolulate, 17-32 cm long, 2.5-3.2 cm wide, herbaceous-chartaceous, margins cartilaginous, slightly ondulate, indument not seen, stomata polocytic; venation areolate, costulae prominent, primary veins prominent and usually stramineous, 55º divergent from the costulae, transverse veinlets prominulous, forming 5-7 primary areoles between the costula and margin, excurrent veinlets 2-3 in each undivided non-costal areole, costal areole with one excurrent veinlet, simple or furcate; sori terminal, paraphyses not seen, spores 40-45 µm long, 20-25 µm wide. Figs. 9; 11; 13; 35.

This species is found in Colombia, Venezuela, Martinica, and southern Brazil, where it grows in forests between 200-950 m elevation.

REPRESENTATIVE SPECIMENS: COLOMBIA. ANTIOQUIA: Río Verde, 14 Jul. 1889, *Kalbreyer s.n.* (S). MAGDALENA: Sierra Nevada de Santa Marta, 1898-1899, *H. Smith 2456* (F).
VENEZUELA. Colonia Tovar, 1854-1855, *Fendler 231* (F).
MARTINICA. Piton Marcel, entre la montagne Pelee et le Pricheur, Jul. 1885, *Duss 1568* (B, US).
BRAZIL. ESPIRITO SANTO: Santa Bárbara de Caparaó, 5 Dec. 1929, *Mexia 4093a* (UC). MINAS GERAIS: Viçosa, 22 Jul. 1930, *Mexia 4892* (B, S, UC). RIO DE JANEIRO: Corcovado, Apr. 1913, *Brade 6461* (UC); Itatiaia, Apr. 1913, *Brade 6461* (UC); Itatiaia, 4-10 Jun. 1913, *Brak 6461* (S); Itatiaia, 23 Jul. 1902, *Dusen 743* (S); Tijuca, 3 Sep. 1904, *Dusen 5144* (S); Rio de Janeiro, *Gaudichaud 2a* (F); Nova Friburgo, 22 Sep. 1947, *Leite 4204* (F); Organ mountains, Jul. 1871, *Luessen 1237* (F); Corcovado, 1911, *Lutzelburg 363* (UC); Corcovado, 17 Jul. 1873, *Mosen 63* (S); Corcovado, 10 Sep. 1874, *Mosen 2683* (B, S); trail between Sylvestre and Paineiras, 14 Apr. 1929, *Smith 2251* (S, UC). SÃO PAULO: Alto da Serra, *Wacket 134* (S); São Paulo, 25 Dec. 1873, *Mosen 2224* (S); Alto da Serra, 1905, *Wacket 134* (UC). PARANA: Porto de Cima, 24 Jul. 1914, *Jonsson 717a* (S).

Campyloneurum decurrens is characterized by its pinnate leaves with more than 5 pairs of narrowly lanceolate pinna. The known distribution of this species appears to be restricted to the presently scarce Atlantic humid forests of South America.

It is closely related to *Campyloneurum magnificum*, but it differs from the latter by its small size, narrowly lanceolate pinnae. Both species may represent an ancient lineage in the genus.

20. *Campyloneurum densifolium* (Hieron.) Lellinger, Amer. Fern J. 78: 19. 1988.
Polypodium angustifolium var. *amphostenon* (Kunze) Baker f. *densifolium* Hieron., Bot. Jahrb. Syst. 34: 532. 1904. Lectoype (chosen by Lellinger, Amer. Fern J. 78: 19-20. 1988): Ecuador, Azuay, near Las Yerbas Buenas, *Lehmann 5723* (US!, isolectotype B!, F!; photo of US, AAU!).

Stem creeping, black, sometimes pruinose, 3-5 (-7) mm wide. Stem scales brown, light brown in mass, 4.5-7 mm long, 2.5-3 mm wide, ovate or broadly ovate, bases auriculate, apices acuminate, subadpressed, slightly clathrate, the cells oblong or ovate, cells along the main axes or irregularlly disposed at the apex, cell walls slightly diffuse, 15-17 µm thick, scales sometimes with marginal hairs. Phyllopodia 1-2 mm long, (1-) 2-3 mm wide, 4-10 mm apart. Leaves 30-70 cm long; petiole stramineous or dark stramineous, 2-14 cm long, slightly ranurate adaxially, plane convex abaxially; laminae linear-lanceolate or narrowly lanceolate, bases and apices attenuate, 1-3 (-5) cm wide, chartaceous or subcoriaceous, margins cartilaginous, slightly sinuate, sometimes revolute, stomata polocytic, indument of bicellular, simple hairs, scattered abaxially; costa prominent, primary veins prominulous on different degree on both sides of the lamina, inconspicuous, partially stramineous or darker when dry, 50-60º (-65)º divergent from the costa, straight or slightly sinuate, 4-7 mm apart, secondary veins inconspicuous or very slightly prominulous, forming 2-4 primary areoles between the costa and margin, symmetrically divided or rarely entire, excurrent veinlets 1-2 in each secondary areole; sori medial or subterminal, paraphyses not seen, spores (50-) 57-60 µm long, (35-) 40-42 µm wide. Figs. 37, 38.

This species is found from Central America to Bolivia. It grows in open areas, among rocks, above 2000 m elevation.

REPRESENTATIVE SPECIMENS: GUATEMALA. Huehuetenango: 5 mi S of San Juan Ixcoy, *Breedlove 8531* (US). EL PROGRESO: between Calera and summit of volcan Siglo, 21 Jan. 1942, *Steyermark 43067* (F).
COSTA RICA. HEREDIA: forest of Río Vueltas, *Gómez 2297* (F); between Sacramento and Laguna de Barba, 12 Apr. 1975, *Utley & Utley 2031* (F). LIMON: Cordillera Talamanca, Cerro Kamuk massif, between Cerro Dudu and Cerro Apri, *Davidse et al. 25897* (MO); unnamed cordillera between the Río Terbi and the Río Sinú, *Davidse et al. 29070* (MO). SAN JOSE: Cerro de la Muerte, N 5 km, 30 Aug. 1983, *Saiki 83* (F); 15-18 km SE of Empalme, 17-26 Mar. 1973, *Stolze 1517* (AAU, F, UC). PUNTARENAS: Cantón de Buenos Aires, Ujarrás, 13 Oct. 1989, *Herrera 3673* (F).
PANAMA. CHIRIQUI: shoulder of El Barú, above Bajo Grande, *Folsom et al. 2140* (MO); 2 km S of Questa Piedra, along Concepción, *Folsom 3966* (UC); vicinity of cerro Punta, above Guadalupe, *McPherson 9399* (MO).
CUBA. ORIENTE: alround Alto del Olimpo, *López-Figueiras 405* (US).
HAITI. Massif de la Selle, Grand-Gosier, slope of M. Commissaires, *Ekman 6862* (C, S); Massif de la Holle, Torbec, *Ekman 7504* (S); Massif de la Selle, Croix des Bouquets, *Ekman 7631* (S, US).
COLOMBIA. ANTIOQUIA: Mun. Helmeira, *Acosta-Arteaga 880a* (AAU); Mun. Caldas, trail La Corrala, *Morales et al. 5869* (F). CUNDINAMARCA: northern end of sabana near Suba, *Cuatrecasas & Jaramillo 25942* (US); Cogua-San Cayetano, 9 May 1967, *Murillo et al. 1052* (F, US). VALLE: Cordillera Central, Río Bugalagrande, Cuchilla de Barragán, 15, 16, 24 Apr. 1946, *Cuatrecasas 20797* (F). CAUCA: Mun. Puracé, Parque Nacional de Puracé, near Laguna San Rafael, 6 Oct. 1984, *Lozano et al. 4682* (F).
VENEZUELA. MERIDA: 25 km from Mérida, along El Valle road, *Breteler 4663* (NY, US). DISTRITO FEDERAL: arriba de Galipán, *Williams 12386* (F, S). Colonia Tovar, *Fendler 226* (US).
ECUADOR. CARCHI: road Julio Andrade-Palestina, *Holm-Nielsen et al. 29704* (AAU, F, USM); Maldonado-Tulcan road, 5 Oct. 1981, *Werling & Leth-Nissen 253* (AAU, F). PICHINCHA: Cerro Pasochoa, *Balslev 2783* (AAU); Los Alpes, N of Cordillera Occidental, *Acosta-Solís 7094* (F); Quebrada Sombría, betweenMagdalena and Chillogallo *Firmin 454* (S); northern slopes of Cerro Corazón, 2-4 km of Aloag, *Holm-Nielsen 18023* (AAU, USM); road Chillogallo-San Juan-Chiriboga-Empalme, 21 Feb. 1986, *Zak 897* (F, MO); between Quito and Santo Domingo de los Colorados, Alisal, 19 Sep. 1989, *Zogg & Gassner 13035* (QCA). COTOPAXI: Quevedo-Latacunga road, *Holm-Nielsen et al. 3262* (AAU, F, GB, MO); road Pilaló-Zumbagua, 10 km above Pilaló, *Holm-Nielsen & Quintana 24647* (AAU, USM). NAPO: Papallacta, *Harling et al. 10329* (F, GB); SE of Playón de San Francisco, on the slopes of cerro Mirador, *Holm-Nielsen et al 29831* (AAU, USM); road San Miguel Salcedo-Puerto Nuevo, 54 km from San Miguel, *Øllgaard & Balslev 9820* (AAU). BOLIVAR: Cerro Negro, Parroquia Chillanes, *Acosta Solís 6793* (F). TUNGURAHUA: Runtún caserío, ca. 3-4 km from Baños, *Lugo 1222* (AAU, GB). CHIMBORAZO: between San Andrés and Cuatro Esquinas, *Fagerlind & Wibom 883* (S). AZUAY: above Sayaus, E of Cuenca, *Correll E339* (S); Cuenca, Paramo Quinoas, *Harling 1481* (S); Paramo de Matanga, km 25 on road Sigsig-Gualaquiza, *Holm-Nielsen et al. 29526* (AAU).
PERU. CAJAMARCA: 25 km from Cajamarca to Bambamarca, 25 Mar. 1960, *Correll & Smith 859* (GH); environs of Huancabamba, Las Huaringas, 20 Feb. 1981, *Davis & Turner 707* (F, GH); Cajamarca, summit between Cajamarca and San Juan, *Gutte & Müller 8915* (USM); Celendín, canyon of the Río Marañón, above Balsas, *Hutchison & Wright 5282* (F, UC); San Miguel, cerro Quillón, Agua Blanca, 5 Jul. 1986, *Mostacero et al. 1287* (F); Contumazá, Pampa de la Sal, 27 Jun. 1983, *Sagástegui et al. 10747* (F). LA LIBERTAD: Otuzco, Llaguen, Shilte, *López 1560* (GH); Otuzco, cerro Chologday, 19 May 1957, *Sagástegui 78* (GH); Santiago de Chuco, Chota, Motil-Shorey, 12 Jun. 1984, *Sagástegui et al. 11699* (F, MO); Santiago de Chuco, Santiago-Shorey road, 26 km from Santiago, *D.N. Smith 2329* (USM). SAN MARTIN: Mariscal Cáceres, P. N. Río Abiseo, Chochos valley, *Young 3800* (USM); *Young 2619* (USM); Chochos forest, *Young 4847* (USM); forest patch C9 above timberline, Chochos valley, *Young 2586* (F, USM); forest patch C10, *Young 2534* (F, USM); C15, *Young 2461* (USM), *Young 2462* (F, USM); forest patch C17, *Young 3655* (USM); entre El Mirador y Puerta del Monte, *Young & León 4443* (USM); Puerta del Monte, P6 forest patch, *Young 1986* (F, USM); Young 1765 (USM); forest patch P10, *Young 1883* (F, USM); forest patch P12, *Young 2056* (USM). ANCASH: Bolognesi, Tinya, Río Fortaleza valley, 28 Apr. 1956, *Cerrate 2585* (GH, USM). HUANUCO: Mito, Bryan 196 (F); *Bryan 365* (F). LIMA: Huarochirí, Río Blanco, *Asplund 11299* (S, US); 23 Jul-14 Aug 1922, *Macbride & Featherstone 1919* (F); Huarochirí, Viso, *Goodspeed et al. 11547* (US). PASCO: 95 km S from Huánuco, *Polylepis* forest, on road to Cerro de Pasco, *Gentry et al. 37489* (F). JUNIN: Tarma, Incatacuna, Tarmatambo-Acolla, *Constance & Tovar 2348* (UC); Jauja, laguna de Paca, *Gracey et al.6* (USM); entre Tarma y San Ramón, 35 km from Tarma, *Gentry et al. 39778* (F, MO, USM); Yauli, Llocllapampa, 22 Oct. 1966, *Saavedra 6317* (GH); La Merced, Aug. 1947, *Soukup 3400* (F). APURIMAC: Abancay, Andahuaylas, *Alvarado s.n.* (USM); quebrada of Juccuchic-chupan, on trail Andahuaylas-Chincheros, *West 3723* (UC). CUSCO: Chincheros, Antakillpa, *Davis et al. 1649* (F, USM); Cusco, 1 Sep.

1914, *Rose & Rose 19062* (US).
BOLIVIA. LA PAZ: Sur Yungas, San Felipe, *Asplund 1782* (S); Omasuyos, Isla del Sol, Yumani, *Asplund 3583* (BM, S, US); vicinity of La Paz, *Bang 140* (UC, US); Murillo, valle de Zongo, Santa Rosa, *Beck 1098* (LPB); Camacho, Puerto Acosta, 6 km hacia La Paz, *Beck 7685* (F, LPB); Nord Yungas, Unduavi, *Buchtien 78* (F, S); Murillo, Río Zongo valley, below dam at Lago Zongo, *Solomon 8386* (LPB, UC); Nor Yungas, 0.9 km W of Chuspipata, *Solomon 9650* (LPB); Murillo, Valle del Río Zongo, 8 Nov. 1987, *Solomon 17272* (MO).

Campyloneurum densifolium is characterized by its adpresed ovate stem scales, these being usually persistent and light brown in color.

It resembles *C. fallax* from Brazil, from which it differs by decurrent leaf bases, and stem scales with acuminate apex. Both*C. densifolium* and *C. fallax* are disjunct in distribution.
Campyloneurum densifolium is closely related to *C. amphostenon*, from which it is easily distinguished by stem scale characters (Fig. 37), which are in the latter lanceolate and with spreading apices.

Campyloneurum densifolium belongs to the *Campyloneurum amphostenon* group.

21. *Campyloneurum ensifolium* (Willd.) J. Sm., Cat. Cult. Ferns 12. 1857.
Polypodium ensifolium Willd., Sp. Pl. 5: 152. 1810. Type. Probably Mexico (as Peru Lima), *Née s.n.* (Herb. Willd. 19610) (holotype, B!; photo BM!, USM!).
Goniophlebium ensifolium (Willd.) Brackenridge *in* Wilkes, U. S. Explor. Exped. 33. 1854.
Polypodium angustifolium var. *ensifolium* Hicken, Revista Mus. La Plata, Secc. Bot. 5: 271. 1908.
Campyloneurum angustifolium var. *ensifolium* (Hicken) Farwell, Amer. Midl. Naturalist 2: 296. 1931.

Stem creeping, pruinose, 2-4 mm wide. Stem scales brown, 3-4 mm long, 1-1.5 mm wide, scales ovate, bases auriculate, apices acuminate, rarely obtuse, clathrate, the cells roundish, cell walls 7.5-12 µm thick. Phyllopodia 1-2 mm long, 1.5-2 mm wide, 1-4 mm apart. Leaves 16-60 cm long; petiole stramineous, 0.5-3 cm long, slightly ranurate on the adaxial side, convex abaxially, glabrate; lamina linear, bases and apices attenuate, 0.4-1 (-1.5) cm wide, chartaceous, lamina margins cartilaginous, usually revolute, indument of inconspicuous hairs, scattered abaxially, stomata polocytic; costa prominent, sometimes with scales similar to those on the stem, primary veins inconspicuous, 1-2 areoles between the costa and margin, excurrent veinlet one per areole; sori medial, paraphyses not seen; spores 45-55 µm long, 30-40 µm wide. Fig. 29.

This species is found from Mexico to Guatemala, Nicaragua, where it grows mainly as an epiphyte, rarely on rocks, between 500 m and 2900 m elevation.

REPRESENTATIVE SPECIMENS: MEXICO. SINALOA: 5 Km N of El Palmito, 28 Oct. 1973, *Breedlove 35732* (MO). JALISCO: Sierra de Manantlán, Cuautitlan, 19 Jan. 1975, *Diaz-Luna 5598* (UC). MICHOACAN: vic. Morelia, Campanario, 14 Sep. 1911, *Arsene 5612* (MO); Uruapan, Tancitaro, 14 Nov. 1940, *Hinton et al. 15685* (MO, US); Tancitaro, Uruapan, 17 Oct. 1940, *Hinton 15543* (MO); Tancitaro, 21 Jul. 1941, *Leavenworth & Hoogstraal 1095* (F, GH, MO). VERACRUZ: Mun. Jalisco, Taxolo, 8 Jun. 1983, *Barnett et al. 85a* (MO); Mun. Acajete, NW of Mazatepec, 9 Jun. 1983, *Barnett t al. 101* (MO); Córdoba, Aug. 1936, *Matuda 208* (MO); Cerro del Aguila, 13 km N of Altotonga, 28 Jun. 1980, *Nee & Hansen 18570* (F); 1 km NE of San Antonio Ixtatetla, 27 Apr. 1983, *Nee & Taylor 26818* (F) Huayacocotla, 26 Jan. 1984, *Nee 29080* (F). CHIAPAS: SE of Cerro Baul, 16 km NW of Rizo de Oro, 3 Nov. 1971, *Breedlove & Smith 21793* (F); finca Irlanda, May 1914, *Purpus 7238* (BM, F, MO). Without locality: Tocuila, 1869, *Hahn 19* (B).
GUATEMALA. ALTA VERAPAZ: San Juan Chameles-Cobán, 19 Aug. 1973, *Dary-Rivera 254* (F). SAN MARCOS: 12 Mar. 1940, *Steyermark 37600* (F). QUEZALTENANGO: slopes of volcán Zunil, at Aguas Amargas, 17 Febr. 1939, *Standley 65432* (F); below Santa María de Jesús, 11 Mar. 1939, *Standley 68419* (F); between Finca Pirineos and Patzulín, 9 Feb. 1941, *Standley 86975* (F, UC), *Standley 87028* (F), *Standley 87095* (F); along quebrada San Gerónimo, lower south-facing slopes of Volcán Santa María, 1-2 Jan. 1940, *Steyermark 33446* (F). SOLOLA: San Lucas, 10 Jun. 1948, *Williams 14343* (BM, F, US). HUEHUETENANGO: near El Reposo, about 8 km from Mexican frontier, 14-18 Dec. 1972, *L.O. Williams et al. 41388* (AAU, F) CHIMALTENANGO: Chimaltenango, *Johnston 1270* (F). SACATEPEQUEZ: just above Barranco Hondo, 11 Mar. 1941, *Standley 88933* (F); lower slopes of Volcán de Fuego, SW of Alotenango, 16 Jan. 1974, *L.O. Williams & Williams 43521* (F). JALAPA: 8 km N of Jalapa, 13 Nov. 1940,

Cutler 4320 (MO, US). SUCHITEPEQUEZ: S lower slopes of Volcán Zunil, E of Pueblo Nuevo, 1 Feb. 1940, *Steyermark 35361* (F). ESCUINTLA: Monte Rey, El Zapote, 27 Apr. 1937, *Muenscher 12119* (F); between Río Jute and Río Pantaleón, on road between Escuintla and Santa Lucia, 24 Jan. 1939, *Standley 63479* (F). SANTA ROSA: Jumaytepequez, Aug. 1892, *J. D. Smith 4087* (B); along road SE of Barbarena, 21 Nov. 1940, *Standley 77870* (F, UC); near Cuilapilla, 23 Nov. 1940, *Standely 78056* (F); near El Molino, 26 Nov. 1940, *Standley 78500* (F); Volcán Tecuamburro, N of Chiquimulilla, 20 Dec. 1939, *Steyermark 33153* (F); up Loma Bandera Shac, lower S facing slopes of Volcán Tajumulco, 9 Mar. 1940, *Steyermark 37351* (F). Finca Naranjo, Chicacao, 14 Mar. 1947, Brenckle 47-94 (F); Coatepeque, 15 Mar. 1944, *Varrelman s.n.* (F)
HONDURAS. EL PARAISO: Quebrada Tapahuasca, 14 Aug. 1964, *Molina 14664* (F).
EL SALVADOR. AHAUACHAPAN: Laguna Verde, 1 Mar. 1979, *Seiler 969* (F, NY, UC); near Ataco, 19 Jan. 1947, Standley & Padilla 2640 (F). SONSONATE: Los Pedregales de San Isidro, 19 May 1977, *Seiler 3* (F). LA LIBERTAD: Mun. Antiguo Cuscatlan, 13 Jul. 1989, *Villacorta & Martinez 310* (MO). SAN SALVADOR: vicinity of San Salvador, 30 Mar.-24 Apr. 1922, *Standley 21824* (MO), *Standley 22660* (MO, S, US), *Standley 22672* (F); near Apulo, near lake Ilopango, 19 Jun. 1949, *L.O. Williams & Molina 16740* (BM, F, MO). SAN MIGUEL: Volcán San Miguel, Las Placitas, 5 May 1979, *Salgado 67* (F)
NICARAGUA. ESTELI: Salto de Estanzuela, ca. 5 km sur de Esteli, 29 Sep. 1980, *Guzman et al. 1215* (MO).

Campyloneurum ensifolium is characterized by its small, adpressed stem scales, with roundish cells.

Although the label of the type collection mentioned Obrajillo, Peru, as the type locality, I agree with Lellinger (1988) that the Nee's specimen was mislabeled.

22. *Campyloneurum falcoideum* (Kuhn *ex* Hieron.) M. Meyer ex Lellinger, Proceed. Biol. Soc. Wash. 89: 708. 1977.

Polypodium falcoideum Kuhn *ex* Hieron. Bot. Jahrb. Syst. 34: 533. 1904. Lectotype (chosen by Lellinger, Proceed. Biol. Soc. Washington 89: 708. 1977). Costa Rica: Río Sucio, 17 Mar. 1882, *Lehmann 1741* (B!, BM!, K!, US!).

Stem long-creeping, not pruinose, 1-1.5 (-2) mm wide. Stem scales 4-7 mm long, usually 1 mm wide, narrowly ovate, slightly falcate, peltate, apices acuminate, cells oblong along the main axes of the scale, central cell walls 10-17 µm thick, marginal cell walls 7.5 µm thick. Phyllopodia 0-1 mm long, 1-1.5 mm wide, 8-20 mm apart. Leaves 10-30 cm long; petiole stramineous or brownish, 3-7 cm long (1/3-1/5 of the total lenght of the lamina), indument not seen, slight ranurate adaxially, convex abaxially; lamina lanceolate to narrow lanceolate, bases attenuate or subcuneate, apices long acuminate, 1.5-2.5 (-4) cm wide, herbaceous or herbaceous-chartaceous, margins cartilaginous, repand or slightly sinuate, indument of scatered hairs on the lamina and caducous scales on the costa; stomata polo or copolocytic; costa prominent on both sides of the lamina, 1.5 mm long 0.5 mm wide, similar to those at the stem, primary veins inconspicuous or slightly prominulous on both sides of the lamina, 3-5 mm apart, flexuous, 50-70º divergent from the costa, transverse secondary veins forming 3-4 primary areoles between the costa and margin, usually entire, excurrent veinlets 1(-2), sometimes forming secondary areoles at the margin of the lamina; sori subterminal, usually one row between secondary veins, paraphyses not seen, spores (50-) 60-70 µm long, 40-50 µm wide. Figs. 5 d, e; 17 d; 36.

This species is known from Costa Rica, Panama and southwestern Colombia, where it grows as an epiphyte between 1300 m and 2500 m elevation.

REPRESENTATIVE SPECIMENS: COSTA RICA. ALAJUELA: from Vara Blanca to La Concordia, between Poas and Barba volcanoes, 23 Jul. 1923, *Maxon & Harvey 8488* (BM); property of R. Gonzales, 28 Jun. 1875, *Polakowsky 201* (BM); Palmira, region of Zarcero, 30 Aug. 1937, *A. Smith F-48* (F); Palmira, 13 Jan. 1938, *A. Smith H82* (F). HEREDIA: Carpintera, 10 Apr. 1908, *A.C. Brade & A. Brade 19* (S, US); N of Heredia, ca. 1 km beyond Porrosati, 18 Aug. 1970, *Lellinger & White 1675* (US); Puerto Viejo, on the Sarapiquí River, 2 Mar. 1956, *Stork 4841* (NY, US). PUNTARENAS: upper Río Burú, 19 Aug. 1983, *Gómez et al. 21491* (MO), *Gómez et al. 21691* (MO, UC). SAN JOSE: Tablazo, 4 Mar. 1908, *A.C. Brade & A. Brade 44* (BM, NY); ca. 15 km N of Tres Ríos, ca. 4 km N of Cascajal, 2 Aug. 1970, *Lellinger & White 1375* (F, US); Río Parrita Chiquita, 5 km N of Santa María de Dota,

10 Oct. 1976, *Lent 3912* (F, NY); near Quebradillas, 24 Dec. 1925, *Standley 42922* (BM); upper slopes of Cerro Daser, Azulillo, 6 km W of rt. 4, 5 km S of Aserri, 19 Mar. 1973, *Stolze 1418* (AAU, F, UC). LIMON: Cordillera de Talamanca, Atlantic slope, canyon of Río Siní, 15 Sep. 1984, *Davidse & Herrera 29159* (MO). Without exactly locality: Cerro del Gallito, 26 Jun. 1926, *Valerio A95* (US).
PANAMA. CHIRIQUI: valley of the Río Caldera, from El Boquete to the Cordillera, 6 Feb. 1918, *Killip 5076* (BM); 2 mi W of Cerro Punta, 22 Jan. 1968, *McDaniel 10222* (GH); valley of the upper Río Chiriquí Viejo, vic. of Monte Lirio, 27 Jun.-13 Jul. 1935, *Seibert 284* (GH); dist. Bugaba, Santa Clara, Cerro Pando, 28 Feb. 1985, *Werff & Herrera 7243* (UC).
COLOMBIA: Putumayo, above Sibundoroy, 4 May 1939, *Alston 8372* (MO).

Campyloneurum falcoideum is easily recognized by the falcate stem scales, remote leaves, and venation of undivided primary areoles with one included free veinlet. It belongs to the *C. sphenodes* group.

23. *Campyloneurum fallax* Fée, Crypt. vasc. Brésil 1: 114. t. 35. f.2. 1869. Type. Brazil: Rio de Janeiro, Serra dos Orgãos, n.d., *Glaziou 2819* (S!, RB!, probably isotype K!, photo BM!). In the label of the specimen at Kew, the date is October 1871. *Non Polypodium fallax* Schlecht, 1830.

Polypodium longipetiolatum Brade, Rodriguesia 3: 115. 1937. *Nomen novum* for *Campyloneurum fallax* Fée.

Stem long-creeping, no pruinose, 3-5 mm wide. Stem scales light brown in mass, 5-7 mm long, 2.5-3.5 mm wide, broadly ovate, adpressed, persistent, slightly clathrate, the cells oblong or broadly oblong, central cells along the main axes of the scale, cell walls 12-16 µm thick, marginal cells transverse or with irregular disposition, cell walls usually 4-8
(-10) µm thick. Phyllopodia 4-5 mm long, 2.5-3 mm wide, 7-10 mm apart. Leaves 25-45 (-75) cm long; petiole stramineous or dark stramineous, (5-) 8-14 (-16) cm long, slightly ranurate on the ventral side, convex on the dorsal, indument of caducous scales; lamina narrowly lanceolate, bases attenuate or subcuneate, rarely cuneate, apices acuminate, 1.5-4.5 cm wide, chartaceous-subcoriaceous, rarely chartaceous, usually bright on both sides, margin cartilaginous, slightly sinuate; stomata polocytic; costa prominent, primary veins very slightly prominulous on the ventral side, slightly flexuosus, 45-50^{o} divergent with the costa, (4-) 5-7 mm apart, secondary veins inconspicuous, 4-5 areoles between the costa and margin, usually 2-3 veinlets, entire or furcate; sori medial or subterminal, paraphyses not seen, spores (55-) 72-87 µm long, 40-50 µm wide. Figs. 7 c; 14 d; 17 c; 38.

This species is known from southern Brazil, where it grows between 1000 m and 2000 m elevation.

REPRESENTATIVE SPECIMENS: BRAZIL. RIO DE JANEIRO: Serra do Itatiaia, n. d, *Brade 6551* (NY, S); Serra dos Orgãos, Pedra Assú 30 Jul. 1940, *Brade 16501* (BM, MO, NY, S, US); Itatiaia, Pousada Nova, 21 Mar. 1943, *Brade 17327* (MO); Mun. Resende, Itatiaia National Park, S face of Mt. Itatiaia, below Macieiras, *Eiten & Eiten 7483* (US); Campo do Itatiaia, 13 May 1906, *Luederwaldt s.n.* (S); vicinity of Itatiaia, 26-30 Jul. 1915, *Rose & Russell 20589* (US). SÃO PAULO: Serra da Bocaina, 21 Apr. 1951, Brade 20676 (MO); Campos do Jordão, 5-20 Feb. 1937, *Campos Porto 3213* (F, BM); São José do Barreiro, Serra da Bocaina, 29 May 1958, *Handro 785* (US); Campos do Jordão, Sep. 1945, *Leite 3632* (MO, UC). PARANA: banks of Rio da Santa, between Curitiba and Joinville, 5 Jan. 1974, Conrad & *Dietrich 2052* (UC). Without locality: 1870, *White s.n.* (BM).

Campyloneurum fallax belongs to the *C. amphostenon* group, which consists os species distributed in the Andes and montane areas of Mexico and Central America. *Campyloneurum fallax* resembles *C. densifolium*, but it differs from it by broader stem scales, and by its oblong, isodiametric cells of the stem scales (Fig. 7 c). *Campyloneurum fallax* is the only disjunct species in the group, and it may have evolved from an early isolation, since the Brazilian shield is geologically older than the Andes.

24. *Campyloneurum fasciale* (Willd.) C. Presl, Tent. Pterid. 190. 1836.

Polypodium fasciale Willd., Sp. Pl. 5: 156. 1810. Type. Caribe, *Humboldt 426* (*Herb. Willd. 19632*) (holotype, B! ; isotype, P).

Polypodium serpentinum Christ, Bull. Herb. Boiss. 2, 6: 51. 1906. Type. Costa Rica: Navarro, *Wercklé s.n.* (holotype, P!, photo of P, BM!).
Campyloneurum serpentinum (Christ) Ching, Sunyatsenia 5: 263. 1940.

Stem long-creeping, not pruinose, brown, greenish-stramineous or black, (1-) 2-3 mm wide. Stem scales brown or dark brown in mass, (1.5-) 2-3 mm long, 0.8-1 mm wide, narrowly oblong, usually pseudopeltate, apices acuminate, clathrate, cell walls sometimes diffuse, cells oblong, along the main axes of the scale, cell walls 8-10 µm thick, without differentiate margins. Phyllopodia 0.5-1 mm long, 1-2.5 mm wide, 0.7-20 mm apart. Leaves 20-40 (-50) cm long; petiole stramineous or brownish, 1-2 cm long, slightly ranurate adaxially or slightly convex abaxially; lamina lanceolate or narrowly lanceolate, bases attenuate, apices acuminate, (1-) 2-5 cm wide, herbaceous-chartaceous, indument of bicellular, simple hairs, inconspicuous; stomata polocytic; costa prominent, primary veins prominulous on both sides of the lamina, stramineous or darker than the leaf tissue, 70-80° divergent from the costa, slightly flexuosous, 5-7 mm apart, secondary veins slightly prominulous on only darker than the leaf tissue, forming (4-) 5-10 primary areoles between the costa and margin, areoles entire, usually with 2 free excurrent veinlets; sori medial or subterminal, paraphyses not seen, spores 47-50 µm long, 32 µm wide. Fig. 39.

This species is known from Mexico, Costa Rica and Panama to Bolivia. It grows as an epiphyte in forests, between 100 m and 2000 (-2500) m elevation.

REPRESENTATIVE SPECIMENS: MEXICO. VERACRUZ: Mun. Hidalgotitlán, NE Hnos. Cedillos camp, 13 Feb. 1974, *Dorantes et al. 2453* (F, MO). OAXACA: Santa María Chimalapa, Río Milagro, 4 Sep. 1985, *Hernandez 1465* (MO). CHIAPAS: 6-8 km N of Ocosingo, along road to Bachajón, 9 Nov. 1971, *Breedlove & A.R. Smith 22151* (F, NY); 45 km N of Ocozocoautla, above lake of Malpaso, 31 Jan. 1973, *Breedlove 32816* (F); Mun. Ocosingo, 1 km SE of Monte Líbano, 8 Aug. 1954, *Dressler 1617* (GH, NY, US); 3 km S de Lacanja-Chanzayab, 11 Aug. 1984, *Martinez 6955* (MO) Finca Mexiquito, Jun. 1913, *Purpus 6751* (F, NY, S, UC). BELIZE: 1907, *Peck 636* (F). HONDURAS. ATLANTIDA: Lancetilla valley, near Tela, 6 Dec. 1927-20 Mar. 1928, *Standley 54150* (F, US). COSTA RICA. ALAJUELA: Santiago, 25 Apr. 1901, *Amz. 14200* (F); colinas de San Pedro de San Ramón, 27 May 1925, *Brenes 4234* (F); San Miguel de San Ramón, 21 Jul. 1934, *Brenes 19258* (F); San Isidro de San Ramón, 22 Oct. 1986, *Herrera 98* (MO); Buena Vista, San Carlos, 21 Jul. 1963, *Jimenez 918* (F); Buena Vista, San Carlos, 14 Aug. 1964, *Jimenez 2295* (F); Santiago, near San Ramón, 21 Apr. 1913, *Tonduz 17572* (BM, F, NY, S, UC). LIMON: cerro Colonel, E of Laguna Danto, 15-20 Sep. 1986, *Stevens & Montiel 24622* (F, MO). SAN JOSE: Río Negro, cerro La Cangreja, 20 Jun. 1986, *Chacón & Chacón 1959* (MO); Zona Protectora La Cangreja, along Quebrada Grande, ca. 2 km NNE of Mastatal de Puriscal, 23 Jul. 1988, *Grayum 8642* (MO); vicinity of El General, Jul. 1936, *Skutch 2663* (GH, NY, S, US). CARTAGO: 2 km W of Orosi, 16 Jan. 1977, *Lent 4056* (F, NY) PUNTARENAS: Reserva Forestal Golfo Dulce, Península Osa, Rancho Quemado, ca. 15 km W of Rincón, 30 May 1988, *Hammel et al. 16891* (MO); slope of Río Java, 20 Nov. 1986, *Hennipman et al. 7069* (MO); San Vito de Java, 24 Jul. 1972, *McAlpin 1474* (F). PANAMA. CHIRIQUI: El Boquete, 5 Feb. 1918, *Cornman 804* (MO, UC, W); around El Boquete, 17 Mar. 1918, *Cornman 1151* (W); on NW side of Cerro Pando, 21 Jul. 1971, *Croat 15933* (AAU, MO); E of Canas Gordas, near Costarican border, 26 Feb. 1973, *Croat 22350* (MO); Ojo de Agua, vicinity of Santa Clara, 17 Jun. 1987, *Croat 66296* (MO); Las Lagunas, 18 Mar. 1983, *Hamilton & Stockwell 3588* (MO, UC); 7.5 mi from bridge over Río Chiriqui Viejo, on road to Río Sereno, 7 Apr. 1979, *Hammel et al. 6855* (MO); valley of Río Caldera, 5-19 Feb. 1918, *Killip 5039* (MO); km 3 on La Unión road, 23 May 1971, *Proctor 32029* (MO). BOCAS DEL TORO: 10-15 mi S from Changuinola river, 18 Dec. 1966, *Lewis et al. 990* (MO), *Lewis et al. 994* (MO, UC). VERAGUAS: along base of Cerro Tute, 10 Sep. 1982, *Hamilton et al. 1310* (MO). COCLE: El Cope on Pacific side, 16 Oct. 1979, *Antonio 2152* (MO); above El Valle, 13 Aug. 1972, *Gentry 5667* (MO); 9 km from El Valle, 12 May 1973, *Kennedy et al. 3221* (MO). PANAMA: 16 km above Pan-Am highway, on road from El Llano to Carti-Tupile, 13 Feb. 1973, *Kennedy et al. 2451* (F, MO); summit of cerro Campana, 31 Mar. 1969, *Porter et al. 4920* (MO). DARIEN: Serranía del Piré, above Cana gold nime, between Río Cana and Río Escucha, 27 Jul. 1976, *Croat 37781* (MO); Serranía del Darién, top of cerro Mali, 17 Jan. 1975, *Gentry & Mori 13685* (MO); W ridge of cerro Mali, 23 Jan. 1975, *Gentry & Mori 13838* (MO); S slope of west peak of cerro Tacarcuna, 28 Jan. 1975, *Gentry & Mori 13967* (MO); trail from cerro Mali to Río Pucuro, 20 Jul. 1976, *Gentry et al. 16838* (MO); E slope of Cerro Sapo, 3 Fb. 1978, *Hammel 1303* (MO); 6 km S from gold mining

camp at Cana, W to Alturas de Nique, 20 Apr. 1980, *Lellinger 1969* (MO, US); Pirre massif, Alturas de Nique, 3 Mar. 1988, *McPherson 12204b* (MO); along ridge trail from Cana up the Cerro Pirre, 3 May 1990, *Moran 5045* (F); Río Tuquesa, at lower Tuquesa mining camp, 4 Jul. 1975, *Mori 6943* (MO); Parque Nacional Darien, slopes of cerro Tacarcuma, 27 Oct. 1987, *Nevers et al. 8532* (MO).
WINDWARD ISLANDS. ST. VINCENT: valley of N fork of Cumbrland river, 2-3 May 1947, *Morton 5542* (MO).
COLOMBIA. CHOCO: Hoya del Río San Juan, Quebrada La Sierpe, 1 Apr. 1979, *Forero & Jaramillo 4454* (MO). VALLE: Pacífic basin, Río Cajambre, 21-30 Apr. 1944, *Cuatrecasas 17180* (F). META: Sierra de la Macarena, between Río Guejar and Sansa, 29 Aug. 1950, *Idrobo 521* (AAU, US).
VENEZUELA. LARA/YARACUY: Sierra de Aroa, 10-13 mi NW of Urachiche, NW from Urachiche to Duaca, 16 Nov. 1982, *A.R. Smith et al. 1343* (MO). Parque Nacional Aragua, 2 Dec. 1938, *L.Williams 10801* (F). TACHIRA: 35 km SSE of San Cristobal, La Buenaña, 6-12 km W of Quebrada Colorada, 20-21 Mar. 1981, *Liesner & Gonzalez 10876* (MO, UC). BOLIVAR: 5 km S of El Paujil, Río Samay, affluent of Icabaru, 21 Oct. 1985, *Liesner & Holst 18843* (MO).
FRENCH GUIANA. Saul: Monts La Fume, 13 Oct. 1982, *Boom & Mori 2016* (CAY, F); camp Tigre, 4.5 km N of Saut Mais , 16 Jan. 1980, *Cremers 6121* (CAY).
ECUADOR. CARCHI: trail from Rafael Quindís finca to Río Verde, 26 Nov. 1987, *Hoover & Wormley 1679* (MO), *Hoover & Wormley 1710* (MO). MANABI: Chone-Santo Domingo road, near Río La Morena, 15 km NNE of Flavio Alfaro, 7 May 1980, *Harling & Andersson 18911* (AAU, F, GB, QCA). PICHINCHA: Tinalanadia, 9.6 km E of Santo Domingo, 3 Apr. 1983, *Croat 55708* (MO); road La Unión del Toachi, San Francisco, 19 Mar. 1985, *Harling & Andersson 23146* (QCA). NAPO: San Pablo de los Secoyas, 6 Aug. 1980, *Brandbyge et al. 32545* (AAU, QCA); Río Aguarico, Tangoy, 29 Aug. 1979, *Holm-Nielsen et al. 20145* (AAU, QCA); Nuevo Rocafuerte, 27 Feb. 1981, *Jaramillo & Coello 4414* (AAU, QCA); San Pablo at Río Aguarico, 5 May 1984, *Laegaard 52083* (QCA); Añangu, Parque Nacional Yasuní, 30 May-21 Jun. 1982, *Øllgaard et al. 39007* (AAU, QCA), *Øllgaard et al. 39110* (AAU); Cabañas Aliniahui, S of Río Napo, 29 Sep. 1989, *Zogg & Gassner 13127a* (QCA). ZAMORA-CHINCHIPE: new road Loja-Zamora, 15 Feb. 1991, *Øllgaard & Moran 98831* (QCA).
PERU. AMAZONAS: Bagua, 12 km E of La Peca, *Barbour 2487* (MO, UC), Barbour 2495 (F, UC); Serranía de Bagua, 14 Jun. 1978, *Gentry et al. 22930* (F, MO, UC); Bongará, SW of Pomacocha, *Wurdack 844* (F, NY, UC, US, USM); Sipabamba, Shillac, 5 May 1981, *Young & Eisenberg 352a* (MO, NY, UC). SAN MARTIN: Monte Campana, Tarapoto, Aug. 1856, *Spruce 4647* (BM). LORETO: Santa Rosa, Yurimaguas, 1-5 Sep. 1929, *Killip & Smith 28927* (S, US). MADRE DE DIOS: Río Manu, Cocha Cashu , 14 Aug. 1978, *Foster & Terborgh 6621* (F); Cocha Cashu, 10 Sep. 1986, *Nuñez 6070* (F, NY).
BOLIVIA. LA PAZ: Larecaja, Consata, 14 Dec. 1981, Beck 4917 (F); Murillo, 44 km below Lago Zongo dam, vic. of Cahua hydroelectric plant, 12-15 Sep. 1983, *Solomon 10853* (MO). COCHABAMBA: Carrasco, junction of Río Leche with Río Isarsama, 5 May 1977, *Beck 1633* (F, LPB).

Campyloneurum fasciale is characterized by clathrate narrowly ovate scales, without differentiated margins. It is closely related to *C. fuscosquamatum*, from which it differs by clear cell lumen in the stem scales. *Campyloneurum fasciale* belongs to the *C. repens* group.

25. *Campyloneurum fuscosquamatum* Lellinger, Amer. Fern J. 78: 21. 1988. Type. Peru: Huánuco, Tingo María on the Río Huallaga, 2 Nov. 1938, *Stork & Horton 9452* (holotype US!; isotypes F!, GH, UC!, photo of US at F!, USM!).

Stem green, geenish-stramineous to black, not pruinose, 2-3 mm wide. Stem scales dark borwn, caducous, persistent only at the growing areas, narrowly ovate or linear, 2.5-3 (-3.5) mm long, 0.5-0.8 mm wide, the cells narrowly oblong along the main axes of the scale, usually not differentiate at the margins, cell walls (8-) 12-16 (-20) µm thick, lumen yellowish or obliterate. Phyllopodia 0.5-1 mm long, 1.5-2 mm wide, 7-10 (-20) mm apart. Leaves 20-40 cm long; petiole 0.5-5 cm long, stramineous, sometimes darker abaxially; lamina narrowly obovate or narrowly elliptic, bases attenuate or narrowly cuneate, apices acuminate, 2-5 (-8) cm wide, herbaceous-chartaceous, margins cartilaginous, slightly revolute or plane, indument of inconspicous, simple, multicellular hairs, 80-96 m long, scattered abaxially; costa prominent, indument of scales similar to those at the stem, primary veins prominent or prominulous, stramineous, (60^{o}-) 70-75^{o} (-80^{o}) divergent from the costa, straight or slightly sinuate, 4-6 mm apart, transverse secondary veins forming 6-10 primary areoles between the costa and margin, excurrent veinlets 2 (-3), irregular marginal areoles present

with 0-1 (-4) excurrent veinlets; stomata copolocytic or polocytic; sori subterminal or medial, paraphyses not seen, spores 56 µm long, 32 µm wide. Figs. 3 b, c; 14 g; 17 e; 40.

This species is known from Colombia to Bolivia, where it grows as an epiphyte in lowland forests between 100 m and 1500 m elevation.

REPRESENTATIVE SPECIMENS: COLOMBIA. META: Cordillera La Macarena, trail between Río Guejar and Guapayita, 20-28 Dec. 1950, *Idrobo & Schultes 817* (GH, US); Sierra de La Macarena, Caño Estrada, 15 Dec. 1949, *Philipson & Idrobo 1753* (BM, US).
ECUADOR. NAPO: Añangu, S bank of Río Napo, 95 km downstream from Coca, 19 Jun.-14 Jul. 1985, *Balslev et al. 60573* (QCA); 2 km downstream from Puerto Aguarico, 6 Apr. 1980, *Brandbyge et al. 30478* (AAU, QCA); San Pablo de los Secoyas, 11 Aug. 1980, *Brandbyge & Asanza 32792* (AAU, QCA); Río Aguarico, San Pablo de los Secoyas, 13 Feb. 1980, *Holm-Nielsen et al. 21061* (AAU, QCA); Añangu, Río Napo, 16-27 Apr. 1983, *Lawesson et al. 39459* (AAU); trail from Santa Cecilia up Río Aguarico, 29 Mar. 1972, *Mac Bryde & Dwyer 1347* (MO, QCA). PICHINCHA: Cantón Santo Domingo, 12 km E of Patricia Pilar, 23 Aug. 1978, *Dodson et al. 7181* (AAU, F, MO); station ENDESA, km 113 along Quito-Puerto Quito, 16-17 Nov. 1989, *Luteyn & Borchsenius 13362* (QCA); ENDESA, km 113 via Quito-Puerto Quito, 23-24 Apr. 1983, *Rodriguez et al. 113* (QCA), 25 Feb. 1984, Rodriguez 293 (QCA). ZAMORA-CHINCHIPE: N side of Río Palanda with Río Zumba, 30 Jan. 1985, *Harling & Andersson 21286* (QCA).
PERU. SAN MARTIN: Mariscal Cáceres, Madre Mía, 16 Mar. 1977, *Boeke & Ramirez 1329* (NY, UC); San Martín, km 28 of Tarapoto-Yurimaguas road, 17 Aug. 1986, *Knapp 8040* (MO, USM), *Knapp & Mallet 8393* (NY); Tarapoto, Alto Pucayacu, *Montes 47* (F); Campanillas, trail to Achiras, SW from Sión, 23 Oct. 1969, *Schunke V. 3556* (F, MO, US, USM); Mariscal Cáceres, Tocache Nuevo, *Schunke V. 3590* (UC, US); San Roque, *Williams 7255* (F, US); Tarapoto, 4 mi E of Tarapoto, *Woytkowski 35235* (MO, S, UC). LORETO: Maynas, near Brilla Nueva, Boro indian village, on upper Río Yaguasyacu, 8 Nov. 1977, *Gentry & Revilla 20412* (MO); Maynas, Quebrada Tamshiyacu, E of Tamshiyacu, 19 Mar. 1979, *Gentry et al. 25837* (F, MO, US); Maynas, Yanamano, Explorama Tourist Camp, on Río Amazonas, between Indiana and mouth of Río Napo, 26 Jul. 1980, *Gentry et al. 29028* (MO); Yurimaguas, lower Río Huallaga, 23 Aug.-7 Sep. 1929, *Killip & Smith 27668* (F, US); Santa Rosa, lower Río Huallaga, below Yurimaguas, 1-5 Sep. 1929, *Killip & Smith 28854* (F, US); San Antonio, Río Itaya, 18 Sep. 1929, *Killip & Smith 29372* (NY, US); above Pongo de Manseriche, left bank of Río Santiago, 23 Nov. 1931, *Mexia 6141a* (MO, UC, US); creek Inche, 3 Jan. 1932, *Mexia 6371a* (UC, US). HUANUCO: Fundo Chela, Sinchono, 3 Aug. 1948, *Aguilar 945* (F, USM); Tingo María, 30 Oct. 1949-19 Feb. 1950, *Allard 22329* (US); Tingo María, 4 Oct. 1972, Croat 21034 (US); Tingo María-Pucallpa, 1971, *Ellenberg 3849* (GH); abajo de la Divisoria, cerca Sinchono, 21 Jul. 1948, *Ferreyra 1101* (F, USM); Huánuco, Tingo María, 24 Sep. 1954, *Ferreyra 10276* (GH, USM); Pachitea, Codo de Pozuzo, 22 Oct. 1982, *Foster 9399* (F, USM); La Divisoria, Tingo María-Pucallpa road, near Loreto border, 29 Mar. 1977, *Gentry et al. 18821* (F, MO); Churubamba, Balsa-Playa, 12 Sep. 1936, *Mexia 8176* (BM, F, GB, GH, MO, NY, S, UC, US); near confluence of Río Cayumba with Río Huallaga, 10 Oct. 1936, *Mexia 8271* (BM, F, GB, GH, MO, NY, S, UC. US); above Río Cayumba, 19 Oct. 1936, *Mexia 8312* (UC); Pachitea, Honoria, Bosque Nacional Iparía, 14 Mar. 1967, *Schunke V. 1762* (F, GH, USM); Tingo María on Río Huallaga, 19 Oct. 1938, *Stork & Horton 9452* (F, MO, UC); Huamalíes, Supte River, N of Tingo María, 2 Nov. 1938, *Stork & Horton 9568* (F, GH, UC, US). PASCO: Puerto Bermudez, 14-17 Jul. 1929, *Killip & Smith 26444* (US); Pozuzo, 20-22 Jun. 1923, *Macbride 4585* (F, US); Oxapampa, vicinity of Chequitavo, Gran Pajonal, 26 Sep. 1983, *D.N. Smith 5625* (UC). JUNIN: Pichis trail, Yapas, 28-29 Jun. 1929, *Killip & Smith 25606* (F, NY, US); Perené, 1960, *Kunkel 618* (GH); Chanchamayo valley, 1924-1927, *C. Schunke 123* (US); above San Ramón, 1923, *C. Schunke 166* (GH, US); La Merced, 1909, *Schunke 25* (S, UC); Chanchamayo, Feb. 1939, *Soukup 1103* (F). AYACUCHO: Río Apurímac, valley near Kimpitiriki, 10-11 May 1929, *Killip & Smith 22861* (F, US); La Mar, along Río Catute, 2 km NW of Santa Rosa, 8 Sep. 1976, *Wasshausen & Encarnación 621* (MO, US, USM). CUSCO: La Convención, 4 km NE from the Hacienda Luisiana, 31 Jul. 1968, *Dudley 11501* (GH, US). MADRE DE DIOS: Tambopata Reserve Zone, 13 Mar. 1988, *Bell & Wiser 88-314* (F); Parque Nacional Manu, Cocha Cashu Biological Station, *Foster P-84-17* (MO); Parque Nacional Manu, Cocha Cashu, 20 Aug. 1976, *Foster & Augsburger 3282* (F); Tambopata, Río Piedras, 17 Jan. 1967, *Vargas 18666* (GH).
BOLIVIA. LA PAZ: Nor Yungas, Polo Polo bei Coroico, Oct.-Nov. 1912, *Buchtien 3535* (UC); Buchtien 3536 (F, S, US); 6 km N (below) Consata, 15 Dec. 1981, *Solomon et al. 6575* (MO). BENI: Ballivian, Río Colorado, 21 Jun. 1989, *Fay & Fay 2083* (F, MO); Ballivian, Río Colorado, 22 Jun. 1989, *Fay & Fay 2092* (F), 24 Jun. 1989, *Fay & Fay 2130* (F). Ballivian, lower slopes of serranía Pilón Lajas, 14.3 km N of the bridge over the Río Quiquibey, *Solomon 13893* (MO); Río

Chaparé, Mamoré, Aug. 1926, *Werdermann 2169* (MO). SANTA CRUZ: Ichilo, Parque Nacional Amboró, along Río Saguayo, 18 Jan. 1988, *Nee & Saldias 36839* (MO); Parque Nacional Amboró, ca. 15 km SE up the Río Pitasama, from the Río Surutú, *Solomon & Urcullo 14090* (MO, US); Sara, bosques del Río Surutu, 1 Oct. 1925, *Steinbach 7246* (F, S, UC). COCHABAMBA: Carrasco, Cantón Chirquioma, Isarsama camp, 3 May 1979, *Beck 1569* (LPB); Antahuacana, N von Cochabamba, Jun. 1909, *Buchtien 2154* (S, UC, US); *Buchtien 2155* (S, US).

Campyloneurum fuscosquamatum is characterized by its dark brown, narrowly ovate or linear stem scales. It is closely related to *C. fasciale*, from which it might be derived. They can be differentiated by the characters provided in the key.

Campyloneurum fuscosquamatum belongs to the *C. repens* group.

26. *Campyloneurum inflatum* Lellinger, Amer. Fern J. 78: 22. 1988. Type. Colombia: Cauca, W slope of Cerro Munchique, *Pérez-Arbelaez & Cuatrecasas 6244* (holotype US!; isotypes COL, F!; photo of US, USM!).

Stem long creeping, green stramineous or black, not pruinose, 2-3 mm wide. Stem scales light brown in mass, 4-5 mm long, 0.9-1 mm wide, lanceolate, bases auriculate, apices acuminate, clathrate, the cells oblong. Phyllopodia 1-2 mm long, 2.5-3 mm wide, 30-40 mm apart. Leaves 30-55 cm long; petiole stramineous to dark stramineous, 9-21 cm long; lamina elliptic, bases acute, apices caudate, 6-10.5 cm wide, subcoriaceous, margins strongly cartilaginous, slightly revolute, indument of scattered bicellular, simple hairs; hypostomatic, stomata polocytic; costa prominent, indument of caducous scales, primary veins slightly prominulous adaxially, prominent abaxially, slightly flexuous, usually stramineous, 65-70° divergent from the costa, 7-8 mm apart, secondary veins forming 6-7 primary areoles between the costa and margin, 2 (-4) free excurrent veinlets in each primary areole, entire, sometimes secondary areoles close to the margin; sori subterminal on the excurrent veinlets, paraphyses absent; spores 67-76 µm long, 37-42 µm wide. Fig. 40.

This species is known only from Colombia and Peru, where it grows in forests between 2200 m and 2400 m elevation.

EXAMINED SPECIMENS: PERU. AMAZONAS: Bongará, WSW of Pomacocha, *Wurdack 868* (US).

27. *Campyloneurum lorentzii* (Hieron.) Ching, Sunyatsenia 5: 263. 1940.
Polypodium lorentzii Hieron., Bot. Jahrb. Syst. 22: 406. 1896. Lectotype (chosen by Sota, Opera Lilloana 5: 102. 1960). Argentina: Tucumán, Tafi, 4 Apr. 1872, *Lorentz 781* (B!, photo BM!).

Stem creeping, dark stramineous, pruinose, 4-6 mm wide. Stem scales light brown in mass, 3-4 mm long, 2.5-3 mm wide, ovate, bases auriculate, apices obtuse or ending in a multicellular hair, scales slightly clathrate, the cells broadly oblong, cell walls diffuse, central cell walls 20 µm thick, marginal cell walls 5 µm thick. Phyllopodia 2.5-4 mm long, 2.5-3 mm wide, 0.6-10 mm apart. Leaves 50-75 cm long; petiole dark stramineous, 5-27 cm long, ranurate adaxially, convex abaxially, indument of caducous scales similar to those on the stem; lamina narrowly lanceolate, bases attenuate, apices long acuminate, 2.5-4.5 cm wide, herbaceous-chartaceous, margins cartilaginous, slightly undulate, indument of inconspicuous, bicellular, simple hairs; stomata polocytic; costa prominent, primary veins prominulous, stramineous, 50-60° divergent from the costa, 5-7 mm apart, secondary veins slightly prominulous, same color as the leaf tissue, transverse secondary veins forming (3-) 4-5 primary areoles between the costa and margin, primary areoles symmetrically divided, (0-) 1-2 free excurrent veinlets in each secondary areole, sometimes free excurrent veinlets at the margin; sori medial, paraphyses not seen, spores 50-65 µm long, 32-40 µm wide. Fig. 36.

This species is found in Bolivia and northern Argentina, where it grows between 1400 m and 3000 m elevation, usually as a terrestrial.

REPRESENTATIVE SPECIMENS: BOLIVIA. LA PAZ: Prov. Murillo, Valle de Zongo, Santa Rosa, 3 km hacia

La Paz, 8 Apr. 1979, *Beck 1099* (F); Nor Yungas, along road between Unduavi and Chulumani, ca. 5 km beyond Aceromarca, 25 Nov. 1980, *Croat 51465* (LPB, UC).
ARGENTINA. CATAMARCA: Río Potrero, 10 Feb. 1949, *Brücher & Brücher s.n.* (S); Rodeo, 30 May 1910, *Castillón s.n.* (GH, US); Ambato-Rodeo, 20 May 1910, *Castillón s.n.* (NY, S, UC). Andalgalá, Esquina Grande, 3 May 1915, *Jörgensen 1497* (UC). TUCUMAN: road from Concepción to Andalgalá (Catamarca), 16 Oct. 1989, *Kramer et al. 10708* (F); Tafí, Tafí del Valle-Los Nogales, 6 May 1947, *Meyer 12110* (W); Tafí, Quebrada de las Sosa, Los Nogales, 12 Nov. 1952, *Petersen & Hjerting 609* (BM); Chicligasta, Quebrada de Cochuna, 17 Oct. 1957, *Sota s.n.* (S); Monteros, Piedra Labrada and Puerto del Pino, 24 Apr. 1949, *Verworst 482* (US, W); Tafí, Taficillo, 13 Mar. 1928, *Venturi 5891* (BM, F, MO). JUJUY: road to Lozano a Tiraxi, 3 Nov. 1974, *Schinini et al. 10210* (UC).

Campyloneurum lorentzii is closely related to *C. densifolium*. The former has stem scales with obtuse apices, while the latter has scales with acuminate or acute apices.

28. *Campyloneurum macrosorum* Fée, Gen. Fil. 96. 1854-1857. Type. Colombia: Ocaña, *Schlim 440* (holotype, not found; isotypes, B!, K!, photo of K, BM!).

Polypodium lindigii Mett., Ann. Sc. Nat. 5: 257. 1864. Cited Syntypes: Colombia, Bogotá, San Antonio, *Lindig 172* (B!, BM!, K!); La Vega, *Lindig 338* (B!, BM!, K!); Ocaña, *Schlim 440* (B!, K!, photo of K, BM!); *Schlim 724 pp* (not seen). Lectotype (chosen here) Colombia: Bogotá, San Antonio, *Lindig 172* (B!, BM!, K!).

Campyloneurum lindigii (Mett.) Ching, Sunyatsenia 5: 263. 1940.

Stem long-creeping, green turning black or stramineous, 2-4 mm wide. Stem scales light brown in mass, persistent, subadpressed, 3-4 mm long, 1 mm wide, lanceolate, bases slightly auriculate, apices acuminate, slightly clathrate, the cells oblong, cell walls diffuse. Phyllopodia 1-2 mm long, 1.5-3 mm wide, 25-30 mm apart. Leaves 30-50 cm long; petiole dark stramineous, 4.5-22 cm long, ranurate adaxially; lamina lanceolate or narrowly lanceolate, bases narrowly cuneate, apices acuminate, 5.5-7 cm wide, margins cartilaginous, slightly sinuate to undulate, indument of inconspicuous, bicellular hairs, scattered abaxially; stomata polocytic; costa prominent, primary veins prominulous on both sides of the lamina, stramineous, slightly flexuosous, 65-70^{o} divergent, 6-7 mm apart, secondary veins forming 6-10 primary areoles between the costa and margin, primary areoles entire, 2 (-3) free excurrent veinlets; sori subterminal, paraphyses filamentosous, branched, same length as sporangia, spores 60-66 µm long, 42 µm wide. Fig. 41.

This species is known from Colombia and Venezuela, where it grows as an epiphyte between 1500 m and 2500 m elevation.

REPRESENTATIVE SPECIMENS: COLOMBIA. CUNDINAMARCA: Salto de Tequendama, 8 Mar. 1939, *Alston 7405* (MO); Cordillera Oriental, WNW of Bogotá, 31 Dec. 1944, *Little & Little 9151* (F, US). Sebastopol, 3 Sep. 1944, *Little & Little 8603* (F). VENEZUELA. TACHIRA. Valencia, Pico de Vela, Buena Vista, 11 Nov. 1945, *Charpin & Jacquemont 13137* (F); Junín, S slopes of Cerro San Isidro, *Davidse & González 22222* (MO); trail leading to summit of Páramo de Tama, 29 Jan. 1978, *Luteyn et al. 5352* (F, UC). YARACUY: Sierra de Aroa, 9 km W of San Felipe, 4 Apr. 1980, *Liesner & González 10010* (MO).

Campyloneurum macrosorum is characterized by lanceolate, long petiolate leaves, with black stems, and by persistent, subadpressed, marginally differentiated stem scales.

Among the synonyms is included *Polypodium lindigii* Mett., which was based on material from Colombia, among them the type collection of *Campyloneurum macrosorum* Fée. During this study three of the four syntypes were studied; they clearly belong to this taxa as defined today.

This species can be differentiated from *C. repens* by having persistent, subclathrate stem scales and a thick stem. In addition, cells of the stem scale run along the axis, and the margin is as broad as the center part of the scale.

Campyloneurum macrosorum belongs to the *C. repens* group.

29. *Campyloneurum magnificum* T. Moore, Ind. Fil. 226. 1861. Type. Venezuela, *Fendler 410* (holotype, K!; isotypes, B!, F!, MO!, NY!). Figs. 1 c; 41.

Polypodium fendleri D. C. Eaton, Mem. Amer. Acad. Arts n.s. 8: 199. 1860. Type. Venezuela, *Fendler 410* (holotype MO!, isortypes B!, F!, K!, NY!). *Non Campyloneurum fendleri* T. Moore, 1861.

Polypodium decurrens Raddi var. *fendleri* (D. C. Eaton) Hook., Sp. Fil. 5: 43. 1864.

Campyloneurum fendleri (D. C. Eaton) J. Smith, Hist. Fil. 97. 1875. *Nom. superfl.*

Campyloneurum juglandifolium Fée, Crypt. Vasc. Br. 1. 1869. Type. Brazil: Rio de Janeiro, *Glaziou 1750* (holotype, P!).

Polypodium magnificum (T. Moore) Hieron., Bot. Jahrb. Syst. 34: 535. 1904.

Stem creeping, not pruinose, 10-15 mm wide. Stem scales light brown in mass, 4-6 mm long, 2 mm wide, ovate, clathrate, the cells oblong, along main axes of the scale, cell walls 10-20 µm thick. Phyllopodia 2-7 mm long, 5-9 mm wide, 5-10 mm apart. Leaves 1.5-3 m long; petiole dark stramineous, 40-95 cm long, ranurate adaxially; lamina 1-pinnate, 4-7 pair of pinnae, pinnae elliptic, base attenuate, apices caudate, 5-11 cm wide, herbaceous-chartaceous, subsessil, margin cartilaginous, sinuate, indument of scattered, simple branched hairs, mainly along veins; stomata polocytic; costula prominent, primary veins prominent, stramineous or darker than the leaf tissue, 55-60º divergent from the costula, 8-10 mm apart, secondary transversal veins forming 8-12 (-15) primary areoles, primary areoles entire, 3-4 free excurrent veinlets in each areole, simple or furcate; sori terminal, paraphyses not seen, spores 35-45 µm long, 22-27 µm wide.

This species is known from Panamá, Trinidad, Colombia, Venezuela to Bolivia and Brazil. It grows in shady forested areas, from sea level to 2100 m.

REPRESENTATIVE SPECIMENS: PANAMA. Darien: cerro Pirre, 10-20 Jul. 1977, *Folsom 4534* (MO). COLOMBIA. DEL VALLE: Western Cordillera, Río Digua, Quebrada de San Juan, below Queramal, 8 Nov. 1946, *Cuatrecasas 22735* (F, S); Mun. Calima, Campo Alegre, Alto Calima, 29 Aug. 1981, *Silverstone 539* (MO). Cordillera Occidental, Quebrada del Río Blanco, Dec. 1942, *Cuatrecasas 13667* (F, UC); San Antonio, Bogotá, *Lindig 307* (B, F). Cerro Pelado, *Stübel 1252* (B). VENEZUELA. YARACUY: Sierra de Aroa, Cerro Tigre, 10 km of Aroa,30 Mar. 1980, *Liesner & González 9722* (MO); Liesner & Gonzalez 9738 (MO). LARA-YARACUY: dist. Urdaneta and Bolívar, 16-17 Feb. 1985, *Ortega & R. F. Smith 2455* (MO). FALCON: Sierra de San Luis, above Santa María, 10 Jan. 1979, *Werff et al. 126* (MO, UC). ECUADOR. PICHINCHA: Cantón Quito, Reserva Maquipucuna, 13 Sep. 1989, *Webster & Addison 27527* (QCA); San Miguel de los Colorados, Oct. 1893, *Sodiro s.n.* (UC). PASTAZA: Baños (Jivaría), *Stübel 983* (B). PERU. SAN MARTIN: Tarapoto, 4 mi E of Tarapoto, *Woytkowski 35218* (MO, UC). PASCO: Oxapampa, Gran Pajonal, trail to Shumahuani from Chequitavo, 24 Sep. 1983, *D.N. Smith 5212* (MO). JUNIN: Chanchamayo, *Schunke 22* (F); *Schunke 683* (F); *Schunke 913* (F); *Soukup 1089* (F). BOLIVIA. LA PAZ: Polo-Polo, Coroico, Oct. Nov. 1912, *Buchtien 3490* (F, S, US); Larecaja, 6 km N of Consata, 15 Dec. 1981, *Solomon et al. 6574* (MO).

Campyloneurum magnificum is one of two species with pinnate leaves; it is characterized by its elliptic pinnae with caudate apices. During this study all southern Brazilian specimens, except the Glaziou specimen (*Glaziou 1750*), belong to *C. decurrens* and not to this taxa, which occurs in more continental areas in South America.

Together with *Campyloneurum decurrens* form the *C. magnificum* group, that may represent an ancient lineage in the genus.

30. *Campyloneurum minus* Fée, Gen. Fil. 258. 1852. Type. America Austral, *Glaziou s.n.* (holotype, n.s.; isotype RB).

Polypodium herbaceum Christ *in* Schwacke, Pl. Nov. Mineiras 2: 22. 1900. Type. Brazil: Rio de Janeiro, Paineiras, *Schwacke 5384* (holotype P!; isotypes BM!).

Campyloneurum herbaceum (Christ) Ching, Sunyatsenia 5: 263. 1940.

Stem long creeping, green turning black, dark stramineous, not pruinose, 1-2 mm wide. Stem scales dark brown in mass, 2-2-5 mm long, 1.2-1.5 mm wide, ovate, slightly clathrate, slightly bullate, bases auriculate, apices acute or obtuse, the cells oblong or ovate, irregularly arranged, cell walls 8-10 µm thick. Phyllopodia 0.5 mm long, 0.5-2 mm wide, 2-7 mm apart. Leaves 15-40 cm long; petiole stramineous or

dark stramineous, 0.7-8 cm long, slightly ranurate adaxially, convex abaxially; laminae narrowly lanceolate, bases and apices attenuate, 1-2.5 (-4.5) cm wide, herbaceous-chartaceous, margins cartilaginous, slightly sinuate or undulate, indument of adaxially scattered bicellular, simple hairs; stomata polocytic; costa prominent, ranurate adaxially, primary veins prominulous, stramineous or darker in color than the leaf tissue, slightly flexuous, 60-65° divergent from the costa, 5-7 mm apart, secondary veins inconspicuous, forming (3-) 5-7 primary areoles between costa and margin, areoles undivided, 2 free excurrent veinlets in each areole, margins sometimes with free excurrent veinlets; sori medial or subterminal, paraphyses not found, spores 40-45 µm long, 25 µm wide. Figs. 17 f; 39.

This species occurs in Brazil, Argentina and Paraguay, where it grows between 100 m and 1800 m elevation.

REPRESENTATIVE SPECIMENS: BRAZIL. MINAS GERAIS: Carangola, trail Araponga to fazenda de Grama, 27 Jan. 1930, *Mexia 4243* (B, F, MO, UC). RIO DE JANEIRO: Guanabara, Paineiras, near Pedra de Beijo, 15 Nov. 1965, *Carauta 285* (F); Rio de Janeiro, 1873, *Mosén 66* (B); Guanabara, 14 Feb. 1945, *Occhioni 20* (F); Parque Nacional Serra dos Orgãos, 6 Aug. 1961, *Pabst 5653a* (B, F); vic. Paineiras, Corcovado, 14 Nov. 1928, *Smith 1213* (GH); Serra dos Orgãos, *Vauthier 605* (F). SÃO PAULO: km 78 on road 116, between Curitiba and São Paulo, 5 Jan. 1974, *Conrad & Dietrich 1980* (MO); São Paulo, Serra da Cantaeira, 18 Jul. 1960, *Eiten et al. 2162* (F); Caraguatuba, 3.5 km NNW of Caraguatuba, 20 May 1961, *Eiten & Eiten 2840* (F); Cunha, 11-14 Feb. 1981, *Filho 528* (MO), Paranapiacaba, 4 Oct. 1956, *Handro 634* (US); Serra da Bocaina, Casa do Peixe, 8 Feb. 1959, *Pabst 4702* (B); 11 Feb. 1959, *Pabst 4786* (B). SANTA CATARINA: Mun. Florianópolis, Rio Tavares, 13 Mar. 1952, *Smith & Reitz 6181* (MO, US). PARANÁ: Iguaçú falls, 16 Sep. 1976, *Davis & Shepherd 60593* (F); Mun. Morretes, Estação Marumbi, 23 Nov. 1984, *Kummrow & Hatschbach 2529* (UC); Estação Marumbi, 1 Feb. 1986, *Kummrow & Cordeiro 2704* (UC).
ARGENTINA. MISIONES; Iguazu, *Osten 7263* (S).
PARAGUAY. ITAPUA: El Tirol, 19.5 km NNE of Encarnación, 16 Oct. 1981, *Foster 81-31* (UC); San Bernandino, 10 Oct. 1893, *Lindman 2191* (F, S). PARAGUARI: Parque Nacional Ybicui, pond Guaraní, 21 Dec. 1980, *Abrell 32* (MO). Cordillera de Altos, 7 Aug. 1902, *Fiebrig 13a* (B, F). Cordillera Mbatobi, Apr. 1881, *Balansa 2882* (B). Without locality. 1885-1895, *Hassler 421* (K).

Campyloneurum minus is characterized by its slightly bullate, ovate lanceolate stem scales. It belongs to the *C. repens* group.

31. *Campyloneurum nitidissimum* (Mett. *in* Triana et Planchon) Ching, Sunyatsenia 5: 263. 1940.
Polypodium nitidissimum Mett. *in* Triana *et* Planchon, Ann. Sc. Nat. n.s. 5: 258. 1864. Type. Colombia: San Antonio, Jan. 1861, *Lindig 363* (holotype B!; isotypes BM!, K!, US!).

Stem long-creeping, not pruinose, 5-10 mm wide. Stem scales dark brown in mass, linear or narrowly ovate, (5-) 7-15 mm long, (0.5-) 1-1.5 mm wide, scales non-clathrate, the cells oblong, marginal cell walls 8 µm thick, central cell walls 12-16 µm thick, sometimes with hairs on the margins 5-7 m long, cell lumen dark yellow. Phyllopodia 0.5-1 mm long, 4-6 mm wide, 5-7 mm apart. Leaves entire; petiole with or without wings, slightly ranurate on the adaxial side, convex on the abaxial side, glabrate; lamina narrowly lanceolate or elliptic-lanceolate, chartaceous or coriaceous, margins cartilaginous, plane or scarcely revolute, sinuous, bases attenuate or abruptly cuneate then decurrent on the petiole, indument of bicellular hairs, entire, inconspicuous, scattered; stomata polocytic, rarely anomocytic; costa prominent, slightly ranurate adaxially, plane or angulate abaxially, primary veins prominent, secondary veins forming 7-15 primary areoles, primary areoles asymmetrically divided, 3-4 simple or furcate excurrent veinlets in each primary areole, 1-2 veinlets connected to the transverse veins forming asymmetrical secondary areoles; sori 2-4 rows between primary veins, sori subterminal or compital; paraphyses not seen.

Campyloneurum nitidissimum grows mainly as a terrestrial plant in disturbed forests. It belongs to the *Campyloneurum brevifolium* group. Morphological variation within this taxon is

found in lamina size and in the division of the primary areoles. These variations appear to be continuous, and they may be a response to environmental conditions, since those specimens growing in open areas have thicker and narrower leaves compared to those growing in forests. Based on the available information, two varieties are recognized, although future studies may allow the recognition of two different species. The typical variety is characterized by narrow lanceolate leaves, and with primary veins more than 70º divergent from the costa. The variety *latius* has more elliptical lanceolate leaves, and primary veins 70º or less divergent from the costa.

- Lamina herbaceous-chartaceous, usually more than 5 cm wide. var. *latius*
- Lamina subcoriaceous, usually less than 5 cm wide. var. *nitidissimum*

31a. *Campyloneurum nitidissimum* var. *nitidissimum*

Stem 10 mm wide, stem scales 10-14 mm long, 1-1.5 mm wide. Leaves 60-90 cm long; petiole dark stramineous, 17-25 cm long; lamina narrowly lanceolate, bases attenuate, apices acuminate, 4-6 cm wide, subcoriaceous; primary veins 75-80º divergent from the costa, 4-9 mm apart, secondary transverse veins forming 7-12 primary areoles between the costa and margin; spores 58-60 µm long, 35-40 µm wide. Fig. 42.

The typical variety is known from Colombia, Peru and Bolivia, where it grows in open areas above 1500 m elevation.

REPRESENTATIVE SPECIMENS: COLOMBIA. CAUCA: Cordillera Central, western side, Hoya del Río Palo, 19 Dec 1944, *Cuatrecasas 19499* (F, GH, MO, US).
PERU. HUANUCO: Muña, *Macbride 4040* (F, GH, US). Without locality: Peruvian Andes, *Ruiz 12* (B).
BOLIVIA. LA PAZ: Murillo, 44 km below Lago Zongo dam, vic. of Cahua hydroelectric plant, 12-15 Sep. 1983, *Solomon 10758* (MO).

31b. *Campyloneurum nitidissimum* var. *latius* (Rosenst.) B. León, Fieldiana Bot. n.s. 1993: in press.

Polypodium nitidissimum Mett. var. *latius (latior)* Rosenst., Repert. Spec. Nov. Regni Veg. 12: 474. 1913. Type. Bolivia: Yungas septentrionalis, Polo Polo, prope Coroico, 900 m, *Buchtien 3526* (holotype not located; isotypes F!, S!, US!).

Stem 5-10 mm wide, stem scales (5-) 7-15 mm long, (0.5-)1-1.5 mm wide. Leaves 60-110 cm long; petiole dark stramineous, 2-7 cm long, with wings 1.5-4 mm wide, lamina lanceolate or elliptic-lanceolate, bases abruptly cuneate or attenuate, then decurrent on the petiole, apices usually caudate, (4.5-) 6.5-13.5 cm wide, herbaceous-chartaceous or chartacea; primary veins (60°-) 65-70° divergent from the costa, (3-) 5-7 (-10) mm apart, secondary transverse veins forming 9-15 areoles between the costa and margin; spores 50-60 µm long, 35-40 µm wide. Figs. 6 a; 42.

This variety is found in Colombia, Ecuador, Peru, and Bolivia. On abundant humus, usually as a terrestrial plant, although sometimes it has been found as a climber, in forested areas between 100 m and 2000 m elevation.

REPRESENTATIVE SPECIMENS: COLOMBIA. TOLIMA: Alto del Consuelo, Honda, Jul. 1923, *Ariste 997* (F, GH). CUNDINAMARCA: near bridge San Antonio de Tena, 10 May 1940, *Cuatrecasas 8270* (F). CAUCA: Central cordillera, basin of Río Palo, betweenTacueyó and La Tolda, 19 Dec. 1944, *Cuatrecasas 19499* (F, GH, US).
ECUADOR. NAPO: Rio Waui Si Ayá, a northern tributary to Río Aguarico, 8 Aug. 1980, *Brandbyge et al. 32661* (AAU); Río Yasuní, Garza Cocha, 12 Apr. 1983, *Lawesson et al. 43536* (AAU). PASTAZA: Río Bufeo, northern tributary of Río Bobonaza, 19 Jul. 1980, *Øllgaard et al. 34779* (AAU, QCA). PICHINCHA: between Nono and Nanegalito, NW of Quito, 4 Sep. 1976, *Croat 38838* (UC). ZAMORA-CHINCHIPE: Shaime at junction of Río Nangaritza. 7 Dec. 1990, *Øllgaard 98440* (QCA).
PERU. HUANUCO: near confluence of Río Cayumba with río Huallaga, 10 Oct. 1936, *Mexia 8272* (BM, F, S, UC, US). PASCO: Oxapampa, canyon of Huancabamba, above Quebrada Honda, 17 Aug. 1985, *León 667* (F, USM). JUNIN: Pichis trail, between Miriatiriani and Yessup, 28 Jun.-8 Jul. 1929, *Killip & Smith 26221* (US); road to Tarma, before Carpapata, 1 Oct. 1982, *León 335* (USM), *León 340* (F, GH, USM); Yaupe, 2 Jul. 1961, *Woytkowski 6401* (MO, US); Manto

and Yaupi, 11 Jul. 1961, *Woytkowski 6542* (MO); Yunguy, 14 Jul. 1961, *Woytkowski 6592* (MO); Yucapata, 17 Jul. 1961, *Woytkowski 6657* (MO). MADRE DE DIOS: Manu, Atalaya, Hacienda Amazonía, 2-3 km W of village, 12 Dec. 1983, *Foster & Waechter 7453* (F). PUNO: San Gavan, *Lechler 2374* (B). BOLIVIA. LA PAZ: Nor Yungas, Polo-Polo, Coroico, Oct-Nov. 1912, *Buchtien 3384* (MO); Larecaja, 6-10 km E of Consata, along new road, 15 Dec. 1981, *Sperling et al. 5451* (MO); Larecaja, 6 km N below Consata, 15 Dec. 1981, *Solomon 6579* (MO).

Campyloneurum nitidissimum var. *latior* has been often misidentified in herbaria as *C. coarctatum* (Kunze) Fée, but it has a much wider stem, with closely spaced phyllopodia, and leaves more than 40 cm long.

32. *Campyloneurum nitidum* (Kaulf.) C. Presl, Tent. Pterid. 190. 1836.
Polypodium nitidum Kaulf., Enum. Fil. 92. 1824. Type. Brazil: *Chamisso s.n.* (B!).
Campyloneurum leuconeuron Fée, Crypt. Vasc. Brésil 113. 1869. Type. Brazil: *Glaziou 1001* (holotype, P!; isotype RB!).
Polypodium phyllitidis f. *minus* (*minor*) Hieron., Bot. Jahrb. Syst. 22: 405. 1896. Type. Uruguay: Misiones, Paggi at Río Alto Uruguay, Aug. 1887, *Niederlein 1947* (holotype, B!).
Polypodium phyllitidis f. *majus* (*major*) Hieron. *ex* Hicken, Rev. Mus. La Plata 15: 272. 1908. Cyted Syntypes. Argentina: Misiones, Ruins at Candelaria, 20 Feb. 1883, *Niederlein s.n.* (B!); El Primer Misionero, von Hernandez, Puck and Fernández, *Niederlein 237* (B!). Lectotype (chosen here) Argentina: Misiones, Arroyo Ñacanguazú, 12 Feb. 1883, *Niederlein* (B!)
Campyloneurum majus (*major*) (Hieron. *ex* Hicken) Lellinger, Amer. Fern J. 78: 26. 1988.

Stem short-creeping, black or stramineous, not pruinose, 3-4 mm wide. Stem scales brown in mass, adpresed or subadpressed, 1.8-2 mm long, 1-2 mm wide, broadly ovate, bases auriculate, apices obtuse, slightly clathrate, cells broadly oblong, cell walls 4-8 µm thick. Phyllopodia 2-3.5 mm long, 1.5-4 mm wide, 2-6 mm apart. Leaves 25-75 cm long; petiole stramineous or dark stramineous, 1.7-8 (-9.5) cm long, ranurate adaxially, with sparse bicellular, simple hairs; lamina lanceolate or narrowly lanceolate, bases and apices attenuate, 2-7 cm wide, margins cartilaginous, repand or slightly undulate; costa prominent, primary veins prominulous or prominent, stramineous on both sides of the lamina, 60-65º divergent from the costa, secondary veins, slightly prominulous, sometimes stramineous, forming (4-) 5-7 primary areoles between the costa and margin, entire or symmetrically divided, 1-2 free excurrent veinlets on each secondary areole; sori medial or subterminal, paraphyses dendritic, shorter than the sporangia, 11-16 µm long, spores 64 µm long, 40 µm wide. Chromosome number: n=37 (as *C. phyllitidis* by Smith & Foster, 1984). Figs. 17 g; 40.

This species is known from the southern part of South America, from southern Bolivia to Argentina, and southern Brazil, where it grows as a terrestrial between 500 m and 1100 m elevation.

REPRESENTATIVE SPECIMENS: BOLIVIA. COCHABAMBA: Cavernas del Repechón, Parque Nacional Carrasco, 9 Oct 1996, Kessler 8336 (LPB). BRAZIL. RIO GRANDE DO SUL: Pelotas, 12 May 1959, *Brauner 74* (F); Pelotas, 22 May 1959, *Costa-Saco 1248* (F); Rio Grande do Sul, Jul. 1940, *Eugenio & Leopoldo 1499* (F); São Leopoldo, 10 Aug. 1930, *Flach 936* (BM, MO); Porto Alegre, 15 Oct. 1982, *Lindman 499* (S); 1865, *Page s.n.* (F); 1897, *Reineck & Czermack 35* (F); Esmeralda, Estação Ecológica de Aracuri, 23 Aug. 1981, *Waechter 1843* (F); Caxias do Sul, Conceição, 24 Oct. 1987, *Wasum et al. 3422* (F). RIO DE JANEIRO: Macaé, Serra do Frade, perto do Rio São João, 18 Oct. 1970, *Carauta 1217* (F); Serra dos Orgãos, entre a Barragem e o Abrigo no. 1, 28 Mar. 1971, *Carauta 1331* (F); Parque Nacional Serra dos Orgãos, 6 Aug. 1961, *Pabst 5662* (B, F); Serra dos Orgãos, 9 Aug. 1964, *Pabst 8139* (F); Mun. Petrópolis, road from Araras to Vale de Videiras, 22 Apr. 1980, *Plowman & Martinelli 10168* (F); Serra dos Orgãos, Teresópolis, 31 Jan. 1983, *Simonis & Martinelli 25* (UC); SE side of Itatiáia, Riberão Campo Belo, 31 Oct. 1965, *Tryon & Tryon 6619* (F). SÃO PAULO: km 78 of road 116, between Curitiba and São Paulo, 5 Jan. 1974, *Conrad & Dietrich 1980* (MO); Ipanema, 29 Sep. 1925, *Freine & Azevedo 153* (UC); Campos do Jordão, Jun. 1947, *Leite 3387* (MO), *Leite 3492* (MO); Estação Biológica Alto da Serra, 14 Feb. 1929, *L.B. Smith 1891* (GH, US). PARANA: banks of the Rio do Santa, between Curitiba and Joinville, 5 Jan.

1974, *Conrad & Dietrich 2052* (MO); Jaguariaíva, 26 Jun. 1910, *Dusén 10057* (BM, S, US); Jacareí, 18 Jul. 1914, *Dusén 15311* (F); Jaguariahyba, 28 Feb. 1915, *Dusén 17354* (F, UC); Mun. Lapa, Rio Passa Dois, 30 Sep. 1969, *Hatschbach 22255* (UC); Mun. Balsa Nova, Serra Santa Ana, 1 Nov. 1969, *Hatschbach 22780* (UC); Mun. Ortiguera, Rio do Barreiro, 7 Aug. 1970, *Hatschbach 24526* (UC); Mun. Catanduvas, 10 Oct. 1974, *Hatschbach & Pelanda 35134* (MO); Jacareí, 20 Aug. 1914, *Jönsson 97a* (F); Mun. Tijucas do Sul, Campina, 46 km S de Curitiba, 14 Feb. 1978, *Krapovickas & Cristóbal 33640* (MO); Mun. Quedas do Iguaçú, 20 Aug. 1974, *Kummrow & Golte 603* (UC); Mun. Lapa, São Carlos, 13 Aug. 1982, *Oliveira 625* (UC); Mun. Quatro Barras, Rio Taquarí, Damata, 25 Aug. 1982, *Oliveira 657* (UC); Mun. São José dos Pinhais, 4 Sep. 1986, *Silva & Silva 182* (UC). SANTA CATARINA: Oct. 1904, *Haerchen s.n.* (Rosenst. 115, S); Frinvihe, 1 Jul. 1901, *Schmalz 8* (F, S); Joinville, 17 Jul. 1901, *Schmalz 49* (F, MO); Joinville, 30 Jul. 1901, *Schmalz 76* (F, MO).
ARGENTINA. CORRIENTES: Santo Tomé, estancia Garruchos, 8 Feb. 1972, *Krapovickas et al. 21365* (QCA). MISIONES: Dep. Libertador General San Martin, Gruta 3 de Mayo, 12 Jan. 1970, *Krapovickas & Cristóbal 15635* (MO, UC); Dep. San Pedro, 20 Jul. 1957, *Montes 27453* (UC); San Pedro, 80 km E of El Dorado, 22 Jan. 1973, *Schinini & Fernandez 5971* (F).
URUGUAY. TACAUREMBO: Gruta Helechos, 28 Sep. 1928, *Herter 1231* (MO, S, UC); Tacuarembo, 24 Aug. 1907, *Herter 3538* (B), Herter 3739 (B); Gruta de los Cuervos, Herter 10225 (B). TREINTA Y TRES: Quebrada de los Cuervos, Serranías de Yerbal, Apr. 1936, *Legrand 716* (F).
PARAGUAY. AMAMABAY: Cerro Corá, 3 Sep. 1978, *Herbst s.n.* (F). ALTO PARANA: 2.8 km W de Puerto Stroessner, *Krapovickas 13403* (MO). ITAPUA: Hotel El Tirol, 19.5 km by road NNE Encarnación, 8 Sep. 1978, *M. Foster 78-(2)-17* (UC), 15 Oct. 1979, *Foster 79-58* (MO). MISIONES: Santiago, Estancia La Soledad, 13 Dec. 1969, *Pedersen-Myndel 9548* (UC). CAAGAZU: Guayaquí, 22 May 1987, *Zardini et al. 2458* (MO). ALTO PARAGUAY: San Pedro, 13 Sep.1959, *Woolston 1118* (UC). GUAIRA: Cordillera Ybytyruzú, cerro Peró, 23 Jul. 1989, *Zardini & Velasquez 13903* (MO). CAAZAPA: Tavai, 29 Oct. 1988, *Basualdo 1688* (MO). Without locality. Cordillera de Altos, 7 Aug. 1902, *Fiebrig 13* (B, F); Río Apa, und Río Aquidaban, 1908-1909, *Fiebrig 5079* (BM); Tobaty, Sep. 1903, *Hassler 6283* (BM, S, UC); Caaguazuensis, 1905, *Hassler 9077* (BM, S, UC); Sapucay, Aug. 1913, *Hassler 12241* (BM, GH, MO, S, UC); 1931, *Jorgensen 4602* (MO, S, US).

Campyloneurum nitidum is characterized by narrow lanceolate leaves, attenuate at both ends, and by stem scales with obtuse apices. It belongs to the *C. phyllitidis* group. This species has been confused with *C. phyllitidis*, but it is smaller, with a narrow stem and with an attenuate leaf apex. In *Campyloneurum nitidum* there are two forms, one has very narrow leaves with the divergent angle of the primary veins less than 55º and they belong to the "leuconeuron" leaf type, and the second has broader leaves with the divergent angle of the primary veins more than 60º and it corresponds to the "nitidum" type; however they are not recognized as different species because of the presence of many intermediate specimens.

33. *Campyloneurum oellgaardii* B. León, sp. nov. ined. Type. Ecuador, Carchi, Cerro Golondrinas, 0º52'N, 78º07'W, 21 Dec. 1987, *Hoover 2211* (holotype MO, isotype QCA).

Species cum habitu *Campyloneurum inflatum*, a qua differt rhizomate longe repente, 5 mm crasso, atrofusco, dense paleaceo, squamis adpressis, brunneolis, foliis amplissimis.

Stem long-creeping, black, not pruinose, 5 mm wide. Stem scales brown in mass, broadly ovate, adpressed, 3-4 mm long, 2-2.5 mm wide, bases auriculate, apices acuminate, margins dentate, scales slightly clathrate, the cells oblong or broadly oblong, cell walls 6-9 µm wide, walls of central cells brown dark, walls of marginal cells yellowish or brownish, cell lumina transparent. Phyllopodia 10-20 mm apart. Leaves erect, 100 cm long, petiole 30-40 cm long, dark stramineous; lamina elliptic, 21 cm wide, herbaceous-chartaceous, base cuneate, apex acuminate, margins cartilaginous, sinuate, leaves puberulous, indument of inconspicuous, bicellular glandular hairs, scattered abaxially; stomata polocytic rarely copolocytic; costa prominent, slightly angular abaxially; primary veins prominent, 75º divergent from the costa, straight, lighter in color than the adjacente tissue, 7-9 mm apart, secondary veins slightly prominulous on both sides of the lamina, transverse secondary veins forming 19 primary areoles between the costa and margin, primary areoles undivided, with 2-3 excurrent veinlets, sometimes with one recurrent veinlet in the areoles close to the margin, veinlets entire, free.

Sori subapical on the excurrent veinlet; paraphyses and spores not seen. Fig. 50.

This species is found in northern Ecuador, at 1200 m. It is known only from the type collection.

Campyloneurum oellgaardii is closely related to *C. inflatum*; they can be distinguished because the former has a 5 mm wide stem; adpressed, broad lanceolate stem scales with undifferentiated margins; and elliptic lanceolate leaves reaching 1.5 m long. The latter species has a 2-3 mm wide stem; spreading, lanceolate stem scales with differentiated margins; and elliptic leaves less than 50 cm long.

This species is named in honor of B. Øllgaard, who with his work on the Ecuadorean plants, especially with the pteridophytes, is contributing to the knowledge of that rich flora.

34. *Campyloneurum ophiocaulon* (Klotzsch) Fée, Gen. Fil. 258. 1852.

Polypodium ophiocaulon Klotzsch, Linnaea 20: 401. 1847. Type. Peru: Junín, Tarma, *Dombey 41* (holotype, B!; photo of B, BM!).

Stem dark stramineous, black, not pruinose, (2-) 2.5-4 mm wide. Stem scales light brown in mass, 3-4 mm long, 2 mm wide, ovate, bases peltate, apices obtuse, scales clathrate, the cells oblong, basal and marginal cells irregular arranged, central cells along main axes of the scale. Phyllopodia 1-2 mm long, 2-3 mm wide, 10-20 mm apart. Leaves 30-50 cm long; petiole dark stramineous, 2.5-4.5 cm long; lamina broad lanceolate, obovate or narrow lanceolate, bases attenuate, apices acuminate, 3.5-7 cm wide, chartaceous, margins cartilaginous, undulate, indument of scattered, inconspicuous, bicellular hairs; stomata not seen; costa prominent, primary veins 65-80^{o} divergent from the costa, stramineous, prominulous, straight, 6-7 mm apart, secondary veins slightly prominulous, inconspicuous, transverse veins forming 8-11 primary areoles between the costa and margin, primary areoles undivided, 2 free excurrent veinlets in each areole; sori medial, paraphyses not seen, spores 50 µm long, 35 µm wide. Fig. 43.

This species is distributed from Colombia and Venezuela to Bolivia, where it grows as an epiphyte mostly between 1500 m and 2500 m elevation.

REPRESENTATIVE SPECIMENS: COLOMBIA. SUR DE SANTANDER: along highway between Pamplona and Bucaramanga, Mun. Tona, Corregimiento Corcova, Vereda La Mariana, 5 May 1983, *Croat 56507a* (MO). VALLE: San Antonio, 18 May 1939, *Alston 8609* (MO). CALDAS: Cordillera Occidental, Pueblo Rico, 21 Dec. 1945, *Sneidern 5258* (F), 11 Jan. 1946, *Sneidern 5437* (F, S). VALLE: Cordillera Occidental, al sur de las Brisas, 27 Oct. 1946, *Cuatrecasas 22663* (F). CAUCA: Munchique, 21 Apr. 1939, *Alston 8175* (MO); Carpinterías, between cerros Munchique and Altamira, 15 Jul. 1939, *Cuatrecasas & Perez-Arbelaez 6136* (F) . Cerro Gualcala, above Piedra Ancha, *Lehmann 5012* (F).
VENEZUELA. TACHIRA: along Quebrada Agua Azul, S of El Reposo, 14 km SE of Delicias, 22-23 Jul. 1979, *Steyermark & Liesner 118424* (MO). Los Venados, Caracas, Aug. 1939, *Elias 21* (F).
ECUADOR. CARCHI: Chical, 16 Nov. 1983, *Barfod et al. 48644* (QCA); Valle de Maldonado, km 60 on road Tulcán-Maldonado, 18 May 1973, *Holm-Nielsen et al. 5775* (F, MO). NAPO: 3.5 km NW of Borja, 20 Sep. 1980, *Holm-Nielsen et al. 26325* (QCA); Francisco de Orellana, near Cañón de los Monos, 1987, *Zak & Jaramillo 3604* (F, MO), *Zak & Jaramillo 3607* (F, MO); Baeza path, 1 km SW of the village,20 Oct. 1976, *Øllgaard & Balslev 10238* (AAU, USM); road Baeza-Tena, in the pass S of Río Salado, 8 Aug. 1980, *Øllgaard et al. 35766* (AAU, QCA), *Øllgaard et al. 35786* (AAU, QCA); Cerro Huacamayos, on road Baeza-Tena, 9-10 Aug. 1980, *Øllgaard et al. 35921* (F, QCA, UC). PICHINCHA: Nono-Nanegalito, N of Cerro Pichincha, 9 May 1982, *Balslev & Boom 2500* (QCA) along road Nono and Nanegal, NW of Quito, 11-12 km NW of Nono, 4 Sep. 1976, *Croat 38818* (MO); km 17 Nono-Tandapaya, road along Río Alambi, 14 May 1981, *Dodson et al. 10793* (F, MO); Estación Científica Guajalito, along road Chiriboga-El Tránsito, 10 Jun. 1990, *Øllgaard 90410* (QCA). TUNGURAHUA: Colonia Mexico, 4 km from Río Topo, 5 Mar. 1969, *Lugo 647* (F). PASTAZA: ca. 5 km E of Mera, 30 Ju;. 1980, *Øllgaard et al. 35581* (AAU, QCA). SANTIAGO-ZAMORA: between La Esperanza and Santa Ana, 15 Feb. 1944, *Acosta-Solís 7436* (F); W side of Río Valladolid, 15 Oct. 1943, *Steyermark 54722a* (F). Without locality: *Mille s.n.* (MO).
PERU. CAJAMARCA: Cutervo, San Andrés de Cutervo, above Saucedal, Chorro Blanco, 3 Aug. 1988, *Diaz & Osores 2963* (MO). AMAZONAS: Bagua, ca. 20

km E of la Peca, 22 Jul. 1978, *Barbour 2812* (AAU, F, MO, UC); Bagua, Cordillera Colán, SE of La Peca, 17 Oct. 1978, *Barbour 4188* (F, MO). SAN MARTIN: Venceremos, near Amazonas border, km 291 on Rioja-Pomacocha road, 12 Feb. 1984, *Gentry et al. 45488* (MO); Rioja, Pedro Ruiz-Moyobamba road, km 390 Venceremos, 29-31 Jul. 1983, *D.N. Smith 4498* (F, MO, NY, UC). HUANUCO: Pampayacu, 28 Jan. 1927, *Kanehira 119* (GH, US); Cushi, 19-23 Jun. 1923, *Macbride 4841* (F); La Divisoria, ca. 25 km NE of Tingo María, 4 Jul. 1984, *Moran & Fernandez 3693* (MO, UC); Leoncio Prado, dist. Hermilio Valdizán, La Divisoria, from Pumahuasi to La Cumbre, 26 Jun. 1978, *Plowman & Schunke 7414* (F); Leoncio Pardo, km 35 on road between Tingo María and Pucallpa, 3 Jun. 1981, *Sullivan & Young 1147* (F, MO). PASCO: Oxapampa, Ulcumanu, SW of Oxapampa, road to María Teresa and Llaupi, 31 Dec. 1983, *Foster et al. 7682* (MO); Oxapampa, 31 Jan. 1983, *León 495* (F, USM); Oxapampa, 5 km SE of Oxapampa, *D.N. Smith 2914* (F, MO). JUNIN: Villa Amoretti, 1960, *Kanehira 524* (GH); in the area of Pichita Caluga, 1-3 May 1957, *Walden 26* (BM). UCAYALI: La Divisoria, ca. 25 km NE of Tingo María, *Moran & Fernández 3693* (MO). CUSCO: valle de Accobamba, Aug. 1922, *Bues 866* (US); 28 May 1915, *Cook & Gilbert 951* (US); Quillabamba, Abra de Málaga, 8-9 Mar. 1971, *Ellenberg 4739* (LPB); ca. 20 km of Pampa Hermosa, 25 Jul. 1978, *Ellenberg 9122* (LPB); valle de San Miguel,near bridge Media Naranja, 20 Jul. 1928, *Herrera 2050* (BM, C, US); Machu Picchu, Oct. 1931, *Herrera 3298* (US); Paucartambo, trail below Buenos Aires, km 136 road Acjanaco-Pilcopata, 16 Feb. 1990, *León 2183* (F, USM), 17 Feb. 1990, *León 2195* (F, USM); Urubamba, above the first waterfall of the Río Mandor, 2.5 km from Machu Picchu, 5 Jun. 1982, *Peyton & Peyton 452* (MO); La Convención, Huayopata, 3 km from village of Incatambo, 31 Jul. 1982, *Peyton & Peyton 844* (GH, MO); Urubamba, Machu Picchu, hillside called Puncuyoj, 10 km SW of Incatambo, 3 Oct. 1982, *Peyton & Peyton 1365* (GH, MO); La Convención, Amaibamba, 23 Nov. 1950, *Vargas 9804* (UC); La Convención, Potrero, Garavito, 13-14 May 1960, *Vargas 13182* (GH).
BOLIVIA. LA PAZ: Sud Yungas, Huancané, 8 Mar. 1980, *Beck 3065* (F, LPB), 9 Mar. 1980, *Beck 3114* (F, LPB); Nor Yungas, Coroico-Yolosa, 1 Apr. 1982, *Beck 7537* (F); Nor Yungas, Polo Polo, Coroico, 1912, *Buchtin 3534* (F); Sud Yungas, La Paz-Chulumani road, 12 km E of Chuspipata, 1 Aug. 1989, *Fay & Fay 2473* (LPB); Nor Yungas, 14.4 km NE Chuspipata, 21 Oct. 1982, *Solomon 8627* (MO, UC); Murillo, 30.5 km N of dam at Lago Zongo, 16-17 Dec. 1982, *Solomon 9103* (MO); Carrasco, Serranía de Bella Vista, 31 Oct. 1984, *Solomon & Nee 12620* (MO); Nor Yungas, 12.8 km NE de Chuspipata, 11 Nov. 1987, *Solomon 17362* (MO, NY). COCHABAMBA: Chapare, road to San Onofre, 1 Nov. 1979, *Foster 79-145* (MO). Without locality: *Bang 2395* (BM, F); Río Tocorani, Jul. 1911, *Herzog 2310* (B, S, UC).

Campyloneurum ophiocaulon is closely related to *C. repens*, but it differs by the ovate lanceolate scales with obtuse apices. The studied specimens of *Campyloneurum ophiocaulon* are mostly distributed above 1500 m elevation. However, two specimens (*Zak & Jaramillo 3604* and *Zak & Jaramillo 3607*) came from 250 m elevation, a very unusual distribution for the species.

35. *Campyloneurum oxypholis* (Maxon) Ching, Sunyatsenia 5: 263. 1940.
Polypodium oxypholis Maxon, J. Wash. Acad. Sci. 14: 140. 1924. Type. Haiti: Morne de Brouet, near Furcy, 13 Jun. 1920, *Leonard 4782* (holotype US!, photo of US, BM!, F!; isotypes B!, BM!, C!).

Stem creeping, 2-2.5 mm wide. Stem scales brown in mass, spreading, 5-6 mm long, narrowly ovate, bases auriculate, apices acuminate, clathrate, the cells oblong, with yellowish lumina, cell walls 14-24 µm thick. Phyllopodia 1.5 mm high, 5-7 mm apart. Leaves 30-40 cm long; petiole stramineous, 2-5 cm long; lamina lanceolate, bases and apices attenuate, 2-3 cm wide, herbaceous-chartaceous, margins sinuate, indument and stomata not seen; costa prominent, primary veins slightly prominulous on both surfaces of the lamina, 45-50^{o} divergent from the costa, secondary veins immersed, darker than the leaf tissue, forming 4-5 primary areoles between the costa and margin, primary areoles with 1-3 included veinlets, undivided or symmetrically divided; sori medial, paraphyses not seen, spores 85-90 µm long, 50 µm wide. Fig. 43.

This species is found in Haiti.

EXAMINED SPECIMENS: HAITI. Morne des Commissaires, Massif de la Selle, 4 Sep. 1926, *Ekman 6884* (B, S, US).

Campyloneurum oxypholis is a rare species, closely related to *C. vulpinum*. It belongs to the

Campyloneurum vulpinum group.

36. *Campyloneurum pascoense* R. Tryon & A. Tryon, Rhodora 84: 125. 1982. Type. Peru: Pasco (as Junín), Oxapampa, *Soukup 2340* (holotype GH!).

Stem short-creeping, black or dark stramineous, not pruinose, 10-30 mm wide. Stem scales brown in mass, 8-10 mm long, 4 mm wide, broadly ovate to ovate, pseudopeltate, bases auriculate, apices acuminate, the cells oblong, central cell walls 8-16 µm thick, marginal cell walls 4-5 µm thick. Phyllopodia 6-10 mm long, 8-10 mm wide, 20 or more mm apart. Leaves 1.50-2 m long; petiole brownish, 8-14 (-75) cm long, ranurate adaxially; lamina lanceolate, bases attenuate or narrow cuneate, apices long acuminate, 10-20 cm wide, chartaceous, margins cartilaginous, sinuate, indument not seen; hypostomatic, stomata polocytic; costa prominent, sometimes with scattered scales abaxially, similar to those on the stem, primary veins prominent, 70-75º divergent from the costa, stramineous, straight, (6-) 9-11 mm apart, secondary veins prominulous, stramineous, forming 12-20 primary areoles between costa and margin, costal areole with 1 free excurrent veinlet, simple or furcate; non-costal primary areole assymmetrically divided with 3-7 excurrent veinlets, 1-2 veinlets forming 2-4 assymmetrical secondary areoles, secondary areoles with 1-3 simple or furcate veinlets, these veinlets forming tertiary areoles; sori subterminal or compital, paraphyses simple, unbranched, spores (50-) 60-65 (-70) µm long, (30-) 35-40 µm wide. Figs. 14 k; 18 b; 19 b; 44.

This species is distributed from Colombia and Ecuador to Bolivia, where it grows between 1500 m and 2500 m elvation, usually as a terrestrial in disturbed forests.

REPRESENTATIVE SPECIMENS: COLOMBIA. SANTANDER: Jan. 1878, *Kalbreyer 451* (B). ECUADOR. GUAYAS-CAÑAR-CHIMBORAZO-BOLIVAR: near village of Bucay, 8-15 Jun. 1945, *Camp E-3688* (F, UC, US). NAPO: road Baeza-Tena, 8 km from Baeza, 28 Oct. 1976, *Balslev & Madsen 10420* (AAU); Cantón Quijos, 28 mi E of Baeza, 29 Jul. 1974, *Plowman et al. 3941* (S); Río Panteor, SW of Borja, 22 Sep. 1980, *Holm-Nielsen et al. 26769* (AAU, QCA); 1 km SW of Baeza,20 Oct. 1976, *Øllgaard & Balslev 10239* (AAU); road Baeza-Lago Agrio, ca. 114 km from Lago Agrio, 8 Aug. 1980, *Øllgaard et al. 35778* (AAU, QCA), *Øllgaard et al. 35788* (AAU, QCA). PICHINCHA: road Quito-Chiriboga-Empalme, km 50, sector Zapadores, 21 Jul. 1987, *Zak & Jaramillo 2199* (F). ZAMORA-CHINCHIPE: above Valladolid,,on road to Yangana, 1 feb. 1985, *Harling & Andersson 21397* (QCA). Without locality: Baños, Rio de Machai, *Stübel 863* (B). PERU. CAJAMARCA: Chota, Huambos, 10 Sep. 1956, *Soukup 4488* (US). AMAZONAS: Bagua, Colán, SE of La Peca, 17 Oct. 1978, *Barbour 4187* (F). SAN MARTIN: Mariscal Cáceres, Parque Nacional Río Abiseo, Río Montecristo, Gran Pajatén ruins, 13 Aug. 1986, *Young 4323* (NY). HUANUCO: Huacahi, near Muña, 20 May-1 Jun. 1923, *Macbride 4082* (F, US); Huánuco, km 468 on Lima-Tingo María road, above San Miguel Chinchao, 2 Jun. 1981, *Young & Sullivan 619* (MO, NY, UC). PASCO: Oxapampa, Cordillera Chanachaga, road over shoulder of Cerro Pajonal, 9 Oct. 1982, *Foster & Smith 9071* (F, MO); Oxapampa, camino a Quebrada San Alberto, 12 Aug. 1985, *León 636* (F, GH, USM); 5 km SE of Oxapampa, 24 Dec. 1983, *D.N. Smith 5361* (F, MO, UC). AYACUCHO: San Miguel, Urubamba valley, 10 Jul. 1915, *Cook & Gilbert 1756* (US). CUSCO: Machu Picchu station, 5 Nov. 1957, *Hutchison 1760a* (UC); Urubamba, Jan. 1936, *Soukup 173* (F). BOLIVIA. LA PAZ: Coroico, 1912, *Buchtien 3526* (F); Murillo, Zongo valley, 0.6 km up valley from Sainani, 5-6 Aug. 1990, *Fay & Fay 2907* (MO); Murillo, 27.4 km below N dam at Lago Zongo, 16 Mar. 1984, *Solomon et al. 11919* (MO, USM).

Campyloneurum pascoense is characterized by large leaves, more than 1 m long, and also by its prominulous secondary veins and the presence of secondary and tertiary areoles.

Campyloneurum pascoense is closely related to *C. brevifolium* and *C. tucumanense*. It can be differentiated from *C. brevifolium* by the prominence of its tertiary veins and the relatively large size of its leaves. It differs from *C. tucumanense*, by having a chartaceous leaf texture.

37. *Campyloneurum phyllitidis* (L.) C. Presl, Tent. Pterid. 190. 1836.

Polypodium phyllitidis L. Sp. Pl. 1083. 1753. Lectotype (chosen by Proctor, *in* R. A. Howard 2: 341. 1977): *Plumier t.38*, Descr. Pl. Amer. 1693.

Polypodium comosum L., Sp. Pl. 1084. 1753. Type. *Plumier t.131*, Descr. Pl. Amer. 1693.
Polypodium conjugatum Poiret in Lam., Encycl. 5: 516. 1804. Type. *Herb. Jussieu 1071* (holotype, P; photo of P, BM!, C!).
Cyrtophlebium phyllitidis (L.) J. Sm., J. Bot. (Hooker) 4: 58. 1841.
Polypodium phyllitidis var. *linneanum* Hook., Sp. Fil. 5: 38. 1864. Type. *Plumier t. 130, 131*, Descr. Pl. Amer. 1693.
Polypodium phyllitidis var. *swartziana* Griseb., Fl. Br. West Ind. 702. 1864. Type. *Plumier t. 130, 131*, Descr. Pl. Amer. 1693.
Polypodium phyllitidis var. *elongata* Hieron., Bot. Jahrb. Syst. 34: 534. 1904. Cited Syntype. Ecuador: Azuay, Cordillera Oriental de Cuenca, Cerro Yanghuan, near Pindilic, *Lehmann 7679* (B!, F!, K!, US!). Lectotype (chosen here) Colombia: Tolima, Río Paez, *Lehmann 5721* (B!, F!, K!, US!).

Stem black, green turning black, not pruinose, (4-) 6-15 mm wide. Stem scales brown in mass, (4-) 6-8 mm long, (1.5-) 2-3 mm wide, ovate or trinagular-ovate, bases auriculate or shortly auriculate, apices acuminate, the cells oblong, central cells along main axes of the scale, marginal cells irregularly arranged, central cell walls 15 µm wide, marginal cell walls 8-10 µm thick. Phyllopodia 1-3 mm long, 1.5-4 mm wide, 2-5 (-7) mm apart. Leaves (25-) 60-150 cm long; petiole stramineous or brownish, 0.7-4 (-6) cm long, ranurate adaxially, convex abaxially; lamina obovate or lanceolate, bases attenuate, apices acuminate or subcaudate, (2.7-) 5-16 cm wide, chartaceous or subcoriacous, margins cartilaginous, slightly sinuate, plane or slightly revolute, indument of abaxially scattered, simple, bicellular hairs; hypostomatic, stomata polocytic; costa prominent, sometimes with scales similar to those on the stem, primary veins prominent or prominulous on both sides of the lamina, stramineous or dark stramineous, straight, (55º-) 65-75º divergent from the costa, (5-) 6-10 mm apart, secondary veins slightly prominulous, same color as the leaf tissue, transversal veins forming (6-) 8-16 primary areoles between the costa and margin, 3 (-4) free excurrent veinlets in each non costal primary areoles, usually one veinlet connected with the transversal vein forming isodiametric secondary areoles; sori subterminal or terminal, paraphyses not seen, spores (57-) 65-70 µm long, 40-50 µm wide. Chromosome number 2n=74. Figs. 18 c, d; 20 b; 45.

This species is distributed from southern United States (Florida), Central America, the Caribbean Islands, Colombia to Bolivia and central Brazil, where it grows as a terrestrial or epiphyte between 100m and 2500 m elevation.

Common names: "ba sú tape" (cayapa).

REPRESENTATIVE SPECIMENS: U.S.A. FLORIDA: Stuart and vicinity, Arch Creek, near Natural Bridge, 20 Feb. 1917, *Atwood s.n.* (MU); Palm Beach, 10 Apr. 1897, *Curtiss 867* (S); Indian River Narrows, *Curtiss 3668* (BM, NY); Collier County, Big Cypress, vic. of Falkahatchee, 7 Jun. 1966, *Lakela & Almeda 29969* (US); Redlands district, Hattie Bauer Hammock, 2 Feb. 1930, *Moldenke 569* (NY, S); Aiken, Key Largo, 30-31 Mar. 1898, *Pollard et al. 204* (BM, MU, NY); Dade County, Nixon Lewis Hammock, 16 Mar. 1915, *Small & Mosier 5885* (GH, MO, NY, S); Merritt's Isalnd hammock, Little River Prairie Miami, 8 Jul. 1915, *Small et al. 6936* (MU); 7 May 1904, *Tracy 9139* (BM, F, US).
MEXICO. SAN LUIS POTOSI: near banks of Moctezuma, 25 May 1939, *Frye & Frye 2657* (UC); mountains along road to Jalpan, 2 mi W of Xilitla, 25 Mar. 1961, *King 4284* (UC). MICHOACAN: Dist. Coalcoman, Huizontla, 9 Aug. 1941, *Hinton 15969* (F, UC); Aquila and Coahuayana, Jan. 1942, *Hinton 16269* (UC). HIDALGO: dist. Huejutla, woods Tehuetlan, 30 May 1947, *Moore 3038* (UC). VERACRUZ: E of Playa Vicente, 21 Sep. 1973, *Mickel 7227* (UC). OAXACA: Santa María Chimalapa, al N de Santa María, 2 Aug. 1984, *Hernández 284* (F); Santa María Chimalapa, Piedra Blanca (Popotzá), E of Santa María, 15 Dec. 1984, *Hernández 728* (MO); Chiltepec, Sierra Juarez, Tuxtepec, 30 May 1966, *Martinez 873* (F). TABASCO: Mun. Tacotalpa, NW de Tapijulapa, 30 May 1982, *Cowan et al. 3540* (UC); San Isidro, Balancan, 7-11 Jun. 1939, *Matuda 3368* (F). CHIAPAS: Esperanza, Escuintla, 23 Feb. 1948, *Matuda 17632* (F). YUCATAN: 1895, *Armour 38* (F); Yuxpeña, Campeche, 30 Jan. 1932, *Lundell 1268* (F, US); Yucatan, *Schott 781* (F).
BELIZE: Yucatan Peninsule, Maskall, Dec. 1933, *Gentle 1108* (F, GH, S).
HONDURAS. FRANCISCO MORAZAN: Quebrada Hierba Buena, 15 km NE of Tegucigalpa, 24 Sep. 1983, *Calderón 55* (UC). EL PARAISO: drainage of the Río Yeguare, Quebrada Dantas, 10 km N of Yuscarán, 12 Mar. 1950, *L.O. Williams 17220* (F). ATLANTIDA: about 15 mi E of Ceiba, 21 Jul. 1938, *Yuncker et al. 8575* (GH). San Pedro Sula, 30 May 1888, *Thieme 6* (UC).

GUATEMALA. PETEN: Puerto Chimino, Laguna Petexbatún, 20 km S of Sayaxchá, Oct-Dec. 1989, *Zomer 95* (F), 26 Apr. 1990. *Zomer 210* (F). SUCHITEPEQUEZ: near Santo Domingo, S of Mazatenango, 5 Mar. 1941, *Standley 88877* (F). Without locality: Finca Panama, 26 Mar. 1947, *Brenckle 47-188* (F).
COSTA RICA. ALAJUELA: W of San Ramón, ca. 1 km S of Socorro, 25 Jul. 1970, *Lellinger & White 1317* (F); Río San Rafael, Cantón Aguas Zarcas, 8 Feb. 1965, *L.O. Williams et al. 29103* (F). PUNTARENAS: about 4 mi W of Rincón de Osa, 4-7 Jun. 1968, *Burger & Stolze 5404* (F, US), *Burger & Stolze 5605* (F). LIMON: between Siquerres and the Río Pacuare, 20-22 Dec. 1969, *Burger & Liesner 6904* (F, GH, NY). SAN JOSE: basin of El General, Jul.-Ago. 1943, *Skutch & Barrantes 5161* (UC); along Río Convento, El General valley, 31 Jan. 1965, *L.O. Williams et al. 28722* (F). CARTAGO: 22 km N of Turrialba, 23 Jul. 1983, *Givens 3230* (F). ISLA DEL COCO: Twin mountains, Mar. 1970, *Gomez 3353* (F); Mar. 1940, *Valerio 1102* (F).
PANAMA. VERAGUAS: Islas Contreras, Isla Brincaneo, 20 Jul. 1984, *Churchill 5739* (MO). COLON: trail to lago Gatún, 17 May 1975, *Salazar 13* (MO). CANAL ZONE: Barro Colorado Island, 7 Nov. 1972, *Kennedy 1905* (F); Barro Colorado Island, 9 Nov. 1931, *Shattuck 359* (F); Parque Nacional Soberanía, 20 Mar. 1980, *Vasquez 165* (F), 4 Jun. 1980, *Vasquez 232* (MO, UC). DARIEN: vic. of gold mine at Cana, 26 Jul. 1976, *Croat 37588* (MO). Without locality: 1860, *Eaton 40* (F).
CUBA. PINAR DEL RIO: source of Río Taco-Taco, Sierra de los Organos, 18 Nov. 1941, *Morton 4339* (UC); vic. of Sumidero, 2-4 Aug. 1912, *Shafer 13501* (F); Guanajay, 19 Sep. 1907, *Wilson 1773* (F). LAS VILLAS: Arroyo Cimarrón, 5 Mar. 1910, *Britton & Britton 5095* (US); Cieneguita, 6 Jul. 1895, *Combs 285* (F); El Junco, above Siguanea, in San Juan mountains, 1-20 Jul. 1950, *Howard et al. 175* (GH, UC); above San Blas, 9-10 Nov. 1941, *Morton 4105* (UC). ORIENTE: SE summit of Yunque de Baracoa, 28 Feb. 1979, *Bisse et al. 40158* (HAJB); slopes and summit of El Yunque, near Baracoa, 30-31 Jan. 1902, *Pollard & Palmer 184* (F, US); vic. of Baracoa, 1-7 Feb. 1902, *Pollard et al. 243* (F, US); La Perla, 9 Feb. 1911, *Shafer 8554* (F); Monteverde, 1859, *Wright 1021* (UC). San Antonio, Mar. 1906, *Hitchcok s.n.* (F).
JAMAICA. ST. ANDREW: about 2 mi NE of Kingston, on road to Newcastle, 15 Jun. 1963, *Crosby et al. 162* (F, UC). ST. ANN: hill on E side of station TL, 8 mi S of Brown's town, 2 Aug. 1977, *Goodfriend s.n.* (F). Point Antonio, 28 May 1891, *Metcalf s.n.* (MU); Port Antonio, Dec. 1898-Mar. 1899, *Millspaugh 999* (F). ST. ELIZABETH: Cooks Bottom, N of Ipswich, 31 Mar. 1920, *Maxon & Killip 1447* (F). Port Moraut, 1890-91, *Rothrock 428* (F).
HAITI. DU NORD: vic. of Dondon, 8 Jan. 1926, *Leonard 8681* (UC); at source of Rivière Tissier, Grand'Anse valley, 6 km SW of Jéremie, 6 May 1941, *Bartlett 17290* (GH, UC).
DOMINICAN REPUBLIC. MACORIS: Consuelo, along the Macoris river, 22-24 Nov. 1909, *Taylor 262* (F). SANTO DOMINGO: Llano costero, banks of Río Ozama, 30 Apr. 1929, *Ekman 12342* (F, S, US); Santo Domingo, 24 Jan. 1899, *Millspaugh 813* (F).
PUERTO RICO. NW of Utuado, 18 Sep. 1941, *Blomquist 11805* (F); Vega Alta, 15 Oct. 1941, *Blomquist 11991* (UC); near The Caves, Aguas Buenas, 12 Oct. 1941, *Blomquist 12015* (UC); vic. of Catano, 1 Apr. 1922, *Britton et al. 6990* (F, US); near Mayaguez, 30 Jan. 1900, *Heller 4438* (F); on the Adjuntas road, 7 mi from Ponce, 2 Dec. 1902, *Heller 6177* (F, US); Río Abajo forest, 2 Apr. 1985, *Luteyn & Lebrón-Luteyn 11486* (UC); Toro Negro recreation area, 3 Jan. 1978, *Tullis s.n.* (MU).
LEEWARD ISLANDS. ANTIGUA: St. Mary, downstream from Walling's dam, 12 jun. 1974, *Holland 8* (F). DOMINICA: bank of the Mantipo river, 21 Jul. 1938, *Hodge 34* (UC). MONTSERRAT: Canan river, 7 Feb. 1907, *Shafer 451* (F, US); in the mountains, 13 Feb. 1907, *Shafer 756* (F). VIRGIN ISLANDS. ST. CROIX: mountain Eagle, 31 Jan. 1896, *Ricksecker 251* (F, MU, UC).
WINDWARD ISLANDS. ST. VINCENT: St. Patrick, upper Rutland river, 15 Jan. 1962, *Cooley 8155* (F, UC, US); .
BAHAMAS. GRAND BAHAMA: Coppice, Baruetts Point, 5-13 Feb. 1905, *Britton & Millspaugh 2636* (F). GREAT ABACO: along Great Abaco highway, ca. 22 mi SE of Marsh Harbour, 12 Mar. 1975, *Correll & Meyer 44541* (F); Vanilla Hummock, edge of Marsh Harbour, 15 Jun. 1981, *Correll & Wasshausen 52030* (F). ANDROS: Conch Sound, 12 May 1890, *Northrop & Northrop 566* (F, GH); Corpice, near Staniard Creek, 1-3 Feb. 1910, *Small & Carter 8869* (F). NEW PROVIDENCE: Midenhead Coppice, 12-24 Mar. 1907, *Britton 6544* (F, US). CROOKED ISLANDS: Salt Hope, 9-23 Jan. 1906, *Brace 4734* (F).
COLOMBIA. CHOCO: Mun. Río Sucio, near to campamento Tilupo, *Forero et al. 1688* (MO); Hoya del Río San Juan, near to Palestina, 23 Mar. 1979, *Forero et al. 3797* (MO); 26 Mar. 1979, *Forero et al. 4059* (MO), *Forero et al. 4066* (MO), 5 Apr. 1979, *Forero et al. 4681* (MO); area of Baudó, 11 Feb.-29 Mar. 1967, *Fuchs & Zanella 22351* (F); Chocó, Nov. 1857, *Schott 10* (F). ANTIOQUIA: 1934, *Daniel 212* (F); Río Samana, Cord. Central, 2 km above Argelia, 29 May-1 Jun. 1944, *Ewan 15773* (UC); carretera Mutatá-Pavarando, before bridge Río Sucio, 3 Mar. 1987, *Fonnegra et al. 1684* (MO); Anori, Providencia hydroelectric station, 6 Jun. 1971, *Soejarto 2901* (F). CALDAS: Santa Cecilia, Cord. Occidental, Tatamá, 17 Apr. 1945, *Sneidern 5128* (F). CUNDINAMARCA: Salto de Tequendama, 1-3 Oct. 1938, *Cuatrecasas 146* (F); Río Magdalena, Quebrada de los Ñeques, 7 Feb. 1962, *Murillo et al. 579* (F, US).

VALLE: Mun. Zarzal, between La Paila and Zarzal, 17 Nov. 1986, *Silverstone et al. 2590* (MO).
VENEZUELA. TACHIRA: along road between San Cristóbal and Delicias, 11 km N of Delicias, 10 Aug. 1982, *Croat 54993* (MO). APURE: dist. Páez, selva de Cutifí, between Catufí on the Río Cutufí and the Río Sanare, 8-12 Nov. 1982, *Davidse & González 21760* (MO); 25 km by car E of El Nula, 2 Jul. 1983, *Werff & Gonzalez 4742* (MO). PORTUGUESA: 50 km WNW of Guanare,15 Mar. 1982, *Liesner et al. 12804* (MO); ESE of Paraiso de Chabasquén, 5 Nov. 1982, *Smith et al. 1008* (MO). MIRANDA: dist. Páez, cerro Riberón, between Río Guapo and Río Chiquito, 1-2 Jun. 1977, *Davidse & Gonzalez 13580* (MO). BOLIVAR: 7 km E of Hato de Nuria, E of Miamo, 14 Jan. 1961, *Steyermark 88474* (F, GH). TERRITORIO FEDERAL AMAZONAS: 25 May 1975, *Berry 701* (MO); Alto Orinoco, 18 Aug. 1951, *Croizat 524* (F). TERRITORIO FEDERAL DELTA AMACURO: Pedernales, Caño Simoina, W of Isla Cocuinma, 8 Oct. 1977, *Steyermark et al. 11348* (MO). ISLA MARGARITA: San Juan mountain, 27 Jul. 1903, *Johnston 151* (F); El Valle, 30 Jul. 1901, *Miller 165* (BM, F).
TRINIDAD. St. Amés, 21 Apr. 1924, *Broadway 5279* (F). TOBAGO. Calder Hall, 27 Jun. 1910, *Broadway 4650* (F, US); Providence road, 27 Apr. 1910, *Broadway 3597* (BM, F, S).
GUYANA. Amakura river, NW district, 23-30 Mar. 1923, *Cruz 3549* (F, MO, UC); Essequibo river, Jun. 1923, *Persaud 356* (F); bassin of Essequibo river, near mouth of Onoro creek, 15-24 Dec. 1937, *A.C. Smith 2724* (F).
SURINAME: station Victoria, Dec. 1843, *Kappler 1386* (F, S); Jodensavanne-Mapane Kreek area, 15 Dec. 1953, *Lindeman 5258* (MO); Table mountain, base S escarpment Arrowhead Basin, 26 Aug. 1944, *Maguire 24495* (F); Nassau mountains, Marowijne river, 3 Jan. 1955, *Maguire et al. 39088* (UC).
FRENCH GUIANA. Saint Jean du Maroni, 26 Mar. 1914, *Benoist 1004* (F). SAUL: Mont La Fumée, 2 Sep. 1982, *Boom & Mori 1594* (CAY). Saint Laurent, km 10 road Paul Isnard, 5 Nov. 1981, *Billiet & Jadin 1309* (CAY). Ytany island, Haut Maroni, 20 Nov. 1977, *Cremers 5098* (CAY); Cayenne, island 17 May 1979, *Cremers 5665* (CAY); 45 km SE from Aul, 31 Aug. 1980, *Cremers 6503* (CAY); Riv. Mana, Ilots du Saut, 22 Jul. 1981, *Cremers 7290* (CAY); Baboune river, affluent of Mana river, 29 Jul. 1981, *Cremers 7358* (CAY); region Paul Isnard, SW Citron, 7 Feb. 1983, *Cremers 7879* (CAY); Salut, Ile Royale, 21 Feb. 1985, *Cremers 8444* (CAY); Haut Oyapock, Saut Cambrouze, 18 Jul. 1975, *Granville 2482* (CAY); 12 km E fromSaul, 10 Jan. 1980, *Granville 3252* (CAY); 18 km S from Saul, 4 Apr. 1983, *Granville 5542* (CAY); Haute Camopi, N of Mont Belvedere, 2 Dec. 1984, *Granville 7106* (CAY); St. Joseph, 6 Feb. 1967, *Oldeman 2502* (CAY); Arataye river, Saut Pararé, 11 Feb. 1969, *Oldeman 3016* (CAY); Saul. L'eaux Claires, 22 Jun. 1988, *Windisch 5283* (F).
ECUADOR. ESMERALDAS: Río Cayapa, Zapallo Grande, 1-2 Aug. 1982, *Kvist & Asanza 40806* (QCA). CARCHI: around Maldonado, W of Tulcan, 5 Sep. 1981, *Balslev 1993* (F, QCA). IMBABURA: between El Pajón and Cachaco, 2 Jun. 1949, *Acosta-Solís 12704* (F). NAPO: Sucumbios, Reserva Faunística Cuyabeno, 6 Apr. 1989, *Balslev 84890* (QCA); laguna Cuyabeno, 21 Aug. 1981, *Brandbyge et al. 33840* (QCA), 22 Aug. 1981, *Brandbyge et al. 33930* (AAU, QCA); Parque Nacional Yasuní, Pozo Amo 2, 9-13 Jan. 1988, *Cerón & Coello 3300* (QCA); at Río Aguarico, 20-21 Jan. 1984, *Laegaard 51544* (QCA); Río Yasuní, Garza Cocha, 8 Apr. 1983, *Lawesson et al. 43344* (AAU, QCA); Lago Agrio, 3.5-4.8 km E of Río Conejo, 1 Apr. 1972, *Mac Bryde & Dwyer 1407* (QCA); Reserva Biológica Jatun Sacha, 8 km ESE of Puerto Misahualli, 23 Jun. 1986, *Miller et al. 2179* (MO); Añangu, Parque Nacional Yasuní, 30 May-21 Jun. 1982, *Øllgaard et al. 38908* (AAU, QCA). PICHINCHA: vía Santo Domingo-Quinindé, 8 Sep. 1949, *Acosta-Solís 13850* (F); road Cotocollao-Pumdupamba-Nono-Nanegalito, 6 May 1980, *Jaramillo et al. 2405* (QCA). LOS RIOS: Jauneche forest, km 70 Quevedo-Palenque road, vía Mocachi, 14 Jul. 1979, *Dodson et al. 7988* (MO). COTOPAXI: Quevedo-Latacunga road, along Río Pilaló, 6 Apr. 1973, *Holm-Nielsen et al. 3098* (AAU, F, QCA). TUNGURAHUA: Baños, over the river to Baños, 2 Nov. 1981, *Madsen et al. 36475* (AAU). CHIMBORAZO: 20 Aug. 1943, *Acosta-Solís 5466* (F). PASTAZA: Ceilán, 6 Jun. 1980, *Brandbyge & Asanza 31633* (QCA); Río Villano, 24 Mar. 1980, *Holm-Nielsen et al. 22662* (AAU, QCA); 3-4 km of Puyopungu, 28 Sep. 1976, *Lugo 5043* (F, GB); Río Bobonaza, near outlet into Río Pastaza, between Destacamento Cabo Pozo and La Boca, 21 Jul. 1981, *Øllgaard et al. 34932b* (AAU, QCA). LOJA: Loja, 31 May 1946, *Espinoza 457* (GH, LOJA). GALAPAGOS ISLAND. Santa Cruz: 17 Apr. 1974, *Adsersen & Adsersen 78* (QCA); 5 mi N Academy Bay, 3 Mar. 1953, *Bowman 98* (UC).
PERU. PIURA: Huancabamba, Canchaque-Huancabamba, km 16-25 from Canchaque, 17 Apr. 1987, *Díaz & Baldeón 2394* (MO, NY, USM); Huancabamba, W side just below summit of Abra Porculla, between Olmos and Río Marañón, 26 Sep. 1957, *Hutchison 1386* (UC); Ayabaca, around Ayabaca, 9 Sep. 1976, *Sagástegui & Cabanillas 8703* (MO). LA LIBERTAD: Otuzco, Chuquizongo, 5 Jun. 1958, *López et al. 2630* (GH). SAN MARTIN: Mariscal Cáceres, dist. Campanilla, Mashuyacu, 12 Aug. 1970, *Schunke V. 4225* (F); Mariscal Cáceres, Tocache Nuevo, Pushurumbo, E of Puente Palo Blanco, 24 Dec. 1972, *Schunke V. 5792* (F); Alto Río Huallaga, Dec. 1929, *L. Williams 5621* (F); Tarapoto, 14 Feb. 1947, *Woytkowski 35070* (MO, UC). LORETO: Maynas, Colonia Río Zumun, near Río

Yahuas-Yacu, 19 Mar. 1980, *Barrier 1959* (USM); Río Ampiaco, 24 Sep. 1972, *Croat 20731* (F, MO, UC); Varadero de Mazán, 27 Sep. 1972, *Croat 20807* (UC); Río Ampiyacu, Brillo Nuevo-Río Yaguasyacu, 13 Mar. 1981, *Davis et al. 900* (F, GH); Alto Amazonas, Río Pastaza, 1 Aug. 1979, *Diaz et al. 1324* (F, MO); Yanamono, Explorama tourist camp, trail to Río Napo, 19 Feb. 1981, *Gentry et al. 31530* (MO, UC, USM); dist. Indiana, quebrada Yanayacu, below Bombonaje, 27 May 1973, *McDaniel & Rimachi 17347* (GH); above Pongo de Manseriche, left bank of Río Santiago, 22 Dec. 1931, *Mexia 6324* (BM, F, GH, MO, NY, S, UC, US); Maynas, dist. Pebas, Río Ampiyacu, 19 Jul. 1976, *Revilla 862* (F, MO, NY, UC); Maynas, Iquitos, 17 Feb. 1968, *Simpson & Schunke 679* (F). HUANUCO: Tingo María, 30 Oct. 1959-19 Feb. 1950, *Allard 22332* (US); Muña, 23 May-4 Jun. 1923, *Bryan 549c* (F); near carretera marginal de la selva, near Puente Colombia, between Río Mayo and Río Huallaga, 10 Jul. 1970, *McDaniel 13846* (GH); Pachitea, dist. Honoria, Bosque Nacional Iparia, río Pachitea, near Miel de Abeja camp, 26 Sep. 1967, *Schunke V. 2181* (F, GH, NY, US); Mariscal Cáceres, Tocache Nuevo, trail to Pushurumbo, 7-8 km E de puente Palo Blanco, 24 Dec. 1972, *Schunke V. 5792* (F, NY, US); Tingo María, 9 Sep. 1956, *Tryon & Tryon 5290* (GH, US). PASCO: Oxapampa, Quebrada Castillo, sobre el Río Omaiz, afluente del Chuchurras, 12 Jun. 1987, *León & Young 1083* (F, USM); Oxapampa, 5 km SE de Oxapampa, 9-11 Dec. 1982, *D.N. Smith 2917* (F, MO); Oxapampa, Palcazú valley, near the confluence of Río Palcazú and Río Iscosacin, 23 Apr. 1983, *D.N. Smith 3874* (UC). JUNIN: Puente Paucartambo to La Merced, 30 Jan. 1983, *Gentry et al. 39804* (F, MO); Satipo, Alto Quimiriqui, 30 Aug. 1982, *León 278* (AAU, F, USM); Chanchamayo, La Merced-Puente Paucartambo road, 3 km from La Merced, 17 May 1983, *D.N. Smith 4051* (MO, UC). CUSCO: La Convención, Rosario Mayo, 10 Aug. 1968, *Chavez 137* (GH); La Convención, Cocalpampa, Chaullay, 29-30 Dec. 1986, *Nuñez et al. 6772* (MO). MADRE DE DIOS: Tambopata, Tambopata Natural Reserve, 14 Apr. 1980, *Barbour 4768* (F, MO), *Barbour 4967* (MO); Parque Nacional Manu, Cocha Cashu Biological Station, 8 Nov. 1984, *Foster P-84-68* (MO, UC); Parque Nacional Manu, Cocha Cashu, 28 Sep. 1979, *Foster et al. 7065* (F); Tambopata, 39 km SW of Puerto Maldonado, 10 Oct. 1985, *S.F. Smith et al. 669* (F, MO, NY).
BOLIVIA. LA PAZ: Antahuacana, Jun. 1909, *Buchtien 2167* (UC); Polo-Polo, Coroico, Oct-Nov. 1912, *Buchtien 3533* (F, S); Casanare, Tipuani-Tali, 6 Oct. 1922, *Buchtien 7078* (MO); Nor Yungas, 32.1 km S of Caranavi, 26 Mar. 1982, *Solomon 7368* (UC, MO).
BRAZIL. RORAIMA: Serra dos Surucus, 17 Feb. 1969, *Prance et al. 9974* (AAU, F); Posto Mucajaí, Rio Mucajaí, vic. of Mucajaí airstrip, 14 Mar. 1971, *Prance et al. 10996* (F, S), 18 Mar. 1971, *Prance et al. 11086* (F, S, US), 25 Mar. 1971, *Prance et al. 11216* (F, MO, S); vic. of Uaicá airstrip, 3 Dec. 1973, *Prance 20008* (F). ACRE: Rio Juruá-Mirim, near Lucania, 14 May 1971, *Maas et al. 12932* (F, S); Cruzeiro do Sul, Rio Juruá and Rio Moa, 28 Apr. 1971, *Prance et al. 12622* (F). PARÁ : Lageira airstrip on Rio Maicuru, 1 Aug. 1981, *Strudwick et al. 3979* (F); Sete Varas airstrip on Rio Curua, 4 Aug. 1981, *Strudwick et al. 4077* (F), 6 Aug. 1981, *Strudwick et al. 4263* (F), 8 Aug. 1981, *Strudwick et al. 4377* (F). GOIAS: Córrego Itaquera, ca. 30 km N of Formosa, 2 May 1966, *Irwin et al. 15586* (F, US); Córrego Itaquera, 2 May 1966, *Irwin et al. 15596* (US). DISTRITO FEDERAL: Córrego Vicente Pires, near Taguatinga, 8 Sep. 1965, *Irwin et al. 8111* (F); Planalto, ca. 15 km W of Brasilia, Riacho Vicente Pires, 12 Jul. 1966, *Irwin et al. 18169* (F, MO, US).

Campyloneurum phyllitidis is characterized by the prominence of its secondary veins and its symmetrically divided primary areoles.

This species has been confused with *C. brevifolium* and *C. nitidum*. However, *C. phyllitidis* differs from *C. brevifolium* by having symmetrically divided primary areoles, and therefore they represent different lineages within the genus. From *C. nitidum*, it differs by having leaves predominantly with caudate or acuminate apices and acuminate stem scales.

Campyloneurum phyllitidis is a widespread species and several phenotypes occur along its range of distribution. Two cytotypes have been reported in this taxa, and this fact may correlate with some of the morphological variation.

38. *Campyloneurum repens* (Aublet) C. Presl, Tent. Pterid. 190. 1836.
Polypodium repens Aublet, Hist. Pl. Guiane 2: 962. 1775. Lectotype (chosen by Proctor,*in* R. A. Howard 2: 340, 1977): *Plumier t.134*, Traité Foug. Amér. 117. 1705.
Polypodium lapathifolium Poiret, Encycl. 5: 514. 1804. Type. America Meridionale, *Jussieu s.n.* (holotype, P, photo of P, BM!, S!).
Campyloneurum lapathifolium (Poiret) Ching, Sunyatsenia 5: 263. 1940.
Polypodium caespitosum Link, Hort. berol. 2. 91. 1833. Type: Cultivated, ex *Hort. Loddiges* (holotype B!).
Campyloneurum caespitosum (Link) Link, Fil. spec. 125. 1841.
Campyloneurum crispum Fée, Gen. Filic. 259. 1852.

Type. Brazil: *Martius 303* (holotype, not found; isotypes, BM!, MO!).

Stem dark stramineous, black, not pruinose, 1-3 (-4) mm wide. Stem scales brown or light brown, 3-4 mm long, 1-1.5 mm wide, ovate, the cells oblong, cell walls 5-7 µm thick, marginal cell walls lighter than the central cell ones. Phyllopodia 1 mm long, 2-2.5 mm wide, 0.7-15 mm apart. Leaves 20-60 cm long; petiole 0.5-7 (-13) cm long, stramineous; lamina lanceolate or obovate lanceolate, sometimes narrowly lanceolate, bases attenuate, apices acuminate or caudate, (2.5-) 3-8 cm wide, chartaceous, margins cartilaginous, slightly sinuate, usually plane, indument of scarce bicellular glandular hairs, scattered abaxially; hypostomatic, stomata polocytic or copolocytic; costa prominent, slightly ranuarte adaxially, angular or convex abaxially, primary veins prominent or prominulous, stramineous or darker than the leaf tissue, slightly flexuous or straight, (65º-) 70-75º divergent from the costa, (3-) 5-7 mm apart, secondary transversal veins forming (4-) 6-12 primary areoles between the costa and margin, 2 (-4) free excurrent veinlets in each non costal areole; sori medial or subterminal, spores 50-70 µm long, 30-40 µm wide. Figs. 1 b; 46.

This species is distributed from Mexico, Central America, Greater Antilles to Bolivia and central Brazil, where it grows mostly as an epiphyte between 100 m and 2000 m elevation.

Common name: "Shan tape" (colorado).

REPRESENTATIVE SPECIMENS: MEXICO. OAXACA: 23.5 mi S of road to Jesus Carranza, 28 Jul. 1966, *Cruden 1113* (UC); dist. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, 13 Aug. 1971, *Mickel 6374* (UC). CHIAPAS: Mun. Las Margaritas, at confluence of the Río Ixcán with the Río Lacantum (Río Jatatí), 14 Mar. 1973, *Breedlove & McClintock 34063* (F, MO); between Palenque and Bonampak, SW of Palenque, 5 Jul. 1977, *Croat 40209* (MO).
BELIZE. CAYO: Vaca Plateau, Blue Hole Camp, 6 Aug. 1980, *Whitefoord 2044* (BM, MO). TOLEDO: vicinity of San Jose, 6.7 mi N of Columbia, 13 Jun. 1973, *Croat 24462* (MO). Maya mountains, vicinity Cockscomb mountains, 8 Jun. 1930, *Schipp 527* (BM, F, NY, S, UC).
HONDURAS. CORTES: Santa Cruz de Yojoa, 26 Oct. 1933, *Edwards 706* (F); Agua Azul, 27 Dec. 1946, *L.O. Williams & Molina 11338* (F).
GUATEMALA. PETEN: Dolores, on Santo Toribio road, 20 Apr. 1961, *Contreras 2138* (MO); between Finca Yalpemech and Chinajá, 28 Mar. 1942, *Steyermark 45437* (F). IZABAL: along trail between Dartmouth and Morales towards lago Izabal, 7 Apr. 1940, *Steyermark 39065* (F). SOLOLA: S facing slopes of volcán Atitlán, 20 Jun. 1942, *Steyermark 47892* (F).
NICARAGUA. RIO SAN JUAN: Río San Juan, 4 Dec. 1982, *Araquistain 3416* (MO). BOACO: cerro Mombacito, 4 km NW de Camoapa, 1 Feb. 1979, *Grijalva & Araquistan 42* (MO).
COSTA RICA. PUNTARENAS: 4 mi W of Rincón de Osa, 4-7 Jun. 1968, *Burger & Stolze 5405* (F, NY), *Burger & Stolze 5536* (F); about 5 km W of Rincón de Osa, 24-30 Mar. 1973, *Burger & Gentry 9014* (F, NY); foothills of the Cordillera de Talamanca, N of Las Alturas, 28 Aug. 1983, *Davidse 24149* (MO, UC); ca. 10 mi SE of Rincón de Osa, along road to Pacific, 18 Jul. 1967, *Evans & Bowers 2806* (MO); Santiago, near San Ramón, 21 Apr. 1913, *Tonduz 17572* (BM, F, NY, S, UC). CARTAGO: Río Chitaria, E of Buenavista, 20 km from Turrialba, 24 Aug. 1983, *Saiki 58* (F).
PANAMA. CHIRIQUI: Burica Peninsula, 10-11 mi W of Puerto Armuelles, in vic. of San Bartolo, 19 Feb. 1973, *Croat 21983* (MO); 25 km W of El Hato del Volcán, 19 Oct. 1980, *Maas & Dressler 4939* (MO); km 3 on La Unión road NW of volcano, 23 May 1971, *Proctor 32029* (F). PANAMA: at headwaters of Río Indio, slopes of Cerro Jefe, 2 Nov. 1979, *Antonio 2433* (MO), 18 Dec. 1980, *Antonio 3229* (MO); over Río Guanche, 19 Jan. 1980, *Antonio 3344* (MO); Río Maje, 20 Apr. 1976, *Croat 34415* (MO); 20 km above Pan. Am. highway, on trail from El Llano to Carti-Tupile, 22 Feb. 1973, *Kennedy 2563a* (MO); Altos de Pacora, 4 Feb. 1979, *Windisch 2199* (F). CANAL ZONE: Limbo Hunt Club road, 1 Nov. 1972, *Kennedy & Andrews 1878* (MO); Parque Nacional Soberanía, trail to oilline, 17 May 1980, *Vásquez 192* (MO). COCLE: vic. of El Valle, 14 May 1939, *Allen 1799* (F, MO); near La Mesa, 11 Feb. 1971, *Croat 13346* (F, MO, NY); road to Coclosito, 12 mi from Llano Grande, 9 Dec. 1983, *Churchill et al. 4019* (MO, UC); El Valle, 11 May 1977, *Folsom 3110* (MO, UC); 7 km N of Llano Grande on road to Coclesito, 19 Apr. 1978, *Hammel 2511* (MO); foot of cerro Pilón, above El Valle de Antón, 28 Mar. 1969, *Porter et al. 4615* (MO). HERRERA: 18 km W of Las Minas, trail to top of Alto Higo, 5 Aug. 1978, *Hammel 4230* (MO); between Las Minas and El Toro, near village of Chepo, 24 Jan. 1987, *McPherson 10290* (MO). LOS SANTOS: trail between Jobero and Río Pedregal, 29 Apr. 1976, *Croat 34517* (MO); from El Cortezo to Arenas, 27 Oct. 1978, *Hammel 5367* (MO). DARIEN: N Punta Guayabo Grande, 21 Apr. 1980, *Antonio & Hahn 4321* (MO); Parque Nacional Darién, at N base of cerro Pirre, 8 Oct. 1987, *Hammel et al. 16153* (MO); RENARE hut in Darien

National Park, 5 Aug. 1986, *McDonagh et al. 444* (MO). JAMAICA. PORTLAND: gorge of the Stony river, below junction of the Macungo river, 24 Jul. 1967, *Proctor 28322* (F, MO). Dollwood, 6 Aug. 1898, *Harris 7273* (F); foothills of John Crow mountains, E of Seamen's valley, 18 Feb. 1920, *Maxon & Killip 235* (F); lower eastern slopes of Mount Diabolo, 29 Feb. 1920, *Maxon & Killip 543* (F); road from Silver Hill Gap to Hardwar Gap, 19 Mar. 1920, *Maxon & Killip 1216* (F, GH); trail from Morces gap to Vinegar hill, 21 Mar. 1920, *Maxon & Killip 1321* (F); Vinegar Hill road, 2 Jun. 1910, *York 115* (MO); Petit Bordel, 9 Jan. 1890, *Eggers 6871* (F, S). Without locality, 1895, *Moore s.n.* (MO); *Mart. 2874* (MO).
WINDWARD ISLANDS. MARTINIQUE: 1869, *Belanger s.n.* (F); 1868, *Husnot s.n.* (F).
COLOMBIA. ANTIOQUIA: Mun. San Luis, Cañón del río Claro, 2 Sep. 1984, *Cogollo 1887* (MO). VALLE: Western Cordillera, hoya del Río Anchicayá, 20 Dec. 1942, *Cuatrecasas 13745* (F); Río Cajambre, 21-30 Apr. 1944, *Cuatrecasas 17111a* (F, S); western cordillera, Hoya del Río Cali, trail to Miralindo, 31 Oct. 1944, *Cuatrecasas 18439* (F); along road between Cali and Buenaventura at km 18.5 on road from Finca Santa Elena, 27 Aug. 1976, *Croat 38504* (MO). CAUCA: valle del Cauca, May 1948, *Dryander 2931* (F); Río Naya, near El Pastico, 23 Feb. 1983, *Gentry & Juncosa 40624* (UC). META: Mun. La Macarena, sobre el Río Guayabero, 11 Aug. 1988, *Callejas & Marulanda 7066* (MO). CHOCO: Mun. Río Sucio, Alto del Limón, 4 Jun. 1976, *Forero et al. 1811* (MO); Hoya del Río San Juan, La Sierpe, 1 Apr. 1979, *Forero & Jaramillo 4454* (MO); Mun. San José del Palmar, Hoya del Río Torito, 1 Mar. 1980, *Forero et al. 6433* (MO); 4 Mar. 1980, *Forero et al. 6619* (MO), *Forero et al. 6683* (MO); Hoya del Río Atrato, Beté, 5 Apr. 1982, *Forero et al. 8889* (MO); area of Baudó, 11 Feb.-29 Mar. 1967, *Fuchs & Zanella 22253* (F). Mutatá, road to Bajirá, Nuevo Oriente, 19 Mar. 1983, *Brand & Ascanio 270* (MO). SANTANDER: between Pamplona and Bucaramanga, 5 May 1983, *Croat 56507* (UC). PUTUMAYO: Puerto Porvenir, above Puerto Ospina, 22 Nov. 1940, *Cuatrecasas 10755* (F). CAQUETA: Eastern cordillera, Sucre, 4 Apr. 1940, *Cuatrecasas 9074* (F).
VENEZUELA. LARA: Moran, between Agua Amarilla and Santo Domingo, 24 Oct. 1987, *Rivero & Diaz 1316* (MO). MIRANDA: Paéz, Fila La Tigra, Quebrada San Juan, 2-7 Sep. 1977, *Ortega & González 386* (MO), *Ortega & González 405* (MO). ANZOATEGUI: along Río León, by Quebrada Danta, 20 Feb. 1945, *Steyermark 61033* (F, MO). BOLIVAR: Caño Pablo, tributary of Río Caura, ca. 6 km ESE of Las Pavas, 8 May 1982, *Liesner & Morillo 13946* (MO); Salto del Para, Medio Caura, 3 Mar. 1939, *L. Williams 11361* (F). TERRITORIO FEDERAL AMAZONAS: Sierra Parima, headwaters of Río Siapa, 11-23 Mar. 1946, *Cardona 1321* (F); trail S from Cerro Neblina camp, 12 Apr. 1984, *Gentry & Stein 46563* (MO); Río Negro, 1.5 km E of Cerro de la Neblina, 2-3 Dec. 1984, *Liesner 17473* (MO); Río Negro, Cerro de la Neblina, valley N base of Pico Cardona, 21-24 Mar. 1984, *Liesner & Stannard 16873* (F, MO). DISTRITO FEDERAL: Colonia Tovar, 1854-55, *Fendler 229* (F); 6 km NE of Colonia Tovar, before turnoff to El Limón on road to Chichiriviche, 7 Apr. 1982, *Liesner & Medina 13546* (MO). Upper Orinoco region, La Mantequilla, 22 Sep. 1951, *Croizat 710* (F, MO); Santa Marta, *H.H. Smith 1040* (MO).
GUYANA. Upper Rupununi river, near Dadanawa, 2 Jun. 1922, *De la Cruz 1449* (F, MO); New River, 1/4 mile S of camp 3, 5 Oct. 1952, *Guppy 6376* (BM, F); Barima-Waini region, 3 mi W of Eclipse Falls, below Wanamaparu, 2 Aug. 1986, *Pipoly & Lall 8172* (F), *Pipoly & Lall 8183* (F).
SURINAM. Haute crique, Waamahpann, 25 Jul. 1972, *de Granville 966* (CAY); Tumac Humac, between Kouaipann and Palouloui, 1 Aug. 1972, *Granville 1067* (CAY); Tafelberg, Arrowhead Basin, 26 Aug. 1944, *Maguire 24507* (F, MO, NY); Nassau mountains, Marowijne river, 7 Jan. 1955, *Maguire et al. 39195* (NY); Tumuc Humuc Mountains, source of Litani river, 7 Nov. 1937, *Rombouts 879* (MO, US).
FRENCH GUIANA: Arataye river, Sauts Parare, 5 Feb. 1981, *Barrier & Feuillet 2524* (CAY); 45 km SE of Saul, summit of Tabulaire, 19 Aug. 1980, *Cremers 6337* (CAY), 21 Aug. 1980, *Cremers 6383* (CAY); riviere Mana, Saut Dalles, 18 Jul. 1981, *Cremers 7220* (CAY); Mont Gauthiot, Yaroupi, 20 Apr. 1970, *Granville 420* (CAY); Monts Galbao, 10 May 1973, *Granville 1594* (CAY).
ECUADOR. CARCHI: valle de Maldonado, km 60 on road Tulcán-Maldonado, 18 May 1973, *Holm-Nielsen et al. 5775* (AAU, F, USM). ESMERALDAS: Río San Miguel, upstream from San Miguel de Cayapas, 1 Sep. 1980, *Holm-Nielsen et al. 25465* (AAU, USM). IMBABURA: Collapi, 4 Jun. 1949, *Acosta-Solís 12795* (F). NAPO: Río Eno al NE de Shushufindi, 11 Apr. 1982, *Balslev 2326* (AAU, QCA); San Pablo de los Secoyas, on the path to Shushufindi, WSW of the village, 6 Aug. 1980, *Brandbyge et al. 32545* (UC), 7 Aug. 1980, *Brandbyge et al. 32633* (AAU, QCA); Río Wai si ayá, 6 km upriver from San Pablo, 10 Aug. 1980, *Brandbyge & Asnza 32739* (AAU, QCA); Reserva Biológica Jatun Sacha, 8 km E de Misahuali, 21-25 May 1987, *Cerón 1436* (MO); along road from Tena, past Muyuna, ca. 5.7 km W of Tena, 1 May 1984, *Croat 58853* (MO); Río Yasuní, 80 km upriver from Rocafuerte, 21 Sep. 1977, *Foster 3794* (F); Río Yasuní, Charapillo, 26 Aug. 1979, *Holm-Nielsen et al. 19954* (AAU, QCA); Río Cuyabeno, near to Río Aguarico, 20 Feb. 1980, *Holm-Nielsen et al. 21609* (AAU, QCA); San Pablo de los Secoyas, 4 Jul. 1980, *Jaramillo & Coello 2793* (AAU, QCA), *Jaramillo & Coello 2821* (AAU, QCA); Río Yasuní, Garza Cocha, 10

Apr. 1983, *Lawesson et al. 43381* (AAU, QCA); Río Yasuní, upstream from Garza Cocha, 11 Apr. 1983, *Lawesson et al. 43439* (QCA); Parque Nacional Yasuní, Anango, 15 Jul. 1982, *Luteyn et al. 8698* (F); below Puerto Misahualli, 18-30 May 1985, *Palacios et al. 407* (QCA). PICHINCHA: road Nono-Nanegalito, N de Cerro Pichincha, 9 May 1982, *Balslev & Boom 2500* (AAU); Tinalandia, 9.6 km E of Santo Domingo de los Colorados, S of highway to Alaog and Quito, 3 Apr. 1983, *Croat 55708* (MO); Centinela, cantón Santo Domingo, 23 Aug. 1978, *Dodson et al. 7181* (F); Congoma Grande, at km 23 on the Santo Domingo-Puerto Limón road, 4 Jun. 1982, *Kvist & Holm-Nielsen 40095* (QCA), 7 Jun. 1982, *Kvist & Holm-Nielsen 40132* (QCA), 21 Jul. 1982, *Kvist 40672* (QCA). COTOPAXI: Tenefuerte, Río Pilaló, Latacunga, 7 Feb. 1982, *Dodson & Gentry 12204* (MO); Tenefuerte, km 52-54 Quevedo-Latacunga, 9 Apr. 1984, *Dodson & Thurston 14228* (MO); road Quevedo-El Corazón, 9 km ENE of Moraspungo, 13 May 1980, *Harling & Andersson 19044* (F, GB, QCA). PASTAZA: Curaray, SE of the airstrip, 20 Mar. 1980, *Holm-Nielsen et al. 22242* (AAU, QCA), 22 Mar. 1980, *Holm-Nielsen et al. 22511* (AAU, QCA); Río Papayacu at Río Curaray, 23 Mar. 1980, *Holm-Nielsen et al. 22595* (AAU, QCA); Río Bobonaza, between Cachitama and the outlet of Río Bufeo, 19 Jul. 1980, *Øllgaard et al. 34718* (AAU, QCA), *Øllgaard et al. 34808* (AAU, QCA); between destacamento Chiriboga and Apachi Entza, 24 Jul. 1980, *Øllgaard et al. 35190* (AAU, QCA). MORONA-SANTIAGO: between La Esperanza and Santa Ana, Huamboya, 15 Feb. 1944, *Acosta-Solís 7436* (F); Guaruma, km 38 carretera Saloya, 20 Aug. 1945, *Acosta-Solís 11010* (F); Taisha, Río Panguientza, 21 Jun. 1980, *Brandbyge & Asanza 32175* (AAU, QCA); Pumpuentza, 1 km E of village, 28 Jun. 1980, *Brandbyge & Asanza 32353* (AAU, QCA); road Limón (General Plaza)-Macas, ca. km 20 from Limón, 26 Mar. 1974, *Harling & Andersson 12909* (GB, MO); Misión Bomboiza, 23 Apr. 1973, *Holm-Nielsen et al. 4288* (AAU, F, MO). ZAMORA-CHINCHIPE: Río Nangaritza, Colina Salada, 8 Dec. 1990. *Øllgaard 98482* (QCA), *Øllgaard 98457* (QCA).

PERU. AMAZONAS: Río Cenepa, Kayamas creek, 5 km N of confluence of Huampani and Cenepa, 4 Dec. 1972, *Berlin 451* (MO); Puerto Nazareth, 22 Dec. 1970, *Ellenberg 3490* (LPB); Nazareth, 14 Sep. 1912, *Osgood 26* (F), *Osgood 27* (F). SAN MARTIN: San Martín, Caserío El Progreso, on Tarapoto-Yurimaguas road,25 Sep. 1986, *Knapp & Mallet 8415* (MO, NY); Mariscal Cáceres, Tocache Nuevo, Puerto Pizana, 14 Jun. 1974, *Schunke V. 6952* (F, MO, UC). LORETO: near Tuta Pishco on Río Napo, 16 Sep. 1972, *Croat 20293* (MO); Maynas, Quebrada Yanamono, Río Amazonas, 15 Nov. 1979, *Gentry & Jaramillo 28084* (MO); Maynas, dist. Iquitos, 11 Aug. 1978, *Hickok 612* (GH); Nauta, Quebrada de Sapira, caserío Florida, 26 May 1979, *McDaniel & Rimachi 22536* (NY); Maynas, Iquitos, 26 Jun. 1984, *Moran 3649* (F, MO, UC); Gamitanacocha, Río Mazan, Feb. 1935, *Schunke s.n.* (US, USM); 9 Feb. 1935, *Schunke 205* (F, GH, NY, S, UC, US). PASCO: Prov. Oxapampa, Palcazú valley, Iscozacin, 10 Jan. 1984, *Foster et al. 7833* (F); Río Alto Iscozacín, Ozuz to Río Pescado, 12 May 1985, *Foster & d'Achille 10113* (F); Prov. Oxapampa, Quebrada Castilla, Amuesha community on Río Omaiz, 10 Jun. 1987, *León & Young 1065* (MO, USM). JUNIN: Pichis trail, Santa Rosa, 6,7 Jul. 1929, *Kiilip & Smith 26176* (US); E of Satipo, Aug. 1940, *Ridoutt s.n.* (US). AYACUCHO: La Mar, between Tambo San Miguel, Ayna and the Hacienda Luisiana, 20 Aug. 1968, *Dudley 11908* (GH). CUSCO: La Convención, along Río Klause, 15 Jun. 1968, *Dudley 10181* (GH); Urubamba, Machu Picchu, on the Río Mandor, 2.5 km from Machu Picchu, 2 Jun. 1982, *Peyton & Peyton 379* (MO); Quispicanchis, Quincemil, May 1951, *Vargas 10090* (UC); Paucartambo, Hacienda Villa Carmen, 19 Jul. 1963, *Vargas 14679* (GH); Quispicanchis, Punkiri, 14 May 1964, *Vargas 15414* (GH). MADRE DE DIOS: Tambopata, SSW of Puerto Maldonado, Tambopata Natural Reserve, 19 Apr. 1980, *Barbour 4853* (F, MO), 10 May 1980, *Barbour 5216* (F, MO); Prov. Manu, Atalaya, vic. Hacienda Amazonía, 12 Dec. 1983, *Foster & Wachter 7428* (F); on trail between lodge and Río La Torre, 2 Jun. 1986, *Funk et al. 8379* (US); Tambopata Wildlife Reserve, 30 km S of Puerto Maldonado, 2 Dec. 1984, *H.J. Young & Stratton 330* (MO); Tambopata, Explorer's Inn, 39 km SW of Puerto Maldonado, 24 Jan. 1989, *S.F. Smith et al. 1576* (US); Tambopata Reserve, junction of Río La Torre and Río Tambopata, 16 Mar. 1981, *Young 121* (MO, NY, UC).

BOLIVIA. PANDO: Manuripi, 21 km from Puerto Rico, towards Conquista, 28 Jan. 1983, *Fernández Casas & Susanna 8513* (MO); Nicolas Suarez, SW of Cobija, on Río Naraueda, 1 Aug. 1982, *Sperling & King 6460* (MO). LA PAZ: Larecaja, Consata, 7 km hacia Mapiri, 14 Dec. 1971, *Beck 4917* (LPB); Antahuacana, Jun. 1909, *Buchtien 2156* (BM, S, UC); Polo Polo bei Coroico, 1912, *Buchtien 3536* (F, S, US); Murillo, 44 km below lago Zongo dam, 12-15 Sep. 1983, *Solomon 10853* (MO).

BRAZIL. ACRE: 25-30 km NW of Rio Branco, on road to Sena Madureira, 25 Feb. 1978, *Anderson 12123* (F). TERRITORIO DO RORAIMA: vic. Auaris, 6 Feb. 1969, *Prance et al. 9657* (AAU, F); Serra dos Surucus, 6 Feb. 1971, *Prance et al. 13516* (AAU, F). PARÁ: Marabá, 1 Jun. 1982, *Secco et al. 404* (F); Serra dos Carajás, 10 Jun. 1982, *Sperling et al. 6068* (F). RONDONIA: Rio dos Pacaás Novos, 22 Mar. 1978, *Anderson 12235* (F).

Campyloneurum repens is characterized by its acuminate stem scales with differentiated margins. It is closely related to *C. ophiocaulon*, from which it differs by the obtuse stem scales.

39. *Campyloneurum rigidum* J. Sm., Cult. Ferns 13. 1857. Type. Cultivated, from Tropical America, *Herb. J. Smith s.n.* (probably type collection, BM!).

Polypodium rigidum (J. Sm.) Lowe, Ferns 2, t.37a. 1858. *Nom. nud.* Not *Polypodium rigidum* Aublet, 1775; Hoffman, 1795; Hooker & Greville, 1829.

Stem creeping, dark stramineous, not pruinose, 2-4 mm wide. Stem scales dark brown in mass, 2-3 mm long, 1-1.5 mm wide, ovate, the cells oblong, central cell walls 10-15 µm thick, marginal cell walls 5 µm wide. Phyllopodia 0.5-1 mm long, 1-2 mm wide, 2-4 mm apart. Leaves 30-55 cm long; petiole green stramineous, (2.5-) 3.5-6 (-7) cm long, slightly ranurate adaxially, convex abaxially, rarely with spreading scales, similar to those on the stem; lamina linear-lanceolate or narrowly lanceolate, bases and apices attenuate, (1-) 1.5-2.5 cm wide, coriaceous, green yellowish shining on both sides of the lamina, margin cartilaginous, repand, indument of inconspicuous, scarce, bicellular, simple glandular hairs scattered abaxially, hypostomatic, stomata not seen; costa prominent, slightly ranurate adaxially, convex or slightly angulate abaxially, primary veins inconspicuous, secondary veins forming 2-3 primary areoles between the costa and margin, primary areoles symmetrically divided, each secondary areole with one free excurrent veinlet; sori subterminal, paraphyses and spores not seen. Fig. 47.

This species is known from southern Brazil, where it grows as a terrestrial between 50 m and 800 m elevation.

REPRESENTATIVE SPECIMENS: BRAZIL. RIO DE JANEIRO: Rio de Janeiro, *Glaziou 2073* (S); Rio de Janeiro, *Sellow 1815* (BM). SÃO PAULO: Ribeira, May 1911, *Brade 5099* (S); Morro das Pedras, 1922, *Brade s.n.* (US); Feb. 1928, *Brade s.n.* (UC); Capivary, Mar. 1897, *Gerdes 38* (UC); Tietê, 23 Dec. 1906, *Gerdes 60* (S); Campinas, 27 May 1905, *Heiner 484* (S); Santos, 20 Mar. 1875, *Mosén 3745* (BM, S); Toledo, 18 Feb. 1903, *Ulricht 24* (S); Santos, Guarujá, Jan. 1907, *Usteri 22087* (BM); Alto da Serra, *Wacket 139* (S). PARANÁ Mun. Antonina, Serrinha, 30 Nov. 1983, *Callejas t al. 1814* (MO); Morretes, 21 Apr. 1904, *Dusén 4458* (S); Jacareí, 24 Sep. 1908, *Dusén 6607* (BM, S); Río Uruguay, 31 May 1911, *Dusén 11782* (S); Porto da Cima, 30 Jul. 1912, *Dusén 14168* (S); Jacareí, 11 Nov. 1915, *Dusén 17327* (BM, GH, S); Paranaguá, Praia de Mendanha, 13 Aug. 1961, *Hatschbach 8205* (US). SANTA CATARINA: Santa Catarina, *Gaudichaud 268* (F); Hammonia, Jun. 1911, *Luederwaldt 634* (BM); Joinville, 1906, *Müller 398* (BM); Brusque, 30 Aug. 1947, *Reitz 1839* (S); Morro da Lagoa, Ilha de Santa Catarina, 2 Aug. 1945, *Hno. Rohr 325* (US); Joinville, 15 Jul. 1901, *Schmalz 38* (F).

Campyloneurum rigidum is characterized by having light-green shiny leaves and adpressed stem scales. It belongs to the *C. amphostenon* group.

40. *Campyloneurum solutum* (Klotzsch) Fée, Gen. Filic. 258. 1852.

Polypodium solutum Klotzsch, Linnaea 20: 399. 1847. Lectotype (chosen here) Colombia, *Moritz 309* (B, BM!). Syntype. Without locality: 1843, *Hartweg 1493* (B!, isolectotypes BM!, LD!).

Polypodium nodosum Klotzsch, Linnaea 20: 400. 1847. Type. Colombia, Páramo de la Culata, *Moritz 310* (holotype B!, isotypes, BM!).

Campyloneurum nodosum (Klotzsch) Fée, Gen. Filic. 258. 1852.

Campyloneurum jamesoni Fée, Gen. Filic. 259. 1852. Type. Ecuador: Pichincha, Quito, *Jameson s.n.* (holotype,probably P, isotypes BM!).

Polypodium angustifolium f. *remotifolium* Hieron., Bot. Jahrb. Syst. 34: 531. 1904. Type: Colombia, Tolima, Mt. Ruiz, May 1882, *Schmidtchen* (B); and Cauca, Páramo de las Delicias, *Lehmann 4439* (B, isosyntype US!, F!).

Campyloneurum remotifolium (Hieron.) Lellinger, Amer. Fern J. 78: 26. 1988.

Stem long-creeping, black, usually pruinose, 1-3 mm wide. Stem scales shiny dark brown in mass, caducous and spreading, (3-) 4-7 mm long, 1-2 (-2.5) mm wide, narrowly ovate, pseudopeltate, bases auriculate or short auriculate, apices acuminate, slightly clathrate, without differentiate margins, except at the base, the cells narrowly oblong, along the main axes of the scale, cell walls 15 µm thick, cellular lumen yellowish ot translucent. Phyllopodia 1-2 mm long, 1.5-2 mm wide, 5-10 mm apart. Leaves 15-

40 (-60) cm long; petiole stramineous or dark stramineous, 4.5-15 cm long; lamina narrowly lanceolate, bases and apices attenuate, 0.7-2.5 (-3) cm wide, chartaceous, margins cartilaginous, slight or strongly revolute, indument not seen, stomata polocytic; costa prominent, primary veins usually slight prominulous abaxially, more or less concolorous with the adjacent tissue, slightly flexuosous, secondary transverse veins forming 2-3 primary areoles between the costa and margin, each primary areole symmetrical divided, with one free excurrent veinlet; sori medial or subterminal, paraphyses not seen, spores 55-60 µm long, 35-40 µm wide. Fig. 47.

This species is distributed in Colombia, Venezuela, Ecuador, and Perú. It grows in open grassland areas, and high montane forest; usually terrestrial, among rocks, usually between 3000 m and 4500 m elevation.

REPRESENTATIVE SPECIMENS: COLOMBIA: CALDAS: Cordillera Central, Río Otún, towards Nevado de Santa Isabel, 24 Nov. 1946, *Cuatrecasas 23146* (F, S, US); road between Manizales andHotel Termales del Ruiz, 8 Jun. 1966, *Forero et al. 523* (F); road Termales-Refugio, 22 Oct. 1961, *Murillo 464* (F); vic. Termales, 20 km SE of Manizales, 22 Oct. 1961, *Tryon & Tryon 6131* (S, UC, US). CUNDINAMARCA: Macizo de Bogotá, páramo de Palacio, El Tablón, 14 Dec. 1959, *Cuatrecasas 25651* (US). VALLE: Cordillera Occidental, Los Farallones, Alto del Buey, 11,12 Oct. 1944, *Cuatrecasas 17969* (F); Cordillera Central, Río Tulua, Quebrada de Las Vegas, 21-23 Mar. 1946, *Cuatrecasas 20385* (F)
VENEZUELA. MERIDA: Páramo de los Leones (La Lagunita, La Cañada Grande), W de Mucurubá, 31 May 1930, *Gehriger 141* (F); dist. Rangel, Cuenca de la Quebrada Las Escaleras, Páramo de Minugú, 10 km SE de San Rafael de Mucuhíes, 16-17 May 1972, *Ruiz-Terán 7239* (UC); Cerro de Turumiquire, 1925, *Tate 192* (US).
ECUADOR. CARCHI: Páramo El Angel, road El Angel-Tulcán, 15 May 1973, *Holm-Nielsen et al. 5480* (AAU, F, GB, UC); base of Volcán Chiles, km 34-36 on road Tulcán-Páramo Maldonado, 19 May 1973, *Holm-Nielsen et al. 5912* (AAU, F, GB, UC). IMBABURA: Lago San Marcos Cayambe, 28 Nov. 1961, *Cazalet & Pennington 5374* (UC); Laguna Mojanda, Laguna Negra, 22 Sep. 1990, *Øllgaard 98197* (QCA). NAPO: N side of cerro Sumaco, loma NW of campsite, 28 Apr. 1979, *Holm-Nielsen et al. 17398* (AAU, QCA); road Quito-Baeza, 17 Jul. 1976, *Øllgaard & Balslev 8022* (AAU, UC, USM). along Río Topo, SE of Aucacocha, 18 May 1982, *Øllgaard & Holm-Nielsen 38784* (AAU, USM). PICHINCHA: Chaparro de Sebritana, 9 Jul. 1944, *Acosta-Solís 8359* (F); N slope of Volcán Pichincha, 24 Jan. 1981, *Balslev et al. 1743* (AAU, NY, UC); road to Yanacocha, NW of Cerro Pichincha, 3 Oct. 1981, *Balslev 2045* (QCA); 30 Sep. 1982, *Balslev & Steere 3264* (QCA); Volcán Cayambe, 3 Jul. 1980, *Holm-Nielsen & Øllgaard 24333* (AAU, UC); Volcán Iliniza, 14 Aug. 1980, *Holm-Nielsen et al. 25018* (AAU, F); Volcán Atacazo, W slope 17 km from San Juan, 25 Aug. 1980, *Holm-Nielsen & Asanza 25143* (AAU); Volcán Pichincha, Cerro Ventanillas, 9-10 Jan. 1984, *Laegaard 51048* (QCA); Páramo de Guamani, 5 km W of Paso de la Virgen, 8 Feb. 1984, *Laegaard 51368* (QCA); Páramo de Guamani, N of road Pifo-Papallacta, W of the pass, 10 Nov. 1990, *Øllgaard 98237* (QCA); Páramo de Guamani, 16 Jan. 1981, *Proctor 38745* (QCA); NW of Volcán Atacazo, 30 Nov. 1985, *Zak 730* (F, QCA); NW of Volcán Pichincha, 21 Mar. 1987, *Zak 1843* (F). COTOPAXI: Parque Nacional Cotopaxi, al lado W de loma Ingapirca, 2 Oct. 1982, *Balslev 3337* (QCA), *Balslev & Muñoz 3398* (AAU); trail from El Corazón to Facundo Vela, 1-3 km from El Corazón, 17 May 1980, *Harling & Andersson 19194* (AAU, GB); Latacunga-Quevedo road, between Pujilí and Zumbagua, 26 May 1979, *Lojtnant et al. 13695* (AAU, GB, QCA). BOLIVAR: road above Balzapamba, 2 May 1942, *Haught 3299* (S). TUNGURAHUA: Páramo of Miniza, 7 Apr. 1939, *Penland & Summers 351* (F). CHIMBORAZO: road Riobamba-Penipe-Bayuschi-Llurarllacu, 18 Feb. 1987, *Jaramillo 9419* (QCA); Cerro Chiguazo, 24 Sep. 1968, *Lugo 474* (F, GB); 10 km NE of Alao, at Cuspipaccha, 6 May 1982, *Øllgaard et al. 38139* (AAU); road 10 km NE of Alao at Cuspicaccha, 6 May 1982, *Øllgaard et al. 38153* (AAU, QCA). AZUAY: Páramo El Cajas, W of Sayausí and Cuenca, 4 Jan. 1981, *Balslev 1443* (AAU, NY, UC); Páramo de Cajas, 27 Dec. 1976, *Boeke & Loyola 635* (UC); 5-6 km above Angas, 5 Mar. 1985, *Harling & Andersson 22750* (QCA); between Molleturo and Quinoas, 15 Jun. 1943, *Steyermark 53106* (F). LOJA: Alamor-Celica road, 2-3 km S of Río Alamor, 5 Apr. 1980, *Harling & Andersson 17939* (AAU, GB); W side of Laguna Parcacocha,18 Mar. 1979, *Lojtnant & Molau 11149* (AAU, GB, QCA). Without locality. Mar. 1906, *Rimbach 2* (S, US, UC); Gualea, 1888, *Sodiro s.n.* (UC).
PERU. CAJAMARCA: *Sánchez V. 438* (AAU).

Campyloneurum solutum is characterized by its spreading narrowly ovate stem scales, which are dark brown and shiny, with 15-20 narrowly oblong cells at the middle part of the scale, and with a yellowish cellular lumen.

Campyloneurum solutum grows in open areas,

and it usually has small narrowly lanceolate leaves, less than 35 cm long, rarely reaching 60 cm (*Cuatrecasas 17969*).

Campyloneurum solutum and *C. asplundii* might be confused because both have shiny dark brown scales, and the latter grows up to 3500 m elevation. But the leaves of *C. solutum* are usually narrowly lanceolate and the stem is pruinose with well-spaced leaves. *Campyloneurum solutum* belongs to the *C. amphostenon* group.

41. *Campyloneurum sphenodes* (Kunze *ex* Klotzsch) Fée, Gen. Filic. 258. 1852.

Polypodium sphenodes Kunze *ex* Klotzsch, Linnaea 20: 402. 1847. Type. Venezuela, *Moritz 304* (holotype B!; isotypes, BM!, K!).

Polypodium wercklei Christ, Bull. Herb. Boissier 2. 5: 7. 1905. Lectotype (chosen by Lellinger, Amer. Fern J. 78: 28. 1988). Costa Rica: *Werclé s.n.* (P, not seen).

Campyloneurum wercklei (Christ) Lellinger, Amer. Fern J. 78: 28. 1988.

Stem long-creeping, green turning black or dark stramineous, (1-) 2-3 (-4) mm wide. Stem scales light brown or brown in mass, subadpressed, 2-3 mm long, 0.8-1 mm wide, narrowly ovate, bases peltate or slightly auriculate, apices acuminate, clathrate or rarely slightly clathrate, concolorous or bicolorous, margins differentiated at the bases or along the scale, the cells narrowly oblong, some times irregularly arranged, cell lumina transparent, cell walls 10 µm thick. Phyllopodia 1-2 mm long, 1-2 mm wide, 7-25 mm apart. Leaves 25-50 (-65) cm long; petiole stramineous or dark stramineous, 5-20 cm long, ranurate adaxially, convex abaxially; lamina narrowly elliptic or lanceolate, bases narrowly cuneate, short attenuate, apices acuminate or subcaudate, (2-) 4-6 (-9) cm wide, herbaceous-chartaceous, margin cartilaginous, slightly undulate, indument of scarce bicellular hairs; stomata polocytic or copolocytic; costa prominent, primary veins prominulous on both sides of the lamina, stramineous or darker than the leaf tissue, (60°-) 65-70° divergent from the costa, 5-7 mm apart, secondary veins forming 7-12 primary areoles between the costa and margin, transverse tertiary veins inconcpicuous or slightly prominulous, primary areoles undivided, 2 (-3) free excurrent veinlets in each areole; sori subterminal or medial, paraphyses not seen, spores 50-57 µm long, 30-37 µm wide. Figs. 3 a; 48.

This species is known from Costa Rica to Peru, where it grows mostly as an epiphyte between 200 m and 1800 m elevation.

REPRESENTATIVE SPECIMENS: COSTA RICA. ALAJUELA: Reserva Río San Lorenzo, below Fila Volcán Muerte, 14-17 Jul. 1983, *Barringer & Pérez-García 3782* (F); La Palma de San Ramón, 24 Nov. 1923, *Brenes 3968* (F), cataratas de San Ramón, 23 Feb. 1931, *Brenes 13472* (F); los Angeles de San Ramón, 21 Jul. 1932, *Brenes 16138* (F); upper drainage of the Río Peñas Blancas below the Monteverde Nature Reserve, 25-26 Feb. 1977, *Burger et al. 10725* (AAU, F); Cordillera de Tilarán, between San Ramón and Bajo Rodriguez, 26 Sep. 1987, *Croat 68038* (MO); Río Sarapiquí at bridge on road to Colonia Virgen del Socorro, 1 Oct. 1987, *Croat 68337* (MO); Cordillera de Tilarán, 5 May 1976, *Dryer 93* (F); Reserva Monteverde, Cordillera de Tilarán, 1 Jun. 1976, *Dryer 113* (F, MO); 7 mi N of San Ramón, 27 Jul. 1967, *Evans & Bowers 2972* (MO); Monteverde Reserve, Peñas Blancas, 13 Jun. 1986, *Haber et al. 5143* (MO); Monteverde Reserve, on the Atlantic slope, 14 Jun. 1986, *Hammel et al. 15409* (MO); Reserva Forestal de San Ramón, Quebrada Cacical, 2 May 1987, *Herrera et al. 595* (MO, UC); NW of Zarcero, ca. 2 km of Zapote, on road to Santa Elena, 27 Jul. 1970, *Lellinger & White 1357* (MO, US); 25 km NNW of San Ramón, on way to San Lorenzo, 24 Apr 1983, *Liesner & Judziewicz 14765* (MO), *Liesner & Judziewicz 14829* (MO); Vara Blanca de Sarapiquí, Jul-Sep. 1937, *Skutch 3139* (F, MO); la Peña de Zarcero, Cantón Alfaro Ruiz, 11 May 1938, *A. Smith 570* (F); ca. 1 km SE of La Balsa de San Ramón, 3 Feb. 1986, *A.R. Smith et al. 2295* (UC); Río San Rafael, cantón Aguas Zarcas, 8 Feb. 1965, *L.O. Williams et al. 29062* (F). HEREDIA: NW slope of Volcán Barba, 2 km NE of los Cartagos, 16 Mar. 1986, *Grayum & Yatskievych 6638* (MO, UC); La Selva, along Río Viejo, 1 Feb. 1988, *Hennipman et al. 7152* (MO); near the Río Segundo, 2 km SW of Cerro Chompipe, 12 Jul. 1970, *Lellinger & White 1110* (F); base of the Cerro Zurquí, 8 Jul. 1973, *Lent 3567* (F); road between San Rafael and Río Las Vueltas, 4 Sep. 1979, *Stevens 13972* (F, MO). ALAJUELA-HEREDIA: Vara Blanca, N slope of Central Cordillera, Poas-Barba, 12 Jul. 1940, *Chrysler 5048* (MO); Vara Blanca de Sarapiquí, N slope of Central cordillera, Jul.-Sep. 1937, *Skutch 3139* (F, MO, NY, S). LIMON: path beyond Río Sucio, May 1984,

Gómez et al. 22753 (MO). PUNTARENAS: W side of Fila Gamba, ca. 6 km from Golfito airport, 6 Mar. 1985, *Croat & Grayum 59921* (MO); Monteverde reserve, along Río Peñas Blancas, 14 Jun. 1986, *Hammel et al. 15409* (MO); Monteverde Reserve, Pacific slope, 5 Nov. 1986, *Haber & Bello 6199* (MO); Monteverde, 19 Jun. 1979, *Koptur SK-150* (UC). SAN JOSE: valley of the Río Hondura, below La Palma, NE of San Jerónimo, 15 May 1968, *Burger & Stolze 4867* (F); La Palma area, NE of San Jerónimo, above La Hondura, 15 Sep. 1978, *Burger & Antonio 11063* (F); Virgen del Socorro-Río Sarapiquí-Cariblanco, 31 Aug. 1983, *Chacón & Herrera 1224* (MO); on western ascent of Cerro de La Muerte, 27 Feb. 1976, *Croat 32849* (MO); 1 mi beyond divide between San Isidro del General and Dominical, 22 May 1976, *Croat 35277* (MO); 10 km N of San Rafael de Heredia, on Volcán Barba, 30 Jul. 1967, *Lellinger 791* (MO); ca. 15 km N of Tres Ríos, ca. 4 km N of Cascajal, 2 Aug. 1970, *Lellinger & White 1393* (US); above Río Cascajal, 3 km NE of Cascajal, 26 Sep. 1971, *Lent 2176* (F); above Río Hondura, 10 Mar. 1973, *Lent 3229* (F); Bajo La Hondura area, 4 Jul. 1972, *McAlpin et al. 1186* (F); Pan Am hwy. above San Isidro de General, 17 Nov. 1973, *McAlpin 2383* (MO); Parque Nacional Bravillo Carrillo, 19 Jul. 1983, *Moran 3281* (F); along the road to La Hondura, 8 Apr. 1956, *Scamman & Holdridge 8074* (GH); vic. of El General, Aug. 1936, *Skutch 2840* (MO, NY, S); along unnamed N fork of Río Zurquí, Cordillera Central, 18 Jan. 1986, *A.R. Smith 1696* (MO); above La Hondura valley, La Palma area, 23 Mar. 1973, *Stolze 1434* (F, UC), *Stolze 1446* (MO); S slopes of Cerro Zurquí, 5 km N of San Luis Norte, 28 Mar.-4Apr. 1973, *Stolze 1561* (UC); Alto de La Palma, ca. 5 km N of San Jerónimo, 18 Aug. 1975, *Utley & Utley 2900* (F). CARTAGO: Carpintera, 10 Apr. 1908, *Brade & Brade 45* (NY, S, UC); 10 km S of Tapantí, above the Río Grande de Orosí, 10-24 Jun. 1968, *Burger & Stolze 5633* (F, MO); Tapantí, near banks of Río Grande de Orosí, 24 Jun. 1968, *Burger & Stolze 6089* (F); along tributary of Quebrada Casa Blanca Tapantí, 6 Aug. 1984, *Grayum & Sleeper 3680* (MO, UC); Tapantí, valley of Río Reventazón, 18 Mar. 1956, *Scamman & Holdridge 8073* (GH); above the Río Grande de Orosí, 25 Mar. 1973, *Stolze 1479* (F); Cerro Carpintera, 7 mi W of Cartago, 7 Mar. 1928, *Stork 1186* (UC, US); Naranjo, S of Cartago, 4 May 1928, *Stork 1822* (UC). CARTAGO-SAN JOSE: NW of Cartago, 3 Apr. 1928, *Stork 1360* (UC); Cerro Carpintera, 23 May 1928, *Stork 2135* (UC).

PANAMA. CHIRIQUI: Cerro Colorado, near Continental divide, 26 Jul. 1979, *Antonio 1463* (MO); road to Fortuna dam, N of Gualaca, 22 Nov. 1979, *Antonio 2766* (MO); road between Gualaca and the Fortune, NW of los Planes de Hornito, 10 Apr. 1980, *Antonio 4171* (MO); Cerro Horqueta, 24 Jul. 1966, *Blum & Dwyer 2615* (MO); Fortuna dam area, at the Continental divide, 6 Feb. 1984, *Churchill et al. 4661* (MO, UC); Fortuna dam area to N of reservoir near Quebrada Bonito, 30 Jul. 1984, *Churchill 5799* (MO); El Boquete, Dexter trail, 7 Feb. 1918, *Cornman 865* (MO); vic. of Planes de Hornito, beyond Gualaca, 28 Nov. 1979, *Croat 48858* (MO); along road between Fortuna lake and Chiriquí Grande, 8 Mar. 1985, *Croat & Grayum 59977* (AAU, MO, UC); Boquete district, Bajo Chorro, 11 Jan. 1938, *Davidson 106* (F); Cerro Horqueta, 1 Jul. 1968, *Dwyer & Lallathin 8763* (MO); La Fortuna hydroelectric project, 20 Mar. 1978, *Hammel 2035* (MO); Palo Alto, 4.5 mi NE of Boquete, along E fork of Palo Alto river, 26 May 1979, *Hammel 7510* (MO); S slopes of Cerro Pate Macho, along Río Palo Alto, 11 Nov. 1981, *Knapp et al. 2028* (MO); near Fortuna dam, along Quebrada de Arena, 6 Dec. 1985, *McPherson 7802* (MO); N of San Felix at Chiriquí-Bocas del Toro border, 4 May 1975, *Mori & Kallunki 5860* (NY, US); Cerro Colorado, 50 km N of San Felix, 17 Aug. 1975, *Mori & Dressler 7808* (MO); along trail between N fork of Río Palo Alto and Cerro Pate Macho, 6 Feb. 1986, *A.R. Smith 2311* (MO, UC); along Río Caldera, ca. 3.5 km NW of Bajo Mono, 8 Feb. 1986, *A.R. Smith 2460 et al.* (MO, UC); SE slopes and summit of Cerro Pate Macho, 4 km NE of Boquete, 26 May 1981, *Sytsma et al. 4886* (MO), 27 May 1981, *Sytsma et al. 4998* (MO). VERAGUAS: NW of Santa Fé, 20 Dec. 1974, *Mori et al. 3958* (MO). BOCAS DEL TORO: 10-15 mi S from mouth of Changuinola river, 18 Dec. 1966, *Lewis et al. 994* (UC). COCLE: La Mesa region, N of Cerro Gaital, 2 Jul. 1978, *Hammel 3862* (MO). DARIEN: S of El Real on trail up Cerro Pirre, 29 Mar. 1985, *McPherson 7036* (MO, UC); on ridge of cerro Pirre, 14 Sep. 1989, *McPherson 14082* (F).

COLOMBIA. CAUCA: near Cerro Munchique, 5 Nov. 1968, *Espinal & Ramos 3201* (MO). CHOCO: Mun. Río Sucio, Alto Limón, 4 Jun. 1978, *Forero et al. 1812* (MO). Without locality: *Triana 99* (W).

VENEZUELA. FALCON: Sierra San Luis, near Hotel Parador, 25 Aug. 1978, *Wingfield & Werff 6565* (MO). TRUJILLO: near Vitú, Cerro El Zamuro, Quebrada El Limón, 23 Nov. 1984, *Ortega & Werff 2292* (MO, UC). LARA: dist. Morán (Andrés Eloy Blanco), 4 mi SE of Sanaré, Parque Nacional Yacambú, 13 Nov. 1982, *A.R. Smith et al. 1195* (MO).

ECUADOR. CARCHI: Maldonado, km 60 on road Tulcán-Maldonado, 18 May 1973, *Holm-Nielsen et al. 5782* (AAU, F, MO, UC); above San Marcos de los Coaiqueres, on trail towards Gualpí Bajo, 7 Feb. 1985, *Øllgaard et al. 57533* (AAU). PICHINCHA: road El Paraíso-Saguangual, 3 km from El Paraíso, 2 May 1982, *Øllgaard et al. 37798* (AAU); along road SE from La Aurora, passing through La Reforma, 24 Jul. 1990, *Øllgaard 98060* (AAU). BOLIVAR: road Chillanes-Bucay, 29 Aug. 1987, *Zak & Jaramillo 2571* (F, MO). CHIMBORAZO: Sibambe, Hacienda La Carmela, 18

Aug. 1943, *Acosta-Solís 5389* (F); valley of the Río Chanchan, about 5 km N of Huigra, 19-28 May 1945, *Camp E-3381* (F, MO, UC). AZUAY: between Cruz Pampa and Loma de Canela, in region of the Río Sadacray, 12 Jun. 1943, *Steyermark 52959* (F, US). SANTIAGO-ZAMORA: between Río Sordo and La Esperanza, road to Huamboya, 13 Feb. 1944, *Acosta-Solís 7318* (F). ZAMORA-CHINCHIPE: río Nangaritza, Colina Salada, c. 2 km of Destacamento Shaime, 8 Dec. 1990, *Øllgaard 98482* (AAU).
PERU. PIURA: Canchaque, near Chorro Blanco, 4 Nov. 1985, *Ramirez & Lamas s.n.* (USM). CAJAMARCA: Santa Cruz, dist. Catache, upper Río Zaña, ca. 5 km above Monte Seco, 2-4 May 1987, *Dillon et al. 4901* (F). AMAZONAS: Bagua, Cordillera Colán, SE of La Peca, 7 Oct. 1978, *Barbour 3893* (MO). HUANUCO: La Divisoria, near Ucayali border, 29 Mar. 1977, *Gentry et al. 18821* (MO). PASCO: Pozuzo, 20-22 Jun. 1923, *Macbride 4581* (F, US); Oxapampa, 4-5 km N of Mallampampa, 22 Jan. 1984, *D.N. Smith & Canne 5802* (MO). JUNIN: E of Quimirí bridge, near La Merced, 1-3 Jun. 1929, *Killip & Smith 23896* (F, GH, US); Colonia Perené, 14-22 Jun. 1929, *Killip & Smith 24917* (F, NY, US). AYACUCHO: Aina, between Huanta and Río Apurímac, 7-17 May 1929, *Killip & Smith 22720* (NY, US).

Campyloneurum sphenodes is recognized here in a broad sense. It is defined by its stem scales with differentiated margins along the length of the scale or at its bases. Stem scales are concolorous or bicolorous, depending on the development of the margin. Stem color is variable in herbarium material and in this study therefore this character is not considered to be taxonomically important.

Campyloneurum sphenodes might be confused with *C. coarctatum*. But stem scales in *C. sphenodes* are adpressed, lanceolate or narrowly lanceolate, and usually more than 0.8 mm wide, with differentiated margins. *Campyloneurum sphenodes* is closely related to *C. sublucidum*, from which can be differen-tiated by the characters used in the key.

42. *Campyloneurum sublucidum* (Christ) Ching, Sunyatsenia 5: 263. 1940.
Polypodium sublucidum Christ, Bull. Herb. Boissier sér. 2, 7: 261. 1907. Type. Costa Rica, *Wercklé 17051* (holotype, P!, isotype BM!).

Stem long creeping, stramineous, dark brown, not pruinose, 2-3 mm wide. Stem scales light brown in mass, persistent, 2-4.5 mm long, 1-1.5 mm wide, ovate, pseudpeltate, bases auriculate, apices acuminate, slightly clathrate, the cells oblong, lumen yellow, cell walls 5-9 µm thick. Phyllopodia 0.5 mm long, 1 mm wide, 10-25 mm apart. Leaves 15-25 cm long; petiole stramineous, (2.5-) 8-10 cm long; lamina elliptic-lanceolate, base cuneate, apices caudate, 2-5 cm wide, chartaceous or subcoriaceous, indument of scattered simple hairs and deciduous scales; stomata polocytic, 49-61 µm long, 67 µm wide; costa prominent, primary veins inconspicuous or slight prominulous adaxially, 50-55º divergent from the costa, 5-7 mm apart, secondary transverse veins forming 5-6 areoles between the costa and margin, primary areoles usually undivided,
(1-) 2 free excurrent veinlet in each areole, sometimes marginal areoles without excurrent veinlets; sori subterminal, paraphyses not seen; spores 55-60 µm long, 30-36 µm wide. Fig. 49.

This species is known from Costa Rica and Ecuador, where it grows pendent in calacareous rocks, in low montane or lowland forests, in very shady places at 700-1500 m elevation.

EXAMINED SPECIMENS: COSTA RICA. SAN JOSE: above the Río La Hondura, 28 Jan. 1979, *Montgomery & Huttleston 79-102* (US). CARTAGO: 12 km S of Turrialba, 4 km SE of Pejibaye, along Río Gato, 16-17 Apr. 1983, *Liesner 14426* (MO, UC); vic. of Pejivalle, 7-8 Feb. 1926, *Standley & Valerio 47108* (US). HEREDIA: road between San Rafael and Río Vueltas, 4 Sep. 1979, *Stevens 13972* (AAU, F).
ECUADOR. MORONA-SANTIAGO: km 35 of road Gualaquiza-Limón, 4 Mar. 1992, *Øllgaard 98* (AAU, F, QCA).

Campyloneurum sublucidum has yellowish, persistent stem scales, and its leaves are chartaceous subcoriaceous with a glossy surface. This species belongs to the *C. sphenodes* group.

43. *Campyloneurum tenuipes* Maxon, Contr. U.S. Natl. Herb. 13: 7. 1909. Type. Guatemala: Alta Verapaz, near Cobán, Sep. 1907, *von Türckheim II 1952* (holotype, US, photo of US, BM!).
Polypodium tenuipes (Maxon) C. Christ., Index Filic. Suppl. 63. 1913.

Stem dark stramineous or black, not pruinose, 4-7 mm wide. Stem scales dark brown or black in mass, 6-10 mm long, 2-2.5 mm wide, narrowly ovate, pseudopeltate, bases auriculate, apices acuminate, clathrate, the cells oblong, along the main axes of the scale, cell walls (5-) 12.5-17.5 µm thick. Phyllopodia 1-2 mm long, 1.5-2.5 mm wide, 2-4 mm apart. Leaves 40-80 cm long; petiole brown stramineous, 8-18 cm long; lamina narrowly lanceolate or lanceolate, bases attenuate or narrowly cuneate, apices usually caudate, 5-8 cm wide, chartaceous, margins slightly cartilaginous, repand or sinuate, indument of scarce bicellular hairs; stomata polocytic and/or copolocytic, rarely anomocytic; costa prominent, slightly ranurate adaxially, angular abaxially, primary veins prominent or prominulous on both surfaces of the lamina, stramineous, slightly flexuosous, (55º-) 60-70º divergent from the costa, 5-6 mm apart, secondary veins inconspicuous or slightly prominulous, same color as the leaf tissue, transverse veins forming 6-9 primary areoles between the costa and margin, primary non-costal areoles usually symmetrically divided, 1 free excurrent veinlet in each secondary areole, marginal areoles sometimes irregularly divided; sori subterminal or supramedial, paraphyses not seen, spores 60-70 µm long, 35-40 µm wide. Chromosome number 2*n*=74. Fig. 24.

This species is distributed from Mexico to Guatemala and Honduras, where it grows mostly as terrestrial between 1200 m and 2400 m elevation.

REPRESENTATIVE SPECIMENS: MEXICO. MICHOACAN: Galena, Río de las Selvas, 3 Jan. 1938, *Hinton et al. 11177* (US). VERACRUZ: Alto Lucero, La Piedra Cuata, between Plan de las Hayas and Rancho Nuevo, 7 Apr. 1981, *Castillo & Vásquez 1354* (F); Teocillo Cañón, just before Teocillo, 11 Aug. 1966, *Knobloch 2195* (US). OAXACA: above San Gabriel, *Mickel s.n.* (UC); Pochutla, 185 km S of Oaxaca, 60 km N of Pochutla, 29 Sep. 1970, *Mickel & Leonard 5097* (UC); dist. Juquila, 96 km S of Sola de Vega, 33 km N of San Gabriel, 9 Aug. 1971, *Mickel 6050* (UC). CHIAPAS: Mun. Berriozabal, 13 km N of Berriozabal, 2 Nov. 1971, *Breedlove & A.R. Smith 21686* (F, NY); Mun. Villa Corzo, SW of Colonia Agrónomos Mexicanos, at the E base of Cerro Tres Picos, 4 May 1972, *Breedlove 25053* (MO); Mun. Ocozocautla de Espinosa, Cerro del Ocote, 30 km NW of Ocozocautla, 14 Oct. 1972, *Breedlove 28894* (F); Mun. San Andrés Larrinzar, near the summit of Chuchil Ton, NE of Bochil, 1 May 1973, *Breedlove 34590* (MO); between Rizo de Oro and Cerro Baul, 9.2-10.4 mi N of Rizo de Oro, 15 Feb. 1979, *Croat 47627* (MO); 1864-1870, *Ghiesbreght 292* (BM); Motozintla, Mt. Boquerón, 1 May 1945, *Matuda 15343* (F); San Juan de Panamá, Escuintla, 28 Jul. 1948, *Matuda 18051* (F, US); Libertad, Acocayagua, 3 Jul. 1948, *Matuda 18145* (F); Simojovel, Tierra Caliente, 1900, *Munch 9* (US); Mun. Unión Juarez, Volcán Tacaná, near trail to Talquián, 4 Feb. 1987, *Martínez et al. 19148* (F). GUATEMALA. ALTA VERAPAZ: 14 mi E of Cobán, 18 Jul. 1977, *Croat 41467* (MO); along Río Carchá, between Cobán and San Pedro Carchá, 26, 27 Mar. 1941, *Standley 90037* (F); along Río Frío, about 8 km below Tactic, 1 Apr. 1941, *Standley 90834* (F); 1-8 km NW of Cobán, 4 Jan. 1973, *L.O. Williams et al. 42001* (AAU, F). SAN MARCOS: 10 mi S of San Marcos, 13 Jul. 1977, *Croat 41011* (MO); 6 mi SW of town Tajumulco, NW slopes of Volcán Tajumulco, 26 Feb. 1940, *Steyermark 36670* (F); Sierra Madre Mountains, between San Rafael Pie de la Cuesta and Palo Gordo, 10-18 Dec. 1963, *L.O. Williams et al. 25807* (F, NY). QUEZALTENANGO: slopes of Volcán Zunil, at and above Aguas Amargas, 17 Feb. 1939, *Standley 65424* (F); Aguas Amargas 14 Jan. 1941, *Standley 83288*I(nr; region of Boxantin, SE of San Martin Chile Verde, 16 Jan. 1941, *Standley 83834* (F, US), along Río Samalá, near Santa María de Jesús, 25 Jan. 1941, *Standley 84586* (UC); along old road betwen Finca Pirineos and Palzulin, 9 Feb. 1941, *Standley 87148* (F); on SE slopes of Volcán Santa María, 18 Jan. 1940, *Steyermark 34372* (F). SOLOLÁ: Sierra Madre Mountains, near Nahuala, 17 Dec. 1962, *L.O. Williams et al. 23211* (F, US). HONDURAS. FRANCISCO MORAZAN: Montaña La Tigra, 30 km NE of Tegucigalpa, 5 Jun. 1977, *Alduvía et al. 266* (MO); Montaña La Tigra, 17 Apr. 1983, *Guerra 152* (MO); 20 km fromTegucigalpa, 5 Jun. 1977, *Ochoa 61* (MO); 20 km from Tegucigalpa, 5 Jun. 1977, *Rubio 94* (MO); Valle de Angeles, 20.8 km NE of Tegucigalpa, Pinares, *Soihet 66* (UC).

Campyloneurum tenuipes is characterized by conspicuously petiolated leaves and linear lanceolate stem scales. It belongs to the *C.phyllitidis* species group.

44. *Campyloneurum tucumanense* (Hieron.) Ching, Sunyatsenia 5: 263. 1940.
Polypodium tucumanense Hieron., Bot. Jahrb. Syst.

22: 405. 1896. Type. Argentina, Tucumán, Quebrada Monteros, 5 Apr. 1872, *Lorentz 304* (holotype, B!; isotype. CORD, n.v.)

Terrestrial or sometimes epipetric. Stem dark stramineous, not pruinose, 8-25 mm wide, scales brown, 5-6 mm long, (1.5-) 2-2.5 mm wide, lanceolate, ovate lanceolate, bases auriculate, apices acuminate, clathrate, cells oblong, marginal cells irregularly arranged, central cells along main axes of the scale, cell walls 15 µm wide. Phyllopodia 5-6 mm long, 6 mm wide, 2-5 mm apart. Leaves (80-) 95-120 cm long; petiole green stramineous, stramineous, 12-20 cm long, ranurate adaxially, convex abaxially, with scales at the base similar to those at the stem; laminae lanceolate, bases attenuate, apices subcaudate or acuminate,
7-9.5 (-14) cm wide, membranaceous or herbaceous, margins sinuate, cartilaginous, indument of inconspicuous, scarce bicellular hairs, stomata not seen; costa prominent, primary veins prominent, stramineous, 65-70º divergent from the costa, 5-8 mm apart, secondary veins slightly prominulous, slightly stramineous or darker than the leaf tissue, transverse veins forming 12 primary areoles between the costa and margin, primary areoles usually asymmetrical divided in 2-3 secondary areoles, 3-4 excurrent veinlets in each primary areole, simple or furcate, ; sori medial or subterminal, 2-3 rows between secondary veins, paraphyses not seen, spores 52 µm long, 35 µm wide. Chromosome number unknown. Fig. 44.

Campyloneurum tucumanense is known only from Bolivia and Argentina. It grows between 1000 m and 1500 m elevation, usually as a terrestrial in shady habitats.

REPRESENTATIVE SPECIMENS: BOLIVIA. LA PAZ: Murillo, Valle de Zongo, Cahua, 7 Apr. 1979, *Beck 1219* (F). ARGENTINA. TUCUMAN: Quebrada Montero, 5 Apr. 1872, *Lorentz 780* (F); Tafí, Rodeo Aspero, 14 Apr. 1926, *Schreiter 4344* (GH); Quebrada de los Sosa, 2 Sep. 1957, *Sota 1672* (S, US). MISIONES: Libertador General San Martín, Gruta 3 de Mayo, 9 Nov. 1974, *Krapovickas & Cristóbal 26638* (MO).

This species belongs to the *Campyloneurum brevifolium* group. It is closely related to *C. pascoense*. Future cytological studies could reveal their affinities. The main difference to recognize *C. tucumanense* as a different species from *C. pascoense* is the remarkable herbaceous texture of the leaf in the former species.

45. *Campyloneurum vulpinum* (Lindman) Ching, Sunyatsenia 5: 263. 1940.

Polypodium vulpinum Lindman, Ark. Bot. 1: 245. 1903. *Nom. nov*. for *Polypodium laevigatum* Cav. var. *crispatum* C. Christ.

Polypodium laevigatum Cav. var. *crispatum* C. Christ., Bot. Tiddskr. 25: 79. 1903. Type. Brazil, Minas Geraes, Serra de Caldas, 25 Oct. 1873, *Mosén 2220* (holotype, S!; isotypes BM!, US!).

Epiphyte. Stem long creeping, not pruinose, 1-2 mm wide, scales ferrugineous, slightly clathrate, 4-7 mm long, 0.6-1.2 mm wide, linear lanceolate, bases peltate, rarely slightly auriculate, apices acuminate, cells oblong along the main axes of the scale. Phyllopodia 0.5-1.5 mm long, 0.5-1 mm wide, 7-15 mm apart. Leaves 15-45 cm long; petiole stramineous to dark stramineous, 4-12 cm long; laminae linear lanceolate or narrowly lanceolate, bases attenuate, apices acuminate, 1.5-3 cm wide, herbaceous, margins slightly cartilaginous, sinuate or undulate, indument formed by scarce bicellular hairs; stomata polocytic; costa prominent, primary veins inconspicuous or slightly prominulous on both sides of the lamina, same color as the leaf tissue, 30-40º divergent from the costa, 4-7 mm apart, primary veins forming 2-4 primary areoles between the costa and margin, primary areole usually isodiametric divided; sori subterminal, paraphyses dendritic, spores (50-) 60-70 (-90) µm long, (30-) 35-40 (-50) µm wide. Figs. 3d; 7 b; 16 b; 49.

This species is known from Haiti, and the Dominican Republic, and from Ecuador to Bolivia and central Brazil, where it grows above 1000 m elevation, mostly as an epiphyte.

REPRESENTATIVE SPECIMENS: HAITI. Massif de la Selle, Morne Trauchant, 13 Sep. 1924, *Ekman 1892* (BM, F, S); Morne des Commissaires, Grand Gosier, at

ravine Fanchon, 4 Sep. 1926, *Ekman 6885* (S); Massif de la Holle, M. Columette, 26 Nov. 1926, *Ekman 7324* (S); Massif de la Selle, Croix des Bouquets, Badeau, 4 Mar. 1927, *Ekman 7781a* (F, S), *Ekman 7781b* (S); Morne des Commissiares, near Petite Source, 17 Apr. 1932, *Holdridge 1134* (US); Morne des Commissaires, Jul. 1942, *Holdridge 1368* (GH, UC); vic. of Furcy, 26 May-15 Jun. 1920, *Leonard 4638* (BM), *Leonard 4778* (F); Ouest Départment, summit of Morne Guimby, above Morne des Commissaires, 16 Sep. 1955, *Proctor 10812* (US).
DOMINICAN REPUBLIC. BARAHONA: Polo, 26 Feb.-12 Mar. 1922, *Abbott 1798* (S, US), *Abbott 1805* (BM, GH); Montiada Nueva, 21 Aug. 1946, *Howard & Howard 8548* (US).
ECUADOR. TUNGURAHUA: Montaña Woma, 11 km E of Baños, 3 Jun 1968, *Holm-Nielsen & Jeppesen 298* (AAU, GH). NAPO: 4 km NW of Borja, 20 Sep. 1980, *Holm-Nielsen et al. 26365* (AAU); Baeza, 1 km S of the village, 20 Oct. 1976, *Øllgaard & Balslev 10211* (AAU, NY, UC, USM). MORONA-SANTIAGO: Pachicutza, km 140 on road Loja-Gualaquiza, 26-27 Apr. 1973, *Holm-Nielsen et al. 4616* (AAU).
PERU. CAJAMARCA: Santa Cruz, Catache, upper Río Zaña valley ca. 5 km above Monteseco on path to Chorro Blanco, 16-18 Mar. 1986, *Dillon et al. 4358* (F), *Dillon et al. 4428* (F). AMAZONAS: Bagua, 12 km E of La Peca, 23 Jun. 1978, *Barbour 2487a* (UC); 12 km E of La Peca, 29 Jun. 1978, *Barbour 2585* (F, UC). HUANUCO: Muña, 23 May-4 Jun. 1923, *Bryan 421* (F); Muña, 8 Mar. 1959, *Woytkowski 5218* (GH); below Río Santo Domingo, *Macbride 4208* (F). PASCO: Oxapampa, S of Oxapampa, 1 Feb. 1983, *León 506* (USM). JUNIN: Yucapata, 17 Jul. 1961, *Woytkowski 6658* (US). AYACUCHO: Ccarrapa, between Huanta and río Apurímac, 5-17 May 1929, *Killip & Smith 22401* (US).
BOLIVIA. COCHABAMBA: Espíritu Santo, NE von Cochabamba, Jun. 1909, *Buchtien 2165* (BM, US), *Buchtien 2208* (S, US). Santa Bárbara, 30 Aug. 1902, *R.S. Williams 1055* (US).

Campyloneurum vulpinum is easily distinguished by its persistent ferrugineous stem scales.

46. *Campyloneurum wurdackii* B. León, Ann. Missouri Bot. Gard. 77: 212-214. 1990. Type: Venezuela, Bolívar, Cerro Pijiguao, Sierra Suapure, E slopes of Cerro Pijiguao (N end of Serranía Suapure), 19 Jan. 1956, *Wurdack & Monachino 41303* (holotype, MO!; isotypes US!).

Polypodium repens Aublet var. *spathulatum* Vareschi, Flora de Venezuela 1, 2: 950. 1968. Type: Venezuela, Bolívar, Cerro Pijiguao, Sierra Suapure, *Wurdack 41130*. *Nomen nudum*.

Stem long creeping, not pruinose, 2-3 mm wide. Stem scales light brown in mass, 3-4 mm long, 1-1.3 mm wide, lanceolate, bases auriculate, apices obtuse or rarely acute, the cells oblong, cell walls 10 µm thick. Phyllopodia 1-1.5 mm long, 1.5-2 mm wide, 5 mm apart. Leaves 19-41 cm long; petiole dark stramineous or stramineous, 4-8 cm long; lamina lanceolate, 4.5-8 cm wide, bases cuneate then long decurrent, apices acuminate to slight caudate; costa prominent, primary veins slight prominulous, darker than the leaf tissue, 60-65^{o} divergent from the costa, 5-7 mm apart, secondary veins inconspicuous, forming 7-8 primary areoles between the costa and margin, 3-4 excurrent veinlets in each primary areole, simple or furcate, central veinlet generally anastomosed with the transverse veins forming assymetric secondary areoles; sori subterminal or medial, paraphyses and spores not seen. Figs. 5 a-c; 44.

This species is known from Venezuela, where it has been found between 90 m and 500 m elevation.

EXAMINED SPECIMEN: VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Atures, 23 km NE of Puerto Ayacucho and 10 km E of the highway, 17-19 Apr. 1978, *Davidse & Huber 15306* (MO).

Campyloneurum wurdackii belongs to the *C. phyllitidis* group. It is characterized by the closely spaced leaves, light brown and persistent stem scales, and undivided primary areoles.

47. *Campyloneurum xalapense* Fée, Gen. Filic. 258. 1852. Type. Mexico, Veracruz, Xalapa, Jun.-Oct. 1840, *Galeotti 6273* (holotype, probably P ; isotype, K!).

Campyloneurum caudatum Fée, Mém. Foug. 8: 96. 1857. Type: Mexico, Cordoba et Huatusco, 1853, *Schaffner 176* (holotype, P; isotype K!).

Polypodium xalapense (Fée) Christ, Bull. Soc. Roy. Bot. Belgique 35: 231. 1896.

Polypodium phyllitidis L. f. *multipunctatum* Christ,

Bull. Herb. Boissier 2, 5: 7. 1905. Type: Costa Rica, Navarro, 1903, *Wercklé 174* (holotype, P!, isotype US, photo of US, BM!).

Polypodium multipunctatum (Christ) Christ, Bull. Herb. Boissier 2: 51-52. 1906.

Polypodium weatherbyanum Seymour, Phytologia 31: 171. 1975. *Nomen novum* for *Campyloneurum caudatum*.

Campyloneurum multipunctatum (Christ) Lellinger, Proc. Biol. Soc. Wash. 89: 708. 1977.

Stem long creeping, dark stramineous, not pruinose, (2-) 4-5 (-10) mm wide. Stem scales (3-) 4-6 mm long, 0.75-2.5 mm wide, narrowly ovate or ovate, bases auriculate, apices acuminate, sometimes obtuse, cell walls 12-24 µm thick, basal margins of the scale with hair-like teeth 48-56 µm long. Phyllopodia 1-2 mm long, 2-2.5 mm wide, 2-7 mm apart. Leaves 30-85 cm long; petiole stramineous or dark stramineous, 2-21 cm long, indument of scales similar to those on the stem; lamina narrowly lanceolate or narrowly oblong, bases attenuate, apices acuminate, long acuminate or subcaudate, 1.7-5 cm wide, chartaceous or subcoriaceous, margins cartilaginous, undulate, indument of scarce, simple, bicellular hairs, 80-96 µm long; stomata polocytic or copolocytic; costa prominent on both sides of the lamina, plane or slight ranurate adaxially, angled abaxially, primary veins slight prominulous adaxially, inconspicuous abaxially, same color as the leaf tissue or prominulous and stramineous at its origin, (60º-) 65-70º (-75º) divergent from the costa, 4-8 mm apart, transverse secondary veins forming 4-7 primary areoles between the costa and margin, primary areoles usually isodiametric divided, 2-4 excurrent veinlets in each primary areole; sori subterminal or medial, paraphyses not seen, spores 60-64 µm long, 35-45 µm wide. Chromosome number 2*n*=74. Figs. 11; 14 f; 18 e; 50.

This species is distributed from Mexico to Costa Rica. It grows between 1000 m and 2500 m elevation, mostly in open areas or disturbed forests.

REPRESENTATIVE SPECIMENS: MEXICO. HIDALGO: Molango, between Calnali and Huazalingo, 39 May 1947, *Moore 3019* (UC). PUEBLA: Siera Madre Oriental, 4 km NE of Villa Juárez, 27 Jun. 1969, *Marcks & Marcks 820* (BM, UC). VERACRUZ: near Jalapa, Hacienda Concepción, 11 Sep. 1906, *Barnes et al. 87* (F); Cerro San Martín, *Calzada 426* (GH); near Fortín above plant Cervecería Moctezuma, 26 Jun. 1977, *Croat 39386* (MO), *Croat 39413* (MO); El Mirador, 21 km E of Huatusco, 23 Aug. 1977, *Croat 44010* (MO, UC); along highway 125 to Huatusco, 15 Jan. 1987, *Croat & Hannon 63103* (MO); Salto del Gato, along Río Sedeño, about 3 km NE of Xalapa, 31 Dec. 1973, *Dorante et al. 780* (GH); Cordoba, *Finck 55* (UC), *Fink 84* (MO); La Luz, Cordoba, 13 Oct. 1882, *Kerber s.n.* (BM); 7.2 km E of Tebanca, 7.2 km E of E side of Lago Catamaco, 2.6 km W of Bastonal lumber camp, 15 Jan. 1981, *Nee & Schatz 19947* (F); Cordoba, 6 Apr. 1910, *Orcutt 3212* (BM, MO); near Orizaba, 29 Jan. 1895, *Pringle 6082* (BM, GH, MO, NY, S, UC); Zacuapán, Nov, 1906, *Purpus 2163* (F, MO, NY); Zacuapán, Nov. 1906, *Purpus 2163* (F); Barranca de Tenampa, Apr. 1934, *Purpus 16479* (F); Zacuapán, Jan. 1908, *Purpus s.n.* (UC); Copatepec, Dec. 1943, *Sánchez 10* (US); Barranca de la Concepción, near Jalapa, 24 Dec. 1984, *C. Smith 2008* (F, GH); Mun. Perote, deroute to Magueyitos, 25 Aug. 1975, *Vásquez 2131* (UC); vic. of El Ejido de Tepetlampa, El Palmar, Zongolica, 6 Jun. 1944, *Vera 3010* (US). OAXACA: along road between Teotitlán to Chichotla, 23 Feb. 1979, *Croat 48412* (MO); dist. Villa Alta, 25 Jul. 1962, *Mickel 964* (NY, UC, US), 27 Jul. 1962, *Mickel 1015* (NY, US). CHIAPAS: Mun. Motozintla de Mendoza, 45-50 km NE of Huixtla, along road to Motozintla, 17 Nov. 1971, *Breedlove & Smith 22658* (F, NY); Selva Negra, 10 km above Rayón Mezcalapa, *Breedlove 26079* (MO); Mun. Cintalapa, 3 km E of Francisco Madero, NE of Cintalapa, 4 Oct. 1974, *Breedlove 38039* (MO); above El Rosario, 8 mi S of Motozintla, 10 Jul. 1977, *Croat 40731* (MO), *Croat 40732* (MO); along road between Motozintla and Siltepec, 26-30 mi N of Motozintla, 12 Feb. 1979, *Croat 47460* (MO); Mun. Las Margaritas, 12 km E of Tziscao, 16 Nov. 1984, *Davidse et al. 29866* (MO); Mun. Ocosingo, near Laguna Ocotal Grande, ca. 25-30 km SE of Monte Líbano, 8 Aug. 1954, *Dressler 1618* (GH, NY, US); Ocozocautla, El Ocote, 14 Feb. 1986, *Palacios-Ríos 2780* (UC). Without locality: Aug. 1855, *Botteri 5* (BM); 1857, *Muller s.n.* (BM). BELIZE. TOLEDO: Edwards road beyond Columbia, 27 Apr. 1948, *Gentle 6515* (F, S, US). GUATEMALA. ALTA VERAPAZ: between San Pedro Carcha and Campur, 20 Mar. 1970, *Harmon & Fuentes 2181* (MO); Montaña Ixocuvain, W of Cubilguitz, 12 Mar. 1942, *Steyermark 44975* (F). SAN MARCOS: Río Mopá, below Rodeo, 14 Mar. 1939, *Standley 68764* (F). QUEZALTENANGO: Aguas Amargas, W slopes of Volcán Zunil, 14 Jan. 1941, *Standley 83353* (F, UC); El Pocito, S of San Martín Chile Verde, on road to Colomba, 27 Jan. 1941, *Standley*

85012 (F, US), above Mujuliá, between San Martín Chile Verde and Colomba, 1 feb. 1941, *Standley 85620* (F). SOLOLA: Atitlán, 16 Feb. 1906, *Kellerman 5779* (US); Volcán Atitlán, 11 Jun. 1942, *Steyermark 47378* (F). CHIMALTENANGO: Volcán Pacayca, 16 Feb. 1947, *Brenckle 4737* (F); 8 km S of Acatenango, 2 Sep. 1972, *Madison 672* (GH); region of Los Ositos, above Las Calderas, 16 Dec. 1940, *Standley 80182* (UC). JALAPA: Volcán Jumay, N of Jalapa, 1 Dec. 1939, *Steyermark 32450* (F). ZACAPA: Sierra de las Minas, between Cerro de Monosand Monte Virgen, 17 Jan. 1942, *Steyermark 42848* (F). SUCHITEPEQUEZ: S slopes of Volcán Zunil, vic. Finca Las Nubes, along Quebrada Chita, E of Pueblo Nuevo, 2 Feb. 1940, *Steyermark 35433* (F). CHIMALTENANGO: 8 km S of Acatenango, 2 Sep. 1972, *Madison 672* (GH); region of Los Positos, above Las Calderas, 16 Dec. 1940, *Standley 80182* (F, UC). ESCUINTLA: between Río Jute and Río Pantaleón, on road between Escuintla and Santa Lucía, 24 Jan. 1939, *Standley 63496* (F). SANTA ROSA: near El Molino, 26 Nov. 1940, *Standley 78511* (F).
HONDURAS. COMAYAGUA: Cerro Azul-Meambar, 8 Aug. 1974, *Horwath 81* (F). CORTES: N side of Lake Yojoa, 10 Apr. 1951, *Morton 7643* (US). SANTA BARBARA: 10 km W de Lago Yojoa, 28-30 Apr. 1973, *Clewell & Hazlett 3796* (MO, US). OCOTEPEQUE: Cordillera Merendón, vic. of El Portillo, 2 Sep. 1975, *Molina 31007* (F).
EL SALVADOR. SANTA ANA: Cerro Monte Cristo, ca. 14 mi NE of Metapan, 31 Jul. 1977, *Croat 42399* (MO, UC); Montecristo, 23 May 1963, *Molina & Molina 12658* (F, NY, US); Parque Nacional Montecristo, 24 Sep. 1988, *Pfeiffer 48* (MO); Montecristo, 11 Oct. 1978, *Seiler 670* (F, NY, UC); Laguna Las Ninfas, 8 Feb. 1979, *Seiler 907* (F, NY). CHALATENANGO: E slope of Los Esesmiles, 14 Mar. 1942, *Tucker 1047* (UC, US). SAN SALVADOR: Volcán San Salvador, 3 Feb. 1946, *Carlson 505* (F, UC); Santa Tecla, Cantón Las Victorias, 1941, *García 109* (UC). SAN VICENTE: Volcán San Vicente, 7-8 Mar. 1922, *Standley 21610* (MO); Volcán San Vicente, 26 Apr. 1978, *Seiler 324* (F); *Seiler 325* (F).
COSTA RICA. GUANACASTE: upper slopes of Cerro San José de Líbano, 15 Feb. 1930, *Dodge et al. 6461* (US); along Río San Juan, W slopes of Volcán Tenorio, 25 Jan. 1985, *Grayum et al. 4963* (MO); Rincón de la Vieja National Park, ridge SE of Quebrada Zopilote, 24 Jan. 1986, *A.R. Smith et al. 1927* (UC), 26 Jan. 1986, *A.R. Smith et al. 1982* (UC). ALAJUELA: San Isidro de San Ramón, 21 Oct. 1986, *Herrera 73* (MO). HEREDIA: Barba, at Volcán Barba, 18 Apr. 1953, *Scamman 7247* (US). PUNTARENAS: Las Cruces Tropical Botanical Garden, 6 mi S of San Vito de Java, Aug. 1974, *Herb. Tropical Studies 885* (US). SAN JOSE: Tablazo, 17 Sep. 1908, *Brade & Brade 243* (BM, NY, S); La Palma, 1909, *Brade & Brade 243a* (S); Llanuras de San Carlos, Apr.-May 1910, *Brade & Brade 710* (S, UC); road from Santa Cruz to Vista de Mar, 22-26 Jul. 1985, *Gómez & Herrera 23667* (MO); Jul. 1857, *Hoffman 894* (S); 58 km from San José, Poas, *Saiki 109* (F); basin of El General, Jul.-Aug. 1943, *Skutch & Barrantes 5161* (MO). CARTAGO: 2 km N of Orosí, 3 Jul. 1967, *Mickel 2283* (NY, US); Navarro valley, 6-8 mi SW of Cartago, 7 Apr. 1928, *Stork 1402* (NY, UC); 3 km SE of Cartago, 10 Aug. 1967, *Taylor 4259* (MO).

Campyloneurum xalapense is characterized by narrowly lanceolate or oblong lanceolate leaves and by 4-7 primary areoles between margin and costa.

It is recognized here in a broad sense, including populations with a wide range of morphological variation in size and shape of stem scales from linear lanceolate scales with bases less than 1 mm wide to lanceolate scales with bases more than 2 mm wide. All this range of variation can be found within an individual specimen (for example *Croat 40732*). Moreover, at any point of its distributional range, a similar amount of variation can be found in stem scale size and shape. For these reasons stem scale characteristics do not have taxonomic value for discerning different taxa within *C. xalapense*.

Stem width, leaf texture, and pattern of venation are also variable in most specimens examined. Some of that variation was used to distinguish *Campyloneurum multipunctatum* as different from *C. xalapense* (cf. Lellinger, 1988). However, for the vast majority of specimens studied these character states are not associated (e.g. *Steyermark 44975*, *Arsene s.n*, *Standley 85012*).

NOMINA DUBIA

1. *Polypodium calaguala* Ruiz, Mem. c tab. 1805.

Moore (1861), included this name as a synonym of *Campyloneurum angustifolium*. Attempts to localize the type specimen were unsuccessful. For this reason it is not attributed here to any particular species.

2. *Polypodium gladiatum* Vellozo, Fl. Flum. 11, t.59. 1827.

The illustration appears to be that of *Campyloneurum nitidum*. However, I have been unable to locate the type specimen.

3. *Campyloneurum lanciforme* (J. S. Presl) C. Presl,

Tent. Pterid. 190.1836.

Polypodium lanciforme J.S. Presl, Deliciae Pragensis 164. 1822. Type: Brazil, Rio de Janeiro, *Sellow s.n.*

According to the description, this name refers to a Brazilian species with narrowly lanceolate leaves. The description applies either to *Campyloneurum minus* or *C. nitidum*.

4. *Campyloneurum loreum* (Kaulfuss ex Kunze) Fée, Mém Foug. 8. 129. 1857.

Polypodium loreum Kaulfuss ex Kunze, Flora 1839.

There were no seen types or descriptions, and therefore it is not included in any species.

5. *Polypodium medicinale* Rojas, Bull. Acad. Int. Géogr. Bot. 28: 156. 1918.

According to Morton (1973), the type specimen is deposited at the herbarium in Asunción, Paraguay, and "by the process of elimination" was determined to be a synonym for *P. phyllitidis*. However, since *C. phyllitidis* does not occur in Paraguay, it is probable that this name is a synonym for *Campyloneurum nitidum*.

6. *Campyloneurum moritzianum* Fée, Gen. Fil. 258. 1852. Type. Venezuela, Caracas, *Moritz 3*. Non *Polypodium* Link.

I have not seen the type specimen, which is deposited at the herbarium of Rio de Janeiro (Windisch, 1982), but attempts to get a loan were not successful. T. Moore (1861) included this name as a synonym of *C. phyllitidis*. However, after reading the description, I can only be sure that it belongs to the group of *C. phyllitidis*.

7. *Campyloneurum polyanthum* C. Presl, Tent. Pterid. 190. 1836. Tab. 7. Fig 16.

Presl mentioned *Polypodium polyanthum* as the basionym of this name. According to the pattern of venation shown in Presl (1836), this name could be a synonym for one of the species in the *C. phyllitidis* species group.

8. *Polypodium rodriguezianum* L.D. Gómez, Rev. Biol. Trop. 17: 107, f. 5-6. 1970. Type: Costa Rica, Cartago, Cerro Carpintera, *Gómez pt.C-2063*.

This name was considered by Lellinger (1988) as a synonym of *Campyloneurum falcoideum*. Although the figures in the original publication clearly show a specimen of *Campyloneurum*, here they are not attributed to any particular species since leaf morphology, especially among narrowly lanceolate does not help to distinguish species. Attempts to localize the type specimen were unsuccessful; according to Pablo Sánchez, curator of CR (pers. comm.) no Gómez types are kept there.

9. *Campyloneurum sieberianum* C. Presl, Tent. Pterid. 190. 1836. Tab. 7. Fig. 17.

According to the pattern of venation shown in Presl (1836) this could be a synonym for a species within the *Campyloneurum brevifolium* group.

10. *Polypodium schnittspahnii* Christ, Bull. Herb. Boissier 6: 836. 1898. Type: Andes, ?*Moritz s.n.*.

In the original description, the stem scales are described as "ovato-lanceolatis" and atrofuscous on a pruinose glaucous stem (farina glauca). These characters, together with the pattern of venation, may apply to the *Campyloneurum angustifolium* group. Lellinger (1988) suggested that this name might be an earlier epithet for *C. falcoideum*. However, based on the available evidence it is not included in any species.

EXCLUDED TAXA

1. *Campyloneurum laevigatum* (Cav.) C. Presl, Tent. Pterid. 190. 1836. =*Polypodium laevigatum* Cav. Descr. Pl. 244. 1802.

2. *Campyloneurum decumanum* (Willd.) Fée, Crypt. Vasc. Brésil 1. 115. 1869. =*Polypodium decumanum* Willd., Sp. Pl. 5: 170. 1810.

3. *Campyloneurum oligophlebium* (Kunze) Fée, Gen. Fil. 258. 1852. =*Polypodium oligophlebium* Kunze, Linnaea 23: 73. 1850. Type. N. Holl. et Tasmannia, *Houtteau 1848*.

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XI. LIST OF TAXA