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A REVISED LIST OF THE PTERIDOPHYTES OF NEVIS

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ABSTRACT

A revised list of the pteridophytes of Nevis in the Lesser Antilles is given. This includes 14 species not previously recorded for the island.

INTRODUCTION

Nevis is a small volcanic island in the West Indian Leeward Islands. No specific list of the ferns has ever been published, although Proctor (1977) does record each of the species known to occur on the island. Proctor's records were largely accumulated from herbarium specimens collected by R A Howard in 1950 and his own collections in 1959. In total he recorded 81 taxa. Collections by one of us (BMG) in 1988 and both of us in 1990 have added a further 14 species plus 3 unnamed species of *Thelypteris* and 4 established garden introductions. Nineteen species recorded in *Proctor* were not seen by either of us on the island. The 98 native or naturalised taxa here recorded for Nevis are still low in comparison with the number recorded for the two larger principal neighbouring islands of St Kitts: 129 (Proctor 1977) and Monserrat: 117 (Proctor 1977).

Nevis is approximately 6 miles from east to west and 8 miles from north to south, a total surface area of 36 square miles. The whole island is dominated by the central mountainous core rising to 3,232 feet at Nevis Peak. About 9,000 people live on the island mostly around the coastal plain and especially in the west near Charlestown, the Capital. The central mountainous area is unpopulated and rarely visited by the local inhabitants.

The climate is tropical with the temperature rarely falling below 20°C. The prevailing winds blow from the south east with most rainfall at high altitudes (more than 100 inches annually), particularly to the north west of the summit peak. Here, cloud frequently hangs all day in the remnants of the summit crater protected from the prevailing winds and occasional hurricanes, e.g. hurricane Hugo in 1989. Rainfall is low (less than 40 inches annually) in southern and eastern coastal areas where semi-desert scrub has developed.

Rodriques (1990) has mapped the vegetation of the island (see Fig. 1) and found that less than 4 square miles (624 hectares) of montane type forest exists on Nevis. He has further subdivided this area into three zones:– Montane forest – 500 hectares, Palm break – 115 hectares, Elfin forest – 9 hectares.

Montane forest would be at an altitude of about 1500-2300 feet, palm brake from 2300-2700 feet and the elfin forest from 2700-3232 feet. At the time of the 1990 collecting much of this forest, especially on the windward side of the island, was still recovering from the damage caused by hurricane Hugo.

Low altitude species – less than 1000 feet

There are few ferns naturally occurring below 1000 feet. Exceptions are *Acrostichum danaefolium* in mangrove swamps at sea level, and ferns of walls and dry rocky areas, e.g. *Cheilanthes microphylla, Anemia adiantifolia, Pteris vittata* and *Pityrogramma calomelanos.*

Middle altitudes in dry evergreen forest – 1000-1500 feet

In sheltered areas several species tolerant of temporary drought are abundant, eg. *Blechnum*
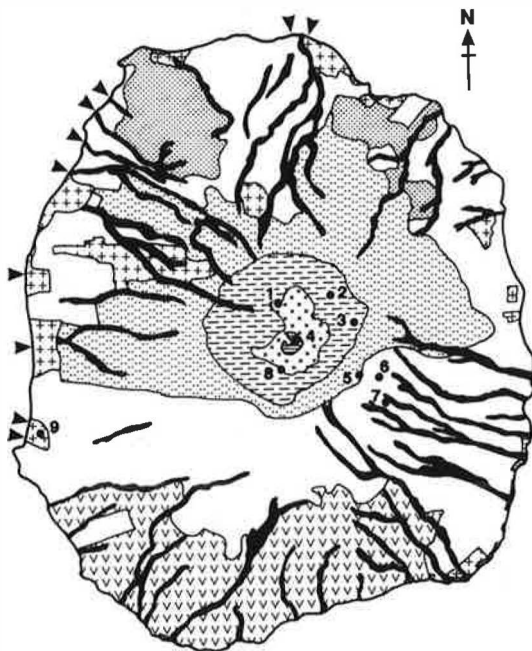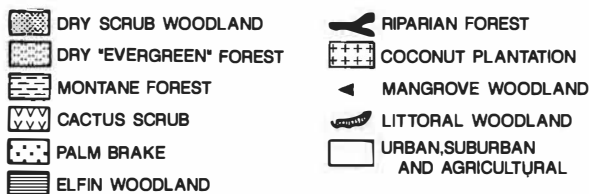
VEGETATION ZONES ON NEVIS

DRY SCRUB WOODLAND   RIPARIAN FOREST

DRY "EVERGREEN" FOREST   COCONUT PLANTATION

MONTANE FOREST   MANGROVE WOODLAND

CACTUS SCRUB   LITTORAL WOODLAND

PALM BRAKE   URBAN,SUBURBAN AND AGRICULTURAL

ELFIN WOODLAND

FIGURE 1. Vegetation zones of Nevis (after Rodriques, 1990).

occidentale, *Nephrolepis rivularis, Selaginella flabellata* and on trees and rocks *Polypodium polypodioides, Polypodium aureum* var. *aureum* and *Polypodium lycopodioides.*

Montane forest – 1500-2300 feet

Here tree-ferns are common, usually *Cyathea muricata* and *C.arborea*, but occasionally in more sheltered areas at higher altitudes the much smaller *Cnemidaria grandifolia* var. *grandifolia* is frequent. The ground vegetation is rich in ferns with *Diplazium spp., Tectaria incisa, Lonchitis hirsutus* and many *Thelypteris* species locally dominant. The striking red young fronds of *Adiantum latifolium* are frequent in forest clearings and a problematical taxon, probably also *A. latifolium*, occurs occasionally on rocks.

In sheltered valleys on tree trunks and where rocks outcrop many species of filmy fern occur. Particularly common are *Trichomanes membranaceum* and *Trichomanes alatum*. Also on rocks, but in more open sites, *Asplenium laetum, A. abscissum* and *A. cristatum* occur occasionally, with in one collection a problematical frond which might possibly be *A.malcolm-smithii* – believed endemic to St Kitts. *Lomariopsis sorbifolia, Grammitis serrulata, Thelypteris reptans* var. *reptans,* several polypodiaceous species and *Vittaria lineata* also grow occasionally on rocks and trees.

Dominant flowering plants include (after Rodriques, 1990) *Sloanea truncata, Miconia spp, Dacryodes excelsa, Euterpe globosa, Beilschmeida pendula, Coccoloba pubescens, Aniba bracteata, Simarouba amara, Ceropia peltata* and *Podocarpus coriaceus.*

Palm brake – 2300-2700 feet

In this zone several species of palm are particularly common, dicotyledonous trees also occur as do many ferns, although none appear to be restricted to the palm break. All three tree-fern species occur, *Hymenophyllum hirtellum* subsp. *gratum* is abundant on many moss festooned trees together with *Trichomanes alatum* and *T. crispum*. Also frequent are *Polypodium loriceum* and *Grammitis seminuda*.

Dominant species of flowering plants (after Rodriques, 1990) are *Euterpe globosa* and *Podocarpus coriaceus*.

FIGURE 2. Moss festooning branches in elfin forest.

Elfin forest – 2700-3232 feet

This zone is the jewel in the crown (See Figs. 2 & 3). In an area perhaps only extending to 9 hectares several of the more interesting species are abundant. *Gleichenia furcata* tangled with *Dicranopteris pectinata* swamp many of the more exposed ridges and invade to some extent the tiny areas of summit heaths where *Lycopodium cernuum* var. *dussii* is common. In the dense almost impenetrable forest all branches, creepers and tree trunks are thickly festooned with mosses, bromeliads and ferns. There appear to be no rock faces as such and species from genera normally considered epipetric are common in these festoons, eg *Hymenophyllum elegans, Grammitis serrulata, G. flabelliformis* and *G. suspensa*. Particularly conspicuous among these epiphytic ferns is *Blechnum binervatum* with its arching fronds, spiralling from the thick scaley rhizomes, climbing around the stems of *Cyathea arborea*. Also magnificent is the terrestrial *Thelypteris decussata* with fronds up to 3 metres in length. *Blechnum ryanii* and *Cnemidaria grandifolia* var. *grandifolia* are abundant, while growing on the dark forest floor *Lindsaea quadrangularis* subsp. *antillensis* and *Trichomanes trigonum* var. *trigonum* are frequent. The fronds of this filmy fern grow erect to a height of 30 or 40 cm and are remarkably tough despite their filmy nature. Less spectacular, but of greater significance, is *Thelypteris muscicola* which occurs only rarely right at the summit of Nevis Peak. This species grows nowhere else in the world.

Dominant species of flowering plants (after Rodriques, 1990) are *Euterpe globosa, Ficus sp., Clidemia umbrasa* and *Podocarpus coriaceus*.

FIGURE 3. *Cyathea arborea* dominating the elfin forest at the summit.

SPECIES LIST

Most determinations have been confirmed by Dr Dennis Adams. Species recorded in Proctor (1977) have been incorporated to give a list of the ferns of Nevis as comprehensive as possible at the present time. Order and nomenclature is usually as in *Flora of the Lesser Antilles - Pteridophyta* (1977) by G R Proctor. Where different, old names are given in brackets. Common names are taken from Jones (1987). Entries of introduced species are preceded by an *. Heights, given in feet, are taken from the map of the island published by the Government of the United Kingdom (Ordnance Survey) for the Government of St Kitts and Nevis (1984).

Representative ranges of herbarium specimens have been placed at the National Museum of Wales, Cardiff (NMW), and the Natural History Museum, London (BM). The numbers are given in the following list. MHR/BMG number is followed by (BM) and/or (NMW + number), eg. 191(BM);192(NMW.V91.115.41).

Psilotum nudum (L.) Griseb. Whisk Fern. Walls on Golden Rock Estate, c.900 feet, 1988 and 1990, 338(NMW.V91.115.72).

Lycopodium taxifolium Sw. Mossy stumps and trunks or branches of trees in moist forests at middle to high elevations. Proctor (1977).

Lycopodiun cernuum L. var. *cernuum*. Nodding Clubmoss. In grassy area at margin of track to the Source, c.1400 feet, 1990, 191(BM);192(NMW.V91.115.41). **New record** *Lycopodium cernuum* L. var. *dussii* Christ. Open areas at high altitude. Above Tower Hill, c.2800 feet, 1990, 531 (NMW.V91.115.75). Summit heath, 3100-3232 feet, 1990, 185(BM); 188(NMW.V91.115.40). (Fig. 4).

Selaginella flabellata (L.) Spring. Very common in forest from c.1000-2000 feet, 1988/90. Route to Source, 1990, 198(NMW.V91.115.42).

Selaginella substipitata Spring. Common at moderate to high altitudes, c.2000-3200 feet. Nevis Peak, 1990, 194(BM); 212(NMW.V91.115.44).

Selaginella serpens (Desvaux) Spring. Frequent in dense forest towards summit, 3000-3200 feet, 1990, 206(NMW.V91.115.43). **New record.**
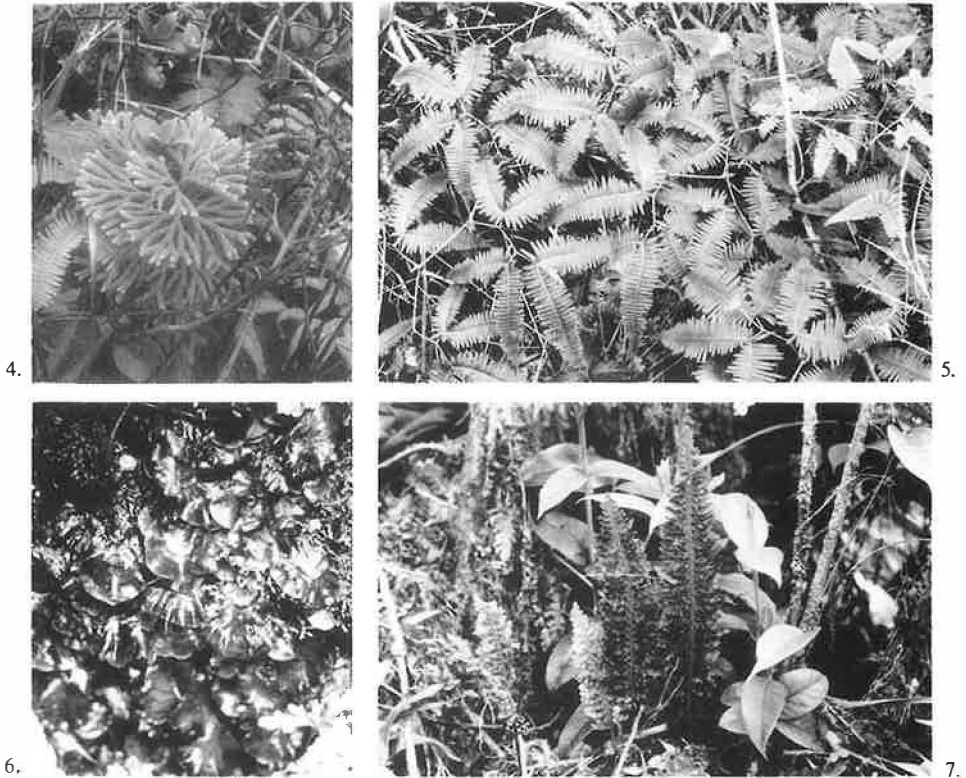
FIGURE 4. *Lycopodium cernuum* subsp. *dussii* in summit heath.
FIGURE 5. *Dicranopteris pectinata* in open area on summit ridge.
FIGURE 6. *Trichomanes membranaceum*.
FIGURE 7. *Trichomanes trigonum* var. *trigonum* in elfin forest.

Anemia adiantifolia (L.) Sw. Pine Fern. Walls at Golden Rock 1988 and 1990 at c. 800 feet, 347(BM); 348(NMW.V91.115.76). Rawlins village, c.900-1200 feet, 1988/90. **New record.**
Dicranopteris pectinata (Willd.) L.M.Underw. Open sites and in forest margins on summit ridges, c.2800-3230 feet. Nevis Peak, 1990, 53(BM); 42(NMW.V91.115.11). **New record.** (Fig. 5).
Gleichenia furcata (L.) Sprengel. Open sites and in forest margins on summit ridges. Above Tower Hill, 2700-2800 feet, 1990. Summit at 3230 feet, 1990, 50(NMW.V91.115.12).
Hymenophyllum lineare (Sw.) Sw. Mossy tree trunks at higher elevations, Proctor (1977).
Hymenophyllum elegans Sprengel. Cloud forest at summit of Nevis Peak, 3220 feet, 1990, 286(BM); 284(NMW.V91.115.57).
Hymenophyllum hirsutum (L.) Sw. Mossy logs and tree trunks at chiefly middle elevations, Proctor (1977).
Hymenophyllum hirtellum Sw. var. *gratum* (Fée) Proctor. Common in forest epiphytic on trees. Above Tower Hill from 1600-2800 feet, 1990, 303(BM); 298(NMW.V91.115.60). Summit at c.3220 feet, 1990, 307(NMW.V91.115.61).
Hymenophyllum macrothecum Fée. On fallen tree at Source, c.1600 feet, 1990, 295(NMW.V91.115.59).
Hymenophyllum polyanthos (Sw.) Sw. var. *polyanthos.* Common in vicinity of Source on rocks and trees, c.1600 feet, 1988 and 1990, 289(NMW.V91.115.58). Also on summit ridge above Tower Hill, c.2800 feet, 1990.
Trichomanes hymenophylloides van den Bosch. Vicinity of Source, c.1600 feet. 1988 and 1990, 217(BM); 218(NMW:V91.115.45); 221(NMW.V9.115.46). Also above Tower Hill, c.1700

feet, 1990.

Trichomanes rigidum Sw. Rare on rocks in ravine near Source, c.1600 feet, 1990, 222(BM);
226(NMW.V91.115.47). **New record.**

Trichomanes membranaceum L. Abundant on rocks and tree trunks along route to Source
and at Source, c.1600 feet, 1988 and 1990, 248(BM); 249(NMW.V91.115.52). (Fig. 6).

Trichomanes punctatum Poiret in Lam. Abundant on rocks and tree trunks. On rocks
in ghut east of Tower Hill, c.1200 feet, 1990. On route to Source and at Source, c.1600
feet, 19888 and 1990, 237(NMW.V91.115.49).

Trichomanes angustifrons (Fée) Wessels Boer in Kramer. At Source, rare, c.1600 feet, 1990,
239(NMW.V91.115.50).

Trichomanes krausii Hook. & Grev. On rocks on route to Source, rare, c.1600 feet, 1990,
228(BM); 230(NMW.V91.115.48). **New record.**

Trichomanes trigonum Desvaux var. *trigonum*. In forest usually at higher altitudes. Above
Tower Hill, c.1700 feet, 1990, 277(NMW.V91.115.55). Common near summit of Nevis Peak
growing on forest floor, 2800-3230 feet, 1990, 278(BM). (Fig. 7).

Trichomanes polypodiodes L. In forest above Tower Hill, c.1700 feet, 1990,
280(NMW.V91.115.56).

Trichomanes alatum Sw. Very common in forest, on rocks, trees or on forest floor. Source
and route to Source, c.1600 feet, 1988 and 1990, 270(BM); 255(NMW.V91.115.53),
265(NMW.V91.115.54). Above Tower Hill, 1700-2700 feet, 1990, 254 (BM).

Trichomanes crispum L. Rocks on route to Source, c.1600 feet, 1988 and 1990, 241(BM).
Damp forest along ridge above Tower Hill, 1700-2600 feet, 1990, 246(NMW.V91.115.51),
516(NMW.V91.115.105).

Cyathea muricata Willd. in L. Common at middle altitudes in forest. Route to Source,
c.1400-1600 feet, 1988 and 1990, 380,388,500(BM); 385(NMW.V91.115.81),
387(NMW.V91.115.82), 501(NMW.V91.115.103). Forest above Tower Hill, 1500-2500 feet,
1990.

Cyathea arborea (L.) Smith. West Indian Tree-fern. In forest at slightly higher altitudes
than   previous   species.   Route   to   Source,   c.1600   feet,   399,498(BM);
391,398,400(NMW.V91.115.83), 499(NMW.V91.115.102). Near Source, c.1700 feet, 1990.
Forest from c.1600 feet to summit at 3230 feet, 1990. (Fig. 8).

FIGURE 8. *Cyathea arborea* in montane forest.

Cnemidaria grandifolia (Willd.) Proctor var. *grandifolia*. Abundant in very damp sheltered forest at middle to high altitudes. Above Tower Hill, 1600-2800 feet, 1990, 409,413,415(NMW.V91.115.86). Above Zetlands, c.1800 feet, 1990. Summit cloud forest c.3230 feet, 1990.

Lindsaea quadrangularis Raddi subsp. *antillensis* Kramer. Occasional on forest floor in damp forest at moderate to high altitudes. Above Tower Hill, 2400-2700 feet, 1990, 479(NMW.V91.115.99). Summit forest 3230 feet.

Lonchitis hirsuta (L.) (*Anisorus hirsutus* (L.) Underw. & Maxon). In damp sites alongside route to Source, c.1600 feet, locally common, 1988 and 1990, 345(BM); 342,346(NMW.V91.115.74). (Fig. 9).

Pteris vittata L. Chinese Brake. Just above sea level to 1000 feet on walls and rockwork. Walls in Charlestown, 1990. Golden Rock Estate, even colonising crevices in concrete by swimming pool c.900 feet, 1988 and 1990, 325(BM);327(NMW.V91.115.68).

Pteris altissima Poiret in Lam. Forest Brake. Occasional in lower altitude forest on banks above streams. Bank above Source reservoir, c.1700 feet, 1990, 322(NMW.V91.115.67). Bank of ghut above Tower Hill, c.1200 feet.

Acrostichum danaeifolium Langsd. & Fischer. Giant Leather Fern. Saline or brackish swamps, Proctor (1977).

Blechnum occidentale L. Hammock Fern. Abundant in dryer forest at lower altitudes. Route to Source, 1200-1500 feet, often dominant, 1988 and 1990, 98(NMW.V91.115.21). Above Tower Hill, c.1200-1500 feet, 1990. Above Zetlands, 1990. Golden Rock Estate in dry forest, c.850 feet, 1988. (Fig. 10). Form with forked pinnae also common along route to Source, 1990, 101(NMW.V91.115.22).

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FIGURE 9. *Lonchitis hirsuta.*
FIGURE 10. *Blechnum occidentale.*
FIGURE 11. *Blechnum binervatum* in elfin forest.
FIGURE 12. *? Thelypteris sancta* near Source.

Blechnum binervatum (Poiret) Morton & Lellinger. Common on trunks of *Cyathea arborea* in cloud forest at summit, 3150-3230 feet, 1990, 103,110(BM); 106(NMW.V91.115.23), 109(NMW.V91.115.24). **New Record**. (Fig. 11).

Blechnum insularum Morton & Lellinger. Mossy montane forests at higher elevations, Proctor (1977).

Blechnum ryanii (Kaulf.) Hieron. Common in cloud forest at high altitudes. Above Tower Hill at c.1600 feet, 1990, 112,113((BM). Summit forest 3200 feet, 1990, coll. Q.Henderson, 114(NMW.V91.115.25).

Pityrogramma calomelanos (L.) Link. Silver Fern. Common from just above sea level to c. 1600 feet on rocks and walls. Route to Source, c.1600 feet, 1988 and 1990, 36(NMW.V91.115.84). Golden Rock Estate, common on walls, 1988 and 1990, 39(BM); 38(NMW.V91.115.10). Charlestown, 1990. **New record**.

Pityrogramma chrysophylla (Sw.) Link. Uncommon on rocky bank. Route to Source, c.1600 feet, 1900, 35(NMW.V91.115.09).

Cheilanthes microphylla (Sw.) Sw. Dry walls. Route to Golden Rock, c.700 feet, 1988 and 1990, 333(BM); 336(NMW.V91.115.71). Gingerland, 650 feet, 1990.

*Adiantum caudatum L. Trailing Maidenhair. Not native, semi-naturalised Golden Rock Estate. c.850 feet, 1988 and 1990, 63(NMW.V91.115.14). **New record**.

Adiantum latifolium Lam. Partly shaded banks, borders of pastures and alluvial thickets at low to middle elevations. (Proctor 1977). Route to Source, 1400-1700 feet 1988 and 1990, 69(BM); 70(NMW.V91.115.15), 74(NMW.V91.115.16). Above Tower Hill, c.1700 feet, 1990. (Det. A C Jermy).

Adiantum tetraphyllum Humb. & Bonpl. ex Willd. in L. Partly shaded banks, borders of pastures and alluvial thickets at low to middle elevations, Proctor (1977).

Adiantum tenerum Sw. Common at foot of shady banks. Golden Rock Estate, 850 feet, 1988 and 1990, 58,59(NMW.V91.115.13). Rawlins village, 100 feet, 1990, 54(BM).

Elaphoglossum petiolatum (Sw.) Urban. Tree branches. Route to source c.1600-1700 feet, 1990, 365(NMW.V91.115.79). Above Tower Hill, c.1700 feet, 1990.

Elaphoglossum schomburgkii (Fée) T. Moore. Shaded mossy ledges, stumps and trees at middle to higher elevations, Proctor (1977).

Elaphoglossum impressum (Fée) T. Moore. Trees at Source, 1700 feet, 1990, 363(BM);364(NMW.V91.115.78).

Elaphoglossum martinicense (Desvaux) T. Moore. Trees. Route to Source and Source, c.1600 feet, 1990, 371(BM); 370(NMW.V91.115.80). Above Tower Hill, c.1700 feet.

Elaphoglossum plumieri T. Moore. On mossy tree trunks at chiefly higher elevations, Proctor (1977).

Elaphoglossum apodum (Kaulf). Schott. On mossy tree trunks, rarely on mossy banks or ledges, at middle to higher elevations, Proctor (1977).

Hymenodium crinitum (L.) Fée. Elephant Ear Fern. On mossy tree trunks, rarely on rocks, at chiefly middle elevations, Proctor (1977).

Lomariopsis sorbifolia (L.) Fée. Climbing on rocks and trees at lower altitudes in forest. On rocks in vicinity of Source, c.1600 feet, 1988 and 1990, 331(BM); 330(NMW.V91.115.70). On trees by side of ghut east of Tower Hill, c.1200 feet, 1990. **New record**.

Olfersia cervina (L.) Kunze (*Polybotrya cervina* (L.) Kaulf.). Common alongside route to Source, c.1600 feet, 1988 and 1990, 340(BM – fertile frond); 341(NMW.V91.115.73).

Nephrolepis rivularis (Vahl). Chr. Abundant in forest from 1000-3230 feet. At summit, 17(NMW.V91.115.04). Equally common in open glades and cloud forest. Also in gardens, eg Golden Rock, 1988 and 1990, 14(NMW.V91.115.03).

*Nephrolepis hirsutula (Forst.) C. Presl cv. 'Superba'. Established in gardens, eg Golden Rock, c.850 feet, 1988 and 1990, 21(NMW.V91.115.05).

Nephrolepis falcata (Cav.) C. Chr. cv. 'Furcans'. Fishtail Fern. Golden Rock garden, c.850 feet, 1988 and 1990, 26(NMW.V91.115.06).

Nephrolepis cordifolia (L.) Presl. cv. 'Duffii'. Golden Rock garden, c.850 feet, 1988 and 1990, 28(NMW.V91.115.07).

Tectaria plantaginea (Jacq.) Maxon. On rocks and clay banks in moist, deeply shaded ravines, or occasionally on floor of tall primary rain forest, at chiefly middle elevations, Proctor (1977).

Tectaria trifoliata (L.) Cav. Moist rocky ravines in rain forest areas at chiefly middle elevations, Proctor (1977).

Tectaria incisa Cav. Base of boulders and damp banks in open forest. Route to Source, c.1600 feet, 1988 and 1990, 32,33(BM); 29(NMW.V91.115.08).

Ctenitis meridionalis (Poiret) Ching. Sheltered bank above ghut east of Tower Hill, four or five plants, 1200 feet, 1990, 482,483(BM); 484,485,486(NMW.V91.115.100). **New Record.**

Diplazium limbatum (Willd.) Proctor. Wet shaded ravines at lower to middle altitudes, Proctor (1977).

Diplazium cristatum (Desr.) Alston. Frequent along route to Source in margin of forest, c.1600 feet, 1990, 7(NMW.V91.15.01).

Diplazium striatum (L.) C. Presl. On shady bank of ravine by side of route to Source, c.1600 feet, 1990, 8(NMW.V91.115.02).

Thelypteris sancta (L.) Ching. On rock face at Source, c.1700 feet, 1990, 123(BM); 124(NMW.V91.115.27). If identification confirmed a **New record.** (Fig. 12).

Thelypteris limbata (Sw.) Proctor. Exposed slopes and low montane thickets on the summits of volcanic mountains, Proctor (1977).

Thelypteris balbisii (Sprengel) Ching. Secret garden at Golden Rock, originally from mountain, c.850 feet. 1988 and 1990, 158(NMW.V91.115.33).

Thelypteris aff. *balbisii.* Indusium dark brown, persistent, large. Sheltered site on route to Source by edge of forest, c.1600 feet, 1990.

Thelypteris aff. *balbisii.* Summit thicket by triangulation point, 3232 feet, 1990, 176(BM); 177(NMW.V91.115.37), 179(NMW.V91.115.38). (Similar to *Thelypteris limbata* (Sw.) Proctor, but lacks indusia).

Thelypteris germaniana (Fée) Proctor. Moist forested slopes at higher elevations, Proctor (1977).

Thelypteris muscicola Proctor. Summit of Nevis Peak. Very rare, endemic to Nevis, c.3220 feet, 1990, 161(BM); 163(NMW.V91.115.34).

Thelypteris decussata (L.) Proctor. Restricted to humid forest and cloud forest. Above Tower Hill, c.2000 feet, 1990, 130, 131, 132(BM). Above Zetlands in ravine, c.2200 feet, 1990. Near summit in cloud forest, c.3220 feet, 990, 139(BM); 134, 135, 136(NMW.V91.115.85), 140(NMW.V91.115.29). Fronds up to 3 metres long. **New record.** (Fig. 13).

Thelypteris clypeolutata (Desvaux) Proctor. Source, c.1600 feet, 1990, 164, 165(NMW.V91.115.35). Above Tower Hill, c.1700 feet, 1990.

Thelypteris glandulosa (Desvaux) Proctor. In deep shaded forest above route to Source, c.1600 feet, 1990, 420, 421, 422(BM); 430, 431(NMW.V91.115.89).

Thelypteris patens Sw. var. *scabriuscula* (C.Presl) A.R. Smith. Forest borders and moist, partly shaded situations along roadsides and gullies at lower to middle elevations, Proctor (1977).

Thelypteris normalis (C. Chr.) Moxley. Route to Source, 1500-1600 feet, 1990, 172(BM). Bank by Rawlins village, 1990, 174(NMW.V91.115.36). **New record.**

Thelypteris dentata (Forssk.) E. St John. Route to Source, 1200-1500 feet, 1990, 181(BM); 180(NMW.V91.115.39). **New record.**

FIGURE 13. *Thelypteris decussata* in elfin forest.

FIGURE 14. *Thelypteris reptans* var. *tenera* at Source.
FIGURE 15. *Asplenium abscissum.*
FIGURE 16. *Polypodium polypodioides* on tree in dry evergreen forest.

Thelypteris reptans (J. F. Gmelin) Morton var. *tenera* (Fée) Proctor. On rock face at Source, c.1600 feet, 1990, 126(BM); 129(NMW.V91.115.28). (Fig. 14).

Thelypteris tetragona (Sw.) Small var. *tetragona*. Base of walls in grounds of Golden Rock, c.900 feet, 1988 and 1990, 116(BM); 120(NMW.V91.115.26). Also in dry forest at around 1000 feet, 1990.

Thelypteris nephrodioides (Klotzsch) Proctor. Source, c.1600 feet, 1990, 155(NMW.V91.115.32).

Thelypteris poiteana (Bory) Proctor. Moist shaded banks, thickets and shady ravines at lower to middle elevations; plants often grow in shaded situations of cultivated areas, Proctor (1977).

Thelypteris reticulata (L.) Proctor. Along route to Source and at Source, 1500-1650 feet, 1988 and 1990, 142(BM); 143(NMW.V91.115.30); 148, 149(NMW.V91.115.31).

Asplenium laetum Sw. Ghut east of Tower Hill, c.1200 feet, 1990. Route to Source on open rock face near dripping water at head of ravine, c.1500 feet, 1990, 88(NMW.V91.115.19).

Asplenium abscissum Willd. in L. On rocks at Source, c.1600 feet, 1990, 80(NMW.V91.115.18). (Fig. 15). One collection at this site was atypical resembling *Asplenium malcolm-smithii* Proctor, 1990, 76(NMW.V91.115.17).

Asplenium auritum var. *rigidum* (Sw.) Hook. On mossy tree trunks, occasionally on boulders, at middle elevations; plants common, Proctor (1977).

Asplenium cristatum Lam. Damp cliff at Source by long ladder, c.1650 feet, 1990, 88(BM); 92(NMW.V91.115.20).

Polypodium pectinatum L. On trees above small reservoir at Source, c.1600 feet, 1990. **New record.**

Polypodium polypodioides (L.) Watt. Resurrection Fern. Walls and trees at low altitudes in light shade. Golden Rock on walls, c.850 feet, 1988 and 1990, 454(NMW.V91.115.94). Above Golden Rock in dry forest scrub on tree trunk, c.950 feet, 1990. (Fig. 16).

Polypodium loriceum L. Epiphytic at medium to high altitudes in damp forest. Above Tower Hill, 1700-2400 feet, 1990, 445(NMW.V91.115.92). Cloud forest at summit of mountain, c.3220 feet, 1990, 448(NMW..V91.115.93).

Polypodium triseriale Sw. Light forest above Tower Hill, c.1700 feet, 1990, 436,437(NMW.V91.115.90). Route to Source, 1500-1600 feet, 1990.

Polypodium aureum L. var. *aureum*. Rabbit's-foot Fern/Golden Polypody. Shady wall at low altitude by road leading up to Golden Rock, c.850 feet, 1988 and 1990, 476,477(BM); 469,470,471(NMW.V91.115.98).

Polypodium piloselloides L. Snake Polypody. On stone walls and tree trunks on route to Source, 1500-1600 feet, 1988 and 1990, 467(NMW.V91.115.97).

Polypodium lycopodioides L. Stone walls and trees. Golden Rock, c.850 feet, 1988 and 1990. Tree trunk in dry forest above Golden Rock, c.950 feet, 1990. Route to Source, 1400-1600 feet, 460(NMW.V91.115.95), 463(NMW.V91.115.96).

Polypodium phyllitidis L. Florida Strap Fern. Trees near Source, c.1600 feet, 1990, 440(NMW.V91.115.91).

Grammitis serrulata (Sw.) Sw. Source, covering rocks above water level in Source reservoir, c.1600 feet, 1988 and 1990, 311(NMW.V91.115.63). Epiphytic in moss on trees above Zetlands, c.2300 feet, 1990. Epiphytic in moss on trees above Tower Hill, c.2800 feet, 1990, 309(NMW.V91.115.62). Epiphytic in moss on trees at summit, c.3220 feet. 1990. Common.

Grammitis serricula (Fée) Proctor. On mossy trees at high elevations, Proctor (1977).

Grammitis flabelliformis (Poiret in Lamarck) Morton (*G.taenifolia* (Jenman) Proctor). Epiphytic in moss festooning trees in summit cloud forest, c.3230 feet, 1990, 320(NMW.V91.115.66).

Grammitis suspensa (L.) Proctor. Cloud forest above Tower Hill, c.2700 feet, 1990, 318(NMW.V91.115.65).

Grammitis asplenifolia (L.) Proctor. Forest above Tower Hill, c.1700 feet, 1990, 315(BM); 314(NMW.V91.115.64).

Grammitis seminuda (Willd.) Willd. (*Cochlidium seminudum* (Willd.) Maxon). Epiphytic on trees often in moss festooning trees. Above Zetland, 1600-2300 feet, 1990, 357(NMW.V91.115.77). Above Tower Hill, 2600-2800 feet, 1990.

Vittaria lineata (L.) Smith. Shoestring Fern. Above Tower Hill epiphytic on tree, c.1200 feet, 1990, 328(NMW.V91.115.69). Route to Source, 1988.

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REVIEW

SPORES OF THE PTERIDOPHYTA by Alice F. Tryon and Bernard Lugardon, 648 pp., 393 figs. 1990. Springer-Verlag, Berlin. ISBN 3-540-97218-8. Price DM 188.

This book is an encyclopaedic reference work to the development and structure of pteridophyte spores. A short but comprehensive Introduction discusses new concepts on sporoderm development and ultrastructure and the relationship between spore and pollen sporoderms, clarifying and describing, often new, terminology of spore wall-layering. There is an interesting section on possible lines of evolution of different spore types. Both SEM and transmission electron micrographs are given for each genus, and the techniques used in preparation are briefly described.

The text describing the spore morphology and commenting on its diversity and relationships is arranged in a family order only remotely similar to that used in Tryon and Tryon (1982). It is not clear whether either the family or the generic arrangement is based on spore morphology although the reader can suspect it is, giving us yet another perspective on this never ending debate; 232 accepted genera are treated, arranged in 35 families. In many larger genera a range of species and micrographs are pictured, e.g. *Asplenium* (73), *Cheilanthes* (55), *Dryopteris* (50), *Isoetes* (52), *Selaginella* (87), *Sphaeropteris* (33), *Thelypteris* (35). Several British species (and specimens) are figured; Figs 38, 39 of *Isoetes echinospora* from English material look very much like the fertile hybrid *I. echinospora × lacustris*, yet to be cytologically confirmed for Britain.

A C JERMY

CHLOROPLAST DNA AND MORPHOLOGICAL VARIATION IN THE FERN GENUS *PLATYCERIUM* (POLYPODIACEAE: PTERIDOPHYTA)

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ABSTRACT

The phylogenetic relationships of 15 species of the pantropical staghorn fern genus *Platycerium* (Polypodiaceae) have been studied, using chloroplast DNA and morphological data. Restriction fragment length polymorphisms (RFLPs) of chloroplast DNA among eleven species of genus *Platycerium* have been examined.

The patterns of interspecific RFLPs were too complex to allow for a direct study of mutational events. Therefore, a simplified method was adopted to reveal the relatedness of the observed restriction fragment patterns: assignment of fragment homology was based upon critical inspection of the fragment patterns. This resulted in the recognition of 215 fragments shared by at least 2 species. A binary data matrix was compiled from the presence/absence distribution of these fragments over the species. Both cladistic analysis using Wagner parsimony and agglomerative clustering analysis of the data revealed the same pattern of relationships among the species. The results from the chloroplast DNA analysis were compared with the results from cladistic and agglomerative clustering analysis of a morphological dataset comprising 85 multistate characters. The results of the study lead to a new hypothesis on the phylogeny of *Platycerium*, that is highly congruent with geographic distributions.

INTRODUCTION

The tropical fern genus *Platycerium* Desv. (staghorn ferns, Polypodiaceae) comprises 15 species (Hennipman & Roos 1982) or 18 species (Joe Hoshizaki 1972), mainly distributed in the Palaeotropics, with only one species in the Neotropics. The genus unambiguously is a monophyletic group, but there has been controversy about the systematic position of the genus among other genera of polypodiaceous ferns and the infrageneric relationships (Hennipman & Roos 1982). *Platycerium* and its sister genus *Pyrrosia* Mirbel constitute one of the two subfamilies within the *Polypodiaceae*, viz. the *Platycerioideae* (Hennipman et al. 1989). Among ferns, this subfamily is characterized by the unique possession of stellate hairs. Most studies on *Platycerium* that have appeared in this century deal with its morphology and taxonomy (Straszewski 1915; Bower 1928; Joe 1964; Joe Hoshizaki 1970, 1972; De Joncheere 1974; De Joncheere & Hennipman 1970 and Hennipman & Ros 1982). The geographical distribution of the species (FIG. 1) have been studied by Hennipman and Roos (1982). The evolutionary relationships within the genus have been studied by both Joe Hoshizaki (1972) and Hennipman and Roos (1982). These authors come to very different conclusions (FIG. 2 and FIG. 3). Joe Hoshizaki (1972) recognizes eighteen species, which she assumes to represent three main lines of evolution in the genus. Her groups coincides with sympatry at a continental level: she recognizes a Javan-Australian (the middle branch in FIG. 2), an Afro-American (the left branch) and a Malayan-Asiatic group (the right branch). Within their respective geographical areas the species mostly have disjunct distributions.
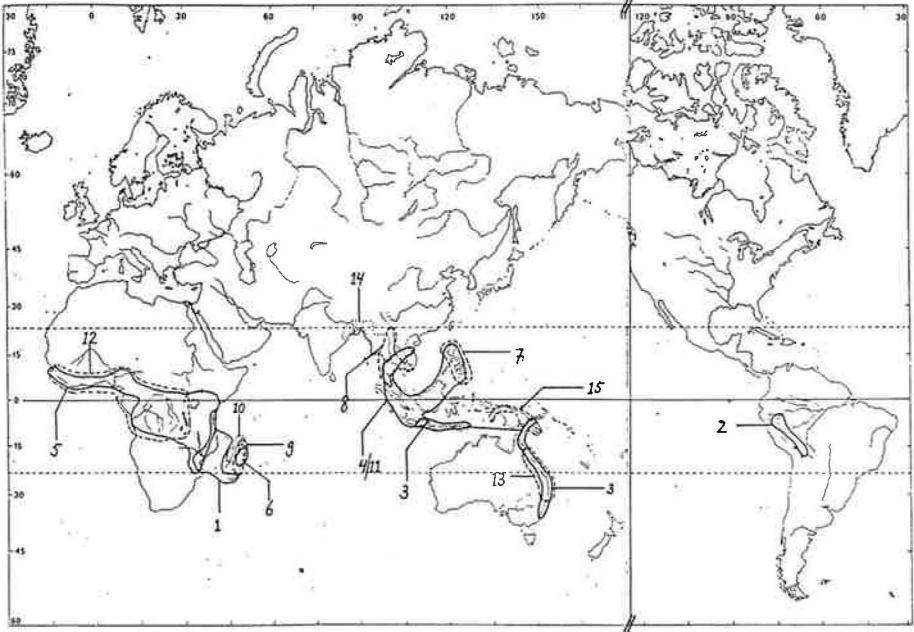
Figure 1. Global geographical distribution of *Platycerium* species descriptions by Hennipman & Roos (1982).
1.. *P. alcicorne* 2. *P. andinum* 3. *P. bifurcatum* 4. *P. coronarium* 5. *P. elephantotis* 6. *P. ellisii* 7. *P. grande* 8. *P. holttumii* 9. *P. madagascariense* 10. *P. quadridichotomum* 11. *P. ridleyi* 12. *P. stemaria* 13. *P. superbum* 14. *P. wallichii* 15. *P. wandae*.
Numbers and abbreviations assigned to the different species are the same in all figures.
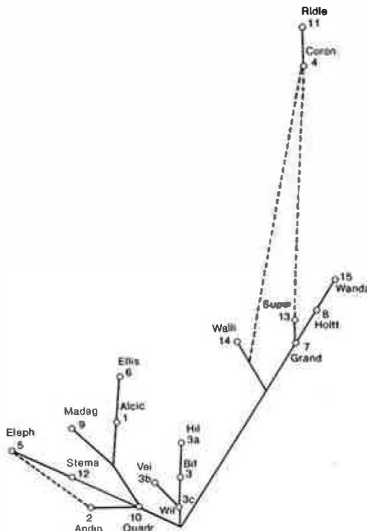
Figure 2. A modified representation of the lines of evolution of *Platycerium* species from Joe Hoshizaki (1972).
1. *P. alcicorne* (alcic), 2. *P. andinum* (andin), 3. *P. bifurcatum* ssp. *bifurcatum* var. *bifurcatum* (bif) 3a. *P. bifurcatum* ssp. *bifurcatum* var. *hillii* (hil) 3b. *P. bifurcatum* ssp. *veitchii* (vei) 3c. *P. bifurcatum* ssp. *willinckii* (wil) 4. *P. coronarium* (coron), 5. *P. elephantotis* (eleph) 6. *P. ellisii* (ellis) 7. *P. grande* (grand) 8. *P. holttumii* (holtt), 9. *P. madagascariense* (madag) 10. *P. quadridichotomum* (guadr), 11. *P. ridleyi* (ridle), 12. *P. stemaria* (stema), 13. *P. superbum* (super), 14. *P. wallichii* (walli), 15. *P wandae* (wanda).
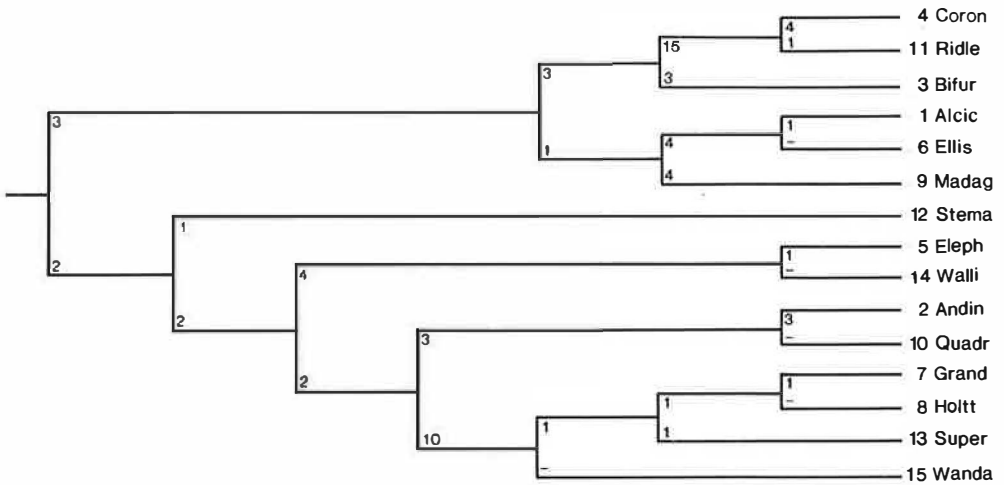
Figure 3. The phylogeny of the genus *Platycerium* according to Hennipman and Roos (1982). The number of apomorphies on which grouping is based are given in the tree.
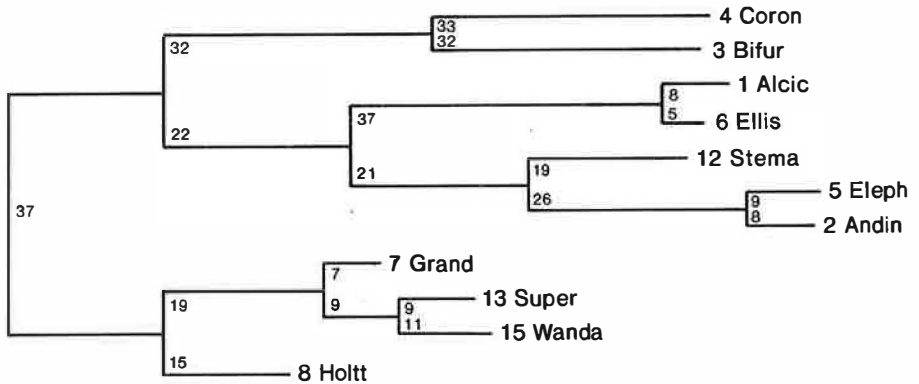
Figure 4. One of the minimal mutation trees found with the BANDB option implemented in the computer program PAUP using the molecular dataset. The next tree found had the three-taxon cluster including *P. andinum* attached to the four-taxon *P. grande*-group (see text). The number of steps or mutations in each branch are given.

Because Hennipman and Roos (1982) have reduced the specific status of four species attributed by Joe Hoshizaki (1970) to the polymorphic *P. bifurcatum*-complex, to infraspecific taxa of *P. bifurcatum* (FIG. 2, 3a-c), they recognise only 15 species. Unlike the three lines of evolution distinguished by Joe Hoshizaki, Hennipman & Roos (1982) recognise two major monophyletic groups, (consisting of lower-ranked taxa that comprise allopatric species at a continental level (FIG. 3). As an example, their *P. elephantotis*-group relates a Central African species to a South East Asian species. In biogeographic terms, this is a less parsimonious solution than Joe Hoshizaki's separation of the species into the Afro-American and Malayan-Asiatic group, respectively.

In the case of allopatric speciation, fragmentation of an ancestral species into two or more different species may result from the physical separation of a distribution area (vicariance; Wiley, 1980) or after long-distance dispersal. Under the assumption that *Platycerium* arose on one of the present-day continents, the distribution pattern of the species is most parsimoniously explained by the phylogeny of Joe Hoshizaki (1972), because it requires a smaller number of dispersal events when compared to the phylogeny of Hennipman and Roos (1982): 2 long- and 2 short- versus 4 long- and 2 short-distance dispersal events, respectively. If the origin of the genus precedes the time of continental fragmentation, then vicariance could have been involved as a mode of allopatric speciation as well as dispersal. Both phylogenies discussed above were inferred from morphological data. Hennipman and Roos (1982) based their phylogeny on a cladistic analysis of selected morphological characters, preceded by *a priori* interpretations of apomorphic and pleisiomorphic character states, using outgroup comparison. Joe Hoshizaki (1972) refers to Wagner's (1962) ground plan divergence method. However, the lack of distinct, informative morphological characters may account for the differences between previous classifications of *Platycerium*.

Comparative data of chloroplast genomes has recently become a major tool for assessing phylogenetic relationships among angiosperm plants at diverse taxonomic levels (Palmer, 1986a, 1987, Palmer et al. 1988 and references therein): the relatively high degree of overall sequence and size conservation of chloroplast DNA (cpDNA) among closely related species as well as among the major lineages of flowering plants makes it an ideal source of variation for evolutionary studies above the population level. In addition, unisexual inheritance, as the most frequent mode of chloroplast transmission in angiosperms (Whatley, 1982), can provide strong evidence for the parentage within hybrids and polyploid complexes (e.g. Palmer et al. 1983a; Stein 1985; Erickson et al. 1983; Kung et al. 1982). The chloroplast genome of ferns is less well studied than that of angiosperms. Most of the studies of fern cpDNA deal only with the characterization of the genome (Palmer & Stein 1986; Hasebe & Iwatsuki 1990). Until recently very few taxonomic studies of pteridophytes using chloroplast DNA have been published: Stein et al. (1986) on the genus *Osmunda* and Yatskievych et al. (1988) and Stein et al. (1989) on the cpDNA evolution of the genera *Cyrtomium, Polystichum* and *Phanerophlebia* (Dryopteridaceae).

In the present study we compare results of an analysis of cpDNA variation in the fern genus *Platycerium* with an analysis based on morphological data. Eleven species of the genus *Platycerium* were examined using restriction endonuclease analysis of their cpDNA. Although an account of the specific mutation events could not be given for the observed restriction fragment variation, relationships are inferred from comparisons of interspecific restriction fragment length polymorphisms. In addition, a morphological dataset of 85 multistate characters, including all fifteen species of the genus was compiled from the literature. Parsimony and cluster analyses were performed on both cpDNA and morphological data matrices. The results of these analyses have been compared with the previous morphological studies, and a new hypothesis on the phylogeny of the genus is presented.

MATERIALS AND METHODS

Plant material

Nineteen specimens of eleven species, representing the eight main groups in the genus as postulated by Hennipman and Roos (1982), were examined (Table 1). The remaining four species *(P. madagascariense, P. quadridichotomum, P. ridleyi* and *P. wallichii)* were either unavailable or of insufficient material.

The sources of plant material for the species of *Platycerium* included in the analysis are shown in Table 1. All investigations were carried out on full-grown specimens, which had been collected in the field and cultivated under tropical greenhouse conditions in the botanic gardens of the Universities of Utrecht and Leiden.

Table 1. Accessions of *Platycerium* included in the analysis of chloroplast DNA variation.

Species	**Garden nr.**
a. *P. alcicorne* Desv.	82.259
b. *P. andinum* Baker	85.164
c. *P. bifurcatum* (Cav.) C. Chr. s.1.	X-1
d. ssp. *bifurcatum* var. *veitchii* (Underwood) Hennipm. & Roos	81-181
e. ssp. *bifurcatum* var. *hillii* (T. Moore) Domin.	20684
f. ssp. *bifurcatum* var. *hillii* (T. Moore) Domin.	20689
g. ssp. *bifurcatum* var. *hillii* (T. Moore) Domin.	82-354
h. *P. coronarium* (Konig ex Muller) Desv.	82-220
i. *P. coronarium* (Konig ex Muller) Desv.	20676
j. *P. coronarium* (Konig ex Muller) Desv.	20679
k. *P. elephantotis* Schweinf.	82-356
l. *P. ellisii* Baker	82-258
m. *P. grande* (Feé) Kunze	23044
n. *P. holttumii* De Jonch. & Hennipm.	16638
o. *P. stemaria* (Beauv.) Desv.	82-178
p. *P. stemaria* (Beauv.) Desv.	82-355
q. *P. stemaria* (Beauv.) Desv.	X-2
r. *P. superbum* De Jonch. & Hennipm.	20681
s. *P. wandae* Racib.	180

Chloroplast DNA isolation

Chloroplast DNA (cpDNA) was isolated according to Sandbrink et al. (1989). Prior to harvesting, plants were kept in the dark for 4 to 8 days to reduce the starch content of the plastids. Leaves were ground at 4°C in a Waring blender with homogenization buffer (HB) (1.25 M NaCl, 3 % PVP, 15mM 2-ME, 0.1% BSA, 7mM EDTA, 10 mM Tris-HCl, pH=8.0). in a 1:5 (w:v) ratio. The chloroplast suspension was filtered through 1 layer of nylon gauze and 4 layers of Miracloth (Calbiochem). Chloroplasts were centrifuged at 1500 x g, resuspended in HB, centrifuged again at 1500 x g and resuspended in a buffer containing 5 mM EDTA, 10 mg/ml proteinase K and 10 mM Tris-HCl, pH=8.0 (8:1 w:v). For leaves that were somewhat aged the chloroplasts were washed twice in HB. An equal volume of lysisbuffer (10 mM 2-ME, 5 mM EDTA, 4% sarkosyl, 1% SDS, 10 mg/ml proteinase K, 10 mM Tris-HCl, pH=8.0) was added. Chloroplasts were lysed by incubation for 30 min at 37°C followed by 30 min. of gentle rotation at room temperature. The lysate was centrifuged for 10 min at 3,000 x g to remove debris and residual starch (mainly in form of amyloplasts). An equal volume of 2 x CTAB buffer (1.4 M NaCl, 20 mM 2-ME, 20 mM EDTA, 2% cetyl trimethyl ammonium bromide, 100 mM Tris-HCl, ph=8.0) was added.

The suspension was incubated for 1 h at 60°C and subsequently extracted twice with chloroform; isoamylalchohol (24:1). DNA was precipitated with isopropanol at -20°C and pelleted by centrifugation at 10,000 x g. Pellets were washed in 76% ethanol, 10 mM ammonium acetate and finally resuspended in TE Buffer pH=8.0 (Maniatis et al., 1982). Restriction endonucleases were purchased from Pharmacia and Boehringer Mannheim.

The following restriction enzymes were used: for infraspecific cpDNA variation: Bgl II, BstE II, Dra I, Hind III, Nco I, Pvu II, Sal I, Sca I, and Sma I, and for interspecific cpDNA variation: Bgl II, BstE II, Mlu I, Nco I, Pst I, Sac I, Sal I, Sca I, and Sma I. Electrophoresis was on 0.3-0.7% TBE agarose minigels (Maniatis et al., 1982).

Restriction fragment pattern analysis
The observed pattern of interspecific restriction fragment variation among the *Platycerium* species examined was too complex to allow a direct study of mutational events. Therefore a simplified method was used to reveal the relationships of the obtained restriction fragment patterns: in our approach every individual band of the digested cpDNA was treated as a discrete phenotypic character of the species in question. Fragments with the same relative migration distance were treated as homologies. The inferred homologous restriction fragments of all cpDNAs examined were compiled into a binary data matrix which was subjected to further analysis. In their study of chloroplast DNA variation in *Silene* sect. *Siphonomorpha*, Sandbrink & Van Brederode (1991) found that the patterns of restriction fragment of cpDNA were also too complex to allow for a direct study of mutational events. They showed, that the method described above resulted in the same shortest Wagner and Dollo trees as the more traditional method of identification of restriction site mutations by the hybridization-overlap method (Palmer 1986b).

Morphological variation
Characters and character state distributions were mainly taken from the species descriptions in Hennipman & Roos (1982). In addition, eight characters, representing 22 character states, were taken from Joe Hoshizaki (1972).

Data analysis
The molecular and morphological data matrices were subjected to two types of analysis: 1) agglomerative clustering analysis using the program system BIOPAT (Hogeweg and Hesper, 1972). A phenetic cluster analysis on the data matrices was performed on mean character differences, using the cluster criteria of Ward's averaging (Ward 1963) and group averaging (UPGMA: Sokal & Sneath 1963), implemented in the BIOPAT program DENDRO. 2) numerical cladistic analysis using the computer program "Phylogenetic Analysis Using Parsimony" (PAUP version 2.4.1) developed by Swofford (1985). In the cladistic analysis of the molecular data matrix the most parsimonious trees were searched for by the brand-and-bound algorithm of Hendy and Penny (1982), implemented in PAUP by the BANDB-option. For the morphological data matrix, most parsimonious trees were searched for by applying the global branch-swapping algorithm (SWAP-GLOBAL-option) with the MULPARS-option to retain all equally parsimonious trees. All characters were treated as unordered. Missing data, due to logistical or technical problems were present in the molecular data matrix. In PAUP, such data do not affect tree-construction procedures, where character states to missing characters are parsimoniously assigned only after the building-up of a tree (Swofford, 1985). Molecular and morphological data matrices with descriptions of the morphological characters and character states are presented in the Appendices 1-3.

RESULTS

Infraspecific cpDNA variation

Infraspecific variation was examined among 3 specimens of *P. coronarium* (acc. h-j), 3 specimens of *P. stemaria* (acc. o-q) and 5 specimens of *P. bifurcatum* (Table 1). One specimen of ssp. *veitchii* (accession d), three specimens of the ssp. *P. bifurcatum* variety *hillii* (acc. e-g) and one specimen of undetermined subspecific rank (acc. c), represented the *P. bifurcatum* accessions. Specimens of *P. bifurcatum* ssp. *willinckii* were not available. For the other species only one appropriate specimen was available for cpDNA analysis. Comparisons between pairs of restriction fragment patterns enabled estimation of infraspecific genetic similarity for the chloroplast genomes of *P. bifurcatum*, *P. coronarium* and *P. stemaria*. As an index of the relative genetic similarity, the fraction of shared restriction fragments was used according to Nei and Li (1979): $F = 2Nxy / (Nx + Ny)$ in which F is the fraction of shared restriction fragments, Nx and Ny are the numbers of fragments in species x and y, respectively and Nxy is the number of fragments shared by x and y. Table 2 shows the values of F for the pairs of specimens compared. The interspecific pairs *P. alcicorne* – *P. ellisii*, *P. alcicorne* – *P. andinum*, *P. alcicorne* – *P. grande* and *P. andinum* – *P. grande* are added for comparison.

Infraspecific variation within species of *Platycerium* as detected in this study, is considerably lower than interspecific variation. Maximal infraspecific divergence was found between the specimen of *P. bifurcatum* ssp. *veitchii* and the three specimens of *P. bifurcatum* ssp. *bifurcatum*. The least diverged species couple *P. alcicorne* – *P. ellisii*, according to the interspecific cpDNA and morphological variation, showed a divergence considerably higher then the scored infraspecific variation.

Table 2. Quantitative analysis of infraspecific cpDNA variation by means of proportions of shared restriction fragments (F) Specimen designations refer to garden numbers (Table 1). For explanations of symbols see text.

Species	Specimen-couple			Nxy	Nx +Ny	F
P. coronarium	82-220	x	20676	114	230	0.991
	82-220	x	20679	86	173	0.994
	20676	x	20679	86	174	0.989
P. bifurcatum	X-1	x	20684	121	242	1.000
	X-1	x	20689	121	242	1.000
	X-1	x	82-354	121	244	0.992
	X-1	x	81-181	96	199	0.965
	20684	x	20689	121	242	1.000
	20684	x	82-354	121	244	0.992
	20684	x	81-181	96	199	0.965
	20689	x	82-354	121	244	0.992
	20689	x	81-181	96	199	0.965
	82-354	x	81-181	96	199	0.965
P. stemaria	82-178	x	82-355	126	256	0.984
	82-178	x	X-2	92	188	0.978
	82-355	x	X-2	84	168	1.000
P. alcicorne x *P. ellisii*				124	272	0.912
P. alcicorne x *P. andinum*				89	308	0.580
P. alcicorne x *P. grande*				50	246	0.410
P. andinum x *P. grande*				50	226	0.442

Interspecific variation

A molecular data matrix was compiled from the restriction fragment patterns by treating each restriction fragment as a separate character. The interspecific comparisons of restriction fragment patterns resulted in the recognition of 215 fragments shared by at least two species. Restriction fragment data were not complete for some accessions, due to the limited amount of proper plant material. The proportions of missing data for each species in the molecular data matrix are listed in Table 3.

Table 3. Proportion of missing data in the molecular data matrix.

Species	Proportion missing
Data (%)	
1. *P. alcicorne*	0.0
2. *P. andinum*	0.0
3. *P. bifuractum* s.l.	0.0
4. *P. coronarium*	0.0
5. *P. elephantotis*	62.8
6. *P. ellisii*	21.4
7. *P. grande*	8.8
8. *P. holttumii*	32.6
9. *P. stemaria*	0.0
10. *P. superbum*	19.5
11. *P. wandae*	19.5

Minimal mutation analysis was performed using the branch and bound algorithm, implemented in the PAUP program (version 2.4.1). Two trees were found requiring a total number of 359 steps with a consistency index (Kluge and Farris, 1969) of 0.599. The first tree is presented in FIG. 4. The second tree was the same except for the linking of the three species of the grouping including *P. andinum* directly to the four species of the *P. grande*-grouping. This second tree, however, has 51 parallel gains of fragments, whereas the first presented tree has only 40 parallel gains. The dendrograms obtained from the agglomerative cluster analysis of the molecular data matrix using different similarity measures (mean character differences, mean square distances, Euclidean distances and correlation coefficients) and 2 different cluster criteria (Ward's averaging and group averaging) were all identical. To avoid redundancy only the dendrogram obtained from group averaging on mean character differences has been given (FIG. 5). Cluster analysis of a subset of the original data matrix (comprising the fragments generated by the enzymes Nco I, Pvu II and Sal I, a total of 83 characters) also gives the same tree.

Hereafter, the pattern of relationships among the species examined for cpDNA variation as shown in the minimal mutation tree (FIG. 4) and the dendrogram of the cluster analysis (FIG. 5) will be referred to as "the molecular tree".

The following groupings present in the molecular tree are also found in the phylogenetic hypotheses of:

A: Both Joe Hoshizaki (1972) (FIG. 2) and Hennipman and Roos (1982) (FIG. 3):
1) the *P. alcicorne*-grouping, comprising the specieis *P. alcicorne* (= *P. vassei* in Joe Hoshizaki (1972)) and *P. ellisii*.
2) the *P. grande*-grouping, comprising the species *P. grande, P. superbum, P. wandae* and *P. holttumii*. Within the *P. grande*-group however, the proposed relationships in the three phylogenetic hypotheses compared differ.
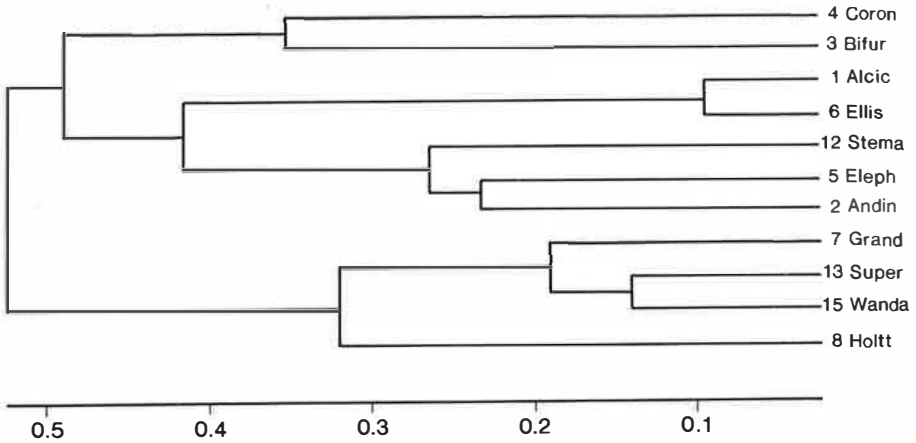
Figure 5. Representation of the clustering pattern found using the group averaging on mean character distances option of BIOPAT on the molecular dataset. The same patterns were found using other clustering criteria or similarity measures.
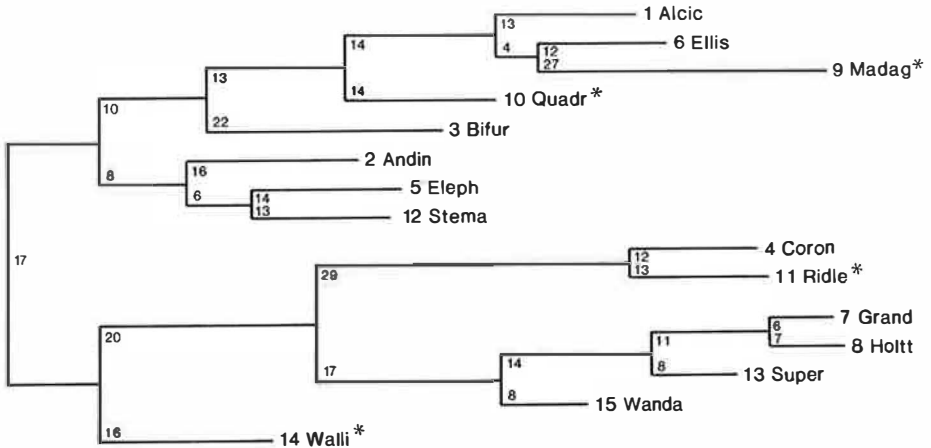
Figure 6. The minimum mutation tree found using the swap-global and mulpars options of PAUP on the morphological dataset. * indicate specifies not included in molecular analysis.

B: Joe Hoshizaki (1972)(FIG. 2):
3) the *P. andinum*-grouping, including the species *P. andinum*, *P. stemaria* and *P. elephantotis* (=*P. angolense*). According to Hennipman and Roos this group of species is paraphyletic.
4) the grouping of the *P. alcicorne*- combined with the *P. andinum*-grouping was found both with both cluster analysis and minimal mutation analysis. Together with the Madagascarian species *P. madagascariense* and *P. quadridichotomum* which are not presented in this cpDNA study, this grouping represents the Afro-American line of evolution within the genus as put forward by Joe Hoshizaki.
C: Hennipman and Roos (1982)(FIG. 3):
5) the *P. coronarium*-group, comprising the species *P. coronarium* and *P. bifurcatum* s.l.

Morphological variation
The morphological data matrix comprised 85 characters representing 344 character states. Character states were unordered in all parsimony analyses. In a search for minimal mutation trees with the morphological data matrix, applying the global branch-swapping algorithm of the PAUP program, yielded 2 most parsimonious trees. Both trees required a total number of 373 steps and had a consistency index (Kluge and Farris, 1969) of 0.678. The trees differed only in one branch, connecting *P. grande* either to *P. superbum* or to *P. holttumii*. The tree connecting *P. grande* to *P. holttummi* is shown in FIG. 6.

Cluster analysis on mean character differences, using group (FIG. 7) and Ward's averaging cluster criteria (not shown) was also performed on the morphological data matrix. This analysis yielded dendrograms which differed slightly from one another and from the minimal mutation trees.

P. madagascariense was monophyletic to *P. ellisii* in the minimal mutation trees and linked to the group including *P. alcicorne, P. ellisii* and *P. quadridichotomum* in the cluster analysis. *P. wallichii* was connected to the *P. grande*-group using group averaging (FIG. 7), and to the *P. andinum*-group when Ward's clustering criterion was used. Interestingly Joe Hoshizaki places *P. wallichii* near the *P. grande*-group, while Hennipman & Roos choose a closer relationship of *P. wallichii* with *P. elephantotis* in 11 species included in the chloroplast DNA study. No differences in topology were found using either clustering or with parsimony analysis (not shown).
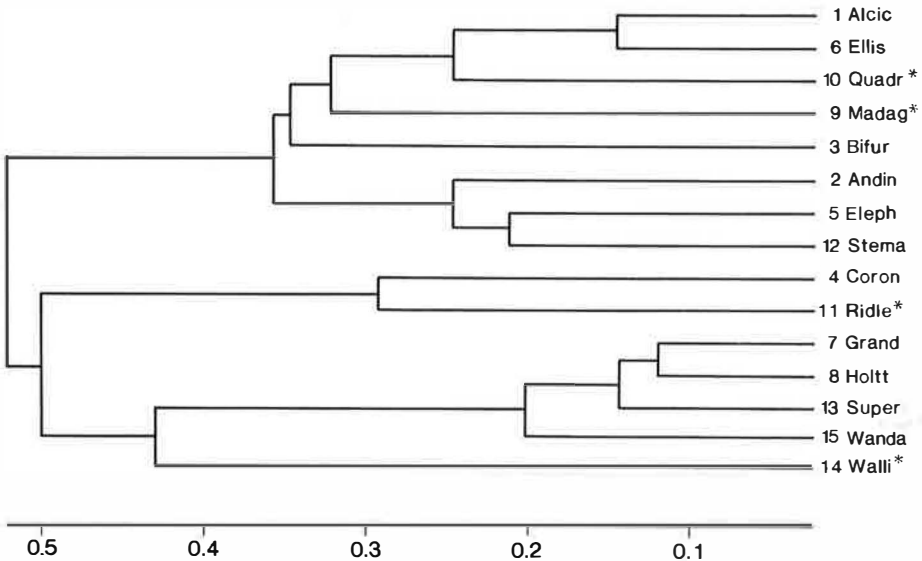
Figure 7. Representation of the clustering pattern found using the group averaging on mean character distances option of BIOPAT on the morphological data. * indicate species not included in molecular analysis.

The phylogenies found with the minimal mutation analysis of the morphological data are very similar to the phylogeny proposed by Joe Hoshizaki (FIG. 2). Corresponding groupings are:
1) the grouping comprising *P. grande, P. superbum, P. holttumii, P. wandae, P. wallichii, P. coronarium* and *P. ridleyi* (the Malayan Asiatic group of Joe Hoshizaki).
2) the grouping comprising *P. alcicorne, P. ellisii* and *P. madagascariense* (one branch in the Afro-American group);

3) the grouping comprising *P. andinum, P. stemaria* and *P. elephantotis*;

4) the grouping relating *P. quadridichotomum* to the species of grouping 2.

The first difference between the phylogenies lies in the position of *P. wallichii* relative to the *P. grande*-grouping and the *P. coronarium*-grouping; although Joe Hoshizaki does not make a decision about either the monophyly or paraphyly of the grouping comprising *P. wallichii* and the *P. coronarium*-group, it is paraphyletic in this study.

The second difference between the phylogenies lies in the position of the *P. bifurcatum*-complex relative to *P. quadridichotomum* and grouping 3: Joe Hoshizaki postulated this species combination as a separate line of evolution (the Javan Australian line), while it is here indicated to be a member of the putative Afro-American group.

There is relatively little correspondence between the cladogram of Hennipman and Roos (FIG. 3) and the morphological minimal mutation-trees. The conformity is restricted to:

1) the monophyly of the *P. grande*-, the *P. coronarium*-, and the *P. alcicorne*-group;

2) the close, though paraphyletic, relationship between *P. andinum, P. stemaria* and *P. elephantotis*.

DISCUSSION

Comparison of molecular to morphological results

When comparing the results of our analyses of the chloroplast DNA restriction fragment variation data with those of the morphological data, the following conclusions can be drawn for the genus *Platycerium*:

1) Both types of data support the presumed monophyly of three groupings of species:

a) the *P. alcicorne*-grouping, comprising the species *P. alcicorne* and *P. ellisii*.

b) the *P. andinum*-grouping, comprising the species *P. andinum, P. stemaria* and *P. elephantotis*.

c) the *P. grande* grouping, comprising the species *P. grande, P. superbum, P. holttumii* and *P. wandae*.

2) Both types of data suggest the descent of a common ancestor of the *P. alcicorne*- and the *P. andinum*-grouping, after the splitting off of the ancestor of the *P. grande*-grouping.

3) Molecular and morphological data are incongruent with regard to the relationships of the species *P. bifurcatum* and *P. coronarium*:

a) the molecular data suggest that these species are monophyletic. At the next level they are related to the united *P. alcicorne*- and *P. andinum*-grouping (FIGS. 4 & 5).

b) analysis of the morphological data suggests a sister relationship between *P. coronarium* (and *P. ridleyi* – not included in the molecular analysis) and the *P. grande*-grouping, though similarity of these taxa appears to be remote. *P. bifurcatum* then is linked to the *P. alcicorne*-grouping, but also only at a considerable level of dissimilarity (FIG. 7).

Phylogeny of the genus

In order to arrive at phylogenetic hypothesis for the genus *Platycerium* that comprises all the species, the topologies presented in this paper have been evaluated, taking into account the existing hypotheses of Joe Hoshizaki (1972) and Hennipman and Roos (1982).

The relationships proposed by the molecular tree are used as the core of this phylogeny, because these relationships are strongly supported by the invariability of the dendrograms found with various types of data analysis. Moreover, where molecular and morphological trees are incongruent the alternatives proposed by the morphological trees involve higher levels of dissimilarity or are mutually incongruent.

The phylogenetic position of the four species not included in the analysis of restriction fragment pattern variation will be discussed below:

1) *P. ridleyi*: the monophyly of the species *P. coronarium* and *P. ridleyi* is unambiguous in that the results of the analysis of morphological variation in the present study as well

as of the previous studies (Joe Hoshizaki, 1972; Hennipman and Roos, 1982) are in agreement on this point.

2) *P. quadridichotomum:* on basis of cluster analysis as well as parsimony analysis a monophyletic relationship of this species to the *P. alcicorne*-grouping is proposed. According to the phylogeny proposed by Joe Hoshizaki this species roots the two branches of the Afro-American line of evolution, thus expressing a close relationship to both the *P. alcicorne*-grouping and the species *P. andinum*. According to Hennipman and Roos *P. quadridichotomum* is monophyletic with *P. andinum* and at the next level with the *P. grande*-grouping.

3) *P. madagascariense:* minimal mutation – and cluster analysis of the morphological data suggests a monophyletic group comprising *P. madagascariense* together with the species *P. alcicorne, P. ellisii* and *P. quadridichotomum*. This monophyly is in good agreement with Joe Hoshizaki (1972) and partially with Hennipman and Roos (1982).

4) *P. wallichii:* the position of this species is not clear. It can be related either to the *P. andinum*- or the *P. grande*-grouping. The first relation is more or less in agreement with Hennipman and Roos (1982) because they propose a monophyletic relationship between *P. wallichii* and *P. elephantotis*, being a member of the *P. andinum*-grouping in the molecular phylogeny. The second relation is in agreement with Joe Hoshizaki. On the basis of the present results no further conclusions can be drawn. The aforementioned alternatives are both acceptable. Integrating the relationships of the 4 species discussed above into a phylogeny with the molecular tree as its core, the tree shown in FIG. 8 can be proposed as hypothesis on the evolutionary history of the genus *Platycerium*. Morphological and molecular four-taxon statements within the *P. grande*-grouping are not congruent. The presented phylogenetic relations within this grouping are based upon the morphological dendrograms and the ideas of Joe Hoshizaki (1972) and Hennipman and Roos (1982). Because the members of the *P. grande*-grouping had relatively high percentages of missing data in the molecular analysis (Table 3), the relationships within this group as proposed by the molecular tree may be questionable.
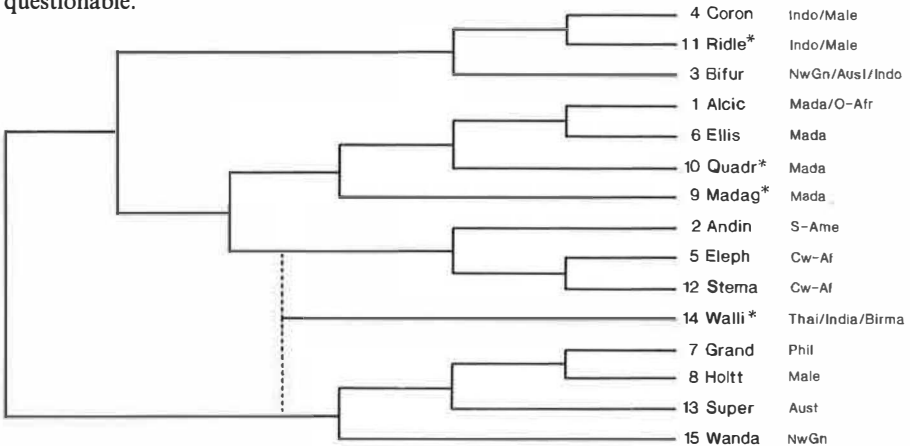
Figure 8. A tentative tree representing the ideas of the authors on the relationships within *Platycerium*. It has been constructed with the tree obtained from the cpDNA analysis as core. The morphological results (and previous phylogenies) have been used to rank the four species not included in the chloroplast DNA study and to determine final branchings in the *P. andinum* group and the *P. grande* group. Note that branch lengths do not represent any form of distance or similarity. * indicate species not included in molecular analysis.

Aust=Australia, Cw-Af=Central-West Africa, Indo=Indonesia, Mada=Madagascar, Male=Malaysia, NwGn=New Guinea, O-Afr=East-Africa, Phil=Philippines, S-Ame=South America, Thai=Thailand.

Comparison of the results with the phylogenies proposed by Joe Hoshizaki (1972) and Hennipman and Roos (1982)

The phylogenetic relationships proposed in this study are in accordance with the phylogeny of Joe Hoshizaki (1972), except for the position of *P. coronarium* and *P. ridleyi* and for details in the relationships in the Afro-American grouping. Hennipman and Roos (1982) used cladistic methods (Hennig, 1966) to elucidate phylogenetic relationships within *Platycerium*. They determined pleisiomorphous and apomorphous states of characters using outgroup comparison or in some cases, ontogeny of the character states. The results of this cladistic analysis deviated from earlier classifications and from the analysis presented in this study, although some groupings are similar. The *P. alcicorne*-grouping and the *P. grande*-grouping are present in the phylogeny of Hennipman and Roos (1982). The most remarkable group, which the phylogeny of Hennipman & Roos (1982) has in common with the phylogeny presented here, is the monophyletic group of *P. coronarium*, *P. ridleyi* and *P. bifurcatum*. Interestingly this group of Hennipman and Roos (1982) was based on characters where the polarity was determined using ontogenetic data. An important difference between the phylogenies of Hennipman & Roos (1982) and Joe Hoshizaki (1970) was the reduction of the specific status of four species attributed by Joe Hoshizaki (1970) to the polymorphic *P. bifurcatum*-complex (her Javan-Australian grouping), to infraspecific taxa of *P. bifurcatum*, viz. a subspecies *bifurcatum*, comprising the varieties *bifurcatum* and *hillii*, a subspecies *veitchii* and a subspecies *willinckii* (formerly *P. bifurcatum* s.s., *P. hillii*, *P. veitchii* and *P. willinckii*, respectively). Because the fraction of shared fragments (0.962) found within *P. bifurcatum* was significantly higher then the maximal fraction of shared fragments found on the species level (0.912 for the species couple *P. alcicorne* and *P. ellisii*), our chloroplast DNA data are in accordance with the interpretation of Hennipman and Roos (1982). However, it should be noted that *P. bifurcatum* ssp. *willinckii* has not been included in this study.

Relationships concerning the *P. andinum*, *P. quadridichotomum*, *P. stemaria* and *P. elephantotis* are totally different in the classification of Hennipman & Roos (1982). They found a sister relationship of *P. andinum* and *P. quadridichotomum* on the basis of three synapomorphic characters, all concerning the foliage fronds and soral patches. The determination of the polarity of the character states of these characters may require a re-interpretation. Parallel changes may have occurred, since these characters are very variable throughout the genus. The sister relationship of *P. stemaria* to the eight species grouping including *P. grande*, as suggested by Hennipman and Roos (1982) has been based on the shape of its base fronds only, which is also a highly variable character in *Platycerium*. The species couple *P. elephantotis* and *P. wallichii* is directly related to the six species grouping including *P. grande* and *P. andinum*, on basis of the pairwise maturing pattern of the foliage fronds only. Although this appears to be a good character, the colour of mature base fronds contradicts this grouping, but this character was omitted from their database. One of these characters must have parallel developed character states and no definite conclusions can be drawn on basis of these characters.

Phylogeny and geographical distribution

One of the interesting aspects of the presented phylogeny for the fern genus *Platycerium* is the over-all congruence of the groups with geographical distribution patterns. Splitting the tree on a four cluster level gives the following distribution:

1) A cluster including *P. alcicorne*, *P. ellisii*, *P. quadridichotomum* and *P. madagascariense* originates from Madagascar, apart from a few locations of *P. alcicorne* in East Africa.

2) A cluster including *P. andinum*, *P. stemaria* and *P. elephantotis* stems from America and Central Africa.

3) These two clusters are connected at the next level to an Afro-American grouping.

4) Geographic relationships within the other two clusters (the *P. grande*-grouping and the *P. coronarium*-grouping) are present although not so clear cut as those concluded in the Afro-American grouping. The *P. grande*-grouping has members in a large but fairly continuous area from Burma to Australia, and the *P. coronarium*-grouping in Australia and South-East Asia.

The results of direct comparison of restriction fragment patterns of widely diverged cpDNA lineages can not be used to calculate genetic divergences or estimate the ages of species (Sandbrink and Van Brederode, 1991). However, the low values of genetic similarity found for distantly related species in the genus (Table 2) indicate an ancient origin of *Platycerium* or an unusual high rate of mutation in chloroplast DNA in *Platycerium*. Assuming that the low genetic similarity is caused by an ancient origin, the breaking-up of the continents may have played an important role in the allopatric speciation within the pantropical genus *Platycerium*. A centre of origin in Gondwanaland was also suggested by Hennipman and Roos (1982). If vicariance has been the most important mode of speciation, sympatry at a continental level of groups of species likely supports the monophyly of such groups. A remarkable result of the analysis of chloroplast DNA variation is the support of the monophyly of the Afro-American group of species as described by Joe Hoshizaki. That the only species that occurs in South-America is related to this group can now be explained in terms of vicariance: speciation must have taken place at the time the migration of this continent away from the African continent started.

Final remarks
Further investigations of chloroplast DNA variation within the genus *Platycerium* are needed to relate the biogeographic data to its evolutionary history. Especially the inclusion of the species *P. quadridichotomum* and *P. wallichii* to the analysis is needed. No satisfying classification of *P. wallichii* could be made on basis of the outcome of the morphological data analysis. *P. wallichii* is in its present distribution restricted to the east of India, Thailand and Burma (FIG. 1), but it is the only species that occurs there. If this species would appear to be more closely related to the Afro-American *P. andinum*-group, than to the *P. grande*-grouping, it is probable that it has evolved on the Indian plate, which broke away from the African continent about 90 million years ago. Thus, vicariance via drift of the Indian plate might have been involved in speciation of the genus.

The power of chloroplast DNA variation in phylogenetic studies is greatly dependent on the taxonomic level of the group under study. This study examplifies that even in ancient or fastly evolving cpDNA lineages directly inspected restriction fragment pattern variation may reveal insight into the evolutionary history of a group of species. Because no restriction site mutation analysis could be performed, an upper limit to this approach has been reached and other techniques adjusted to the amount of divergence encountered may be used. For *Platycerium* this can be achieved by 1. choosing relatively slow evolving regions of the chloroplast genome for detailed restriction-site mapping, 2. the hybridisation overlap procedure (e.g. Jansen & Palmer, 1988) or 3. nucleotide sequencing of specific chloroplast DNA regions (e.g. the RbcL gene, Palmer et al. 1988).

Appendix 1

The binary molecular datamatrix. Every individual band of the digested cpDNA was assigned 1. Missing data are assigned 9. Abbreviations of the taxa are as in figure 1.

```
alcic  11010101110110000100100011101100100100011001000000011100010
       011000101100110000100101010001111100010110110100101010000101
       001010010101100011001010000101000001000110000011110011011101
       0010100000000001010010101011010111001
andin  11010000111100000101100100000100011000010011010111010001001
       110011011100100000100110001100111000001100110001000101001000
       101001000101100100001000000011001000001001010100000101001001
       000110001101110111001100010010010110000
bifur  00101010101011110100100000001000001011100010100000101100010
       100001100010000000001000100001010001010100000001000011000101
       0101000000001100011110100011011110101101010100111000100101011
       010000000100000101101110101010100110010
coron  00101101001110000001100000000010000110000011100000100101100
       0101011000100000011100010000111001101010000000000011000011000
       001000100010010001000000011010000000000010010100010000001011
       000000100100010110100010001000101001100
eleph  99999999999999999999999999999999999999999999999999999999
       99999999990010000010010001100111000010100100001010001000000
       10100100000010000101100110010110199999999999999999999999999999
       99999999999999999999999999999999999999
ellis  11010110110110000100100011101110000100011099999999999999999
       99999999990011000011010101000111110001011011010010101000010
       001010010101100011001010000101000000000010000000110011010101
       00101009999999999999999999991011110001
grand  010100001010000101001100001000101001000011100000000001100
       0100001010101101101101010000010010010100100000001000001010000
       100000000111001001001000011010000110010000100011000100100101010
       100001199999999909999999999990001011000
holtt  001000000101000010100110000100010000100001999999999999999
       99999999990100111110110000010000000000000010010001100011010010
       00100000110100010100110000000000099999999999999999999999999
       99999990001100100000000000009999999999
stema  110100001101000000001100100101010100010010010010011011001000
       101101001100100001101100000100111000000100010000010001101000
       101000010001100000000100010000000010101000101010011000
       10011000000010011010101001010001100010
super  99999999999999999999999999999999999999999991100110010001001
       010001010001000111101000000000001001010110000000010000010100000
       101000101010001001001100011000000010010001001110001001001010
       10000111101000000001000100000000001100
wanda  99999999999999999999999999999999999999999999991100100010001001
       0100110100010001010010000000100000001011010010010000010000000
       101000100110000000100010001101000011001000100111000100100101010
       100001111010000100001100100000100001000
```

Appendix 2

Character state distributions used in the morphological analysis. Character states were mainly taken from the species descriptions in Hennipman & Roos (1982). Descriptions of the characters are given in appendix 3. Abbreviations of the taxa are as in figure 1.

Alcic	21322	11232	41121	22232	12331
31034	11122	01200	02111	11121	13111
22111	13112	32212	12132	22532	14133
Andin	21226	11112	52200	00233	22341
21032	11211	11111	12112	22122	11211
25112	22114	33545	12322	22672	13242
Bifur	21324	11332	33121	12223	12131
11035	11344	31120	02111	15321	12211
24115	82617	35344	12365	22892	15255
Coron	22141	42111	63112	31121	12132
11011	31233	51111	12121	14211	20212
26123	54421	21751	31687	11161	26446
Eleph	21226	11122	52121	12232	22321
31012	11211	01111	12122	12122	11220
22223	31214	13544	12443	22362	11062
Ellis	21212	11212	21121	12231	12131
31034	11122	01200	02111	11121	13331
22111	41114	32121	12122	22712	15312
Grand	12142	21132	12200	00113	21244
21011	22415	42112	22112	23311	20112
13123	61116	25357	22322	22222	15234
Holtt	12132	21132	32200	00113	21234
21011	22415	42112	22112	23311	20212
15123	61116	25657	22552	22542	14532
Madag	21214	11212	23200	00231	12114
32224	11122	03112	31201	11121	11111
21131	73116	12132	12354	22332	12232
Quadr	21212	11242	21121	12232	12144
31032	11211	01200	02112	22122	11211
21112	22112	14213	12111	22392	11242
Ridle	12121	52111	62112	42121	12122
12114	11122	01200	01201	11211	20212
22123	54424	41251	31776	11481	25416
Stema	21223	11132	22121	12232	22323
21032	11211	01111	12112	14122	11111
24114	41313	13444	12222	22742	15222
Super	12142	32132	11200	00113	21223
21011	22415	22112	22113	23311	20112
16123	61115	25456	22787	22752	16211
Walli	12125	11132	42121	12300	00005
01033	11216	41111	12112	12311	11212
12223	61516	33847	12622	22492	11263
Wanda	12143	32112	31121	12113	23222
21011	22415	42112	42112	23311	20212
16123	61116	24434	22111	22762	23233

Appendix 3
List of characters and character states

Social behaviour
1. Growth form
solitary 1
in clusters 2

2. ability to reproduce from buds on roots
present 1
absent 2

Rhizome
3. stele-type
dictyostele 1
polycyclic-dictyostele 2
both 3

Rhizome scales
4. Length
  10 mm 1
  17 mm 2
  17 mm 3
  10 mm 4

5. Index
  5 1
  10 2
  5-15 3
  15 4
  10 5
  5 6

6. Width
  2.0 mm 1
2.0-4.5 mm 2
  4.5 mm 3
  4.5 mm 4
  2.0 mm 5

7. Widest
near the base 1
near the middle 2

8. Base
truncate 1
truncate, but also rounded 2
truncate, but also cordate 3

9. Margin,
(slightly) convex 1
straight 2
both convex and straight forms 3
concave 4

10. Flabelloid margin
present 1
absent 2

11. Apex
acute 1
acuminate 2
both acute and acuminate 3
filiform 4
both acuminate and filiform 5
rounded 6

12. Texture
thin coriaceous 1
(thin) papery 2
papery to thin coriaceous 3

13. Midrib
present 1
absent 2

14. Division in midrib
present 1
absent 2
no midrib 0

15. Shape midrib
linear or/to narrow triangular 1
broad triangular 2
no midrib 0

16. Midrib in cross-section
rounded 1
elliptic, rounded 2
dumpbell-shaped 3
flattened 4
no midrib 0

17. Lateral ridges
present 1
absent 2
no midrib 0

18. Hairs
(very) densely set 1
sparsely set 2
absent 3

19. Placement of hairs
in narrow marginal zone 1
marginally 2
marginally and abaxially 3
no hairs 0

20. Length of hairs
25-150 µm 1
25-250 µm 2
  25 µm 3
no hairs 0

21. Branches on hairs
present 1
absent 2
no hairs 0

22. Proturberances on hairs
present   1
absent   2
both forms present   3
no hairs   0

23. Apical cell of hairs
glandular   1
non-glandular   2
both types present   3
no hairs   0

24. Length of apical cell
　30 μm   1
30-60 μm   2
　60 μm   3
　30 μm   4
no hairs   0

25. Presence of trichomes on hairs
always (present)   1
commonly   2
occasionally   3
rarely   4
absent   5

26. Apical cell of trichomes
glandular   1
non-glandular   2
both types present   3
no trichomes   0

Base fronds
27. Attachment
sessile   1
stalked   2

28. Stalk
conspicuous   1
inconspicuous   2
not stalked   0

29. Colour of mature fronds
green   1
green, darkening   2
withering   3

30. Position of old fronds
recurving   1
erect   2
both recurving and erect forms present   3
appressed   4
both erect and appressed forms present   5

31. Length
　80 cm   1
　80 cm   2
forms both longer and shorter than 80 cm   3

32. Width
　60 cm   1
　60 cm   2

33. Position upper frond part
appressed   1
erect   2
both appressed and erect forms present   3
spreading   4

34. Shape upper frond part
wedge-like   1
kidney-like   2
elliptical   3
both kidney-like and elliptical forms pres.   4

35. Incisions
with 2 main lobes   1
slightly lobed   2
strongly lobed, many dissimilar lobes   3
slightly lobed, many dissimilar lobes   4
many similar lobes   5
many ascending lobes of varying shape   6

36. Number of forkings
1,2   1
3,4   2
1-4   3
3-6   4
1-6   5
no forkings   0

37. Margin lower part
entire   1
sinuate   2
minutely dentate   3

38. Fringe
present   1
absent   2

39. Exhibition of fringe
conspicuous   1
inconspicuous   2
no fringe   0

40. Position of fringe
above the stipe only   1
encircling the stipe   2
no fringe   0

41. Margin
entire   1
sinuate   2
minutely dentate   3
with aphlebia like structures   4
no fringe   0

42. Veins
prominent   1
immersed   2

43. Water storage tissue
present   1
absent   2

44. Cells of water storage tissue
spherical   1
cilindrical   2
no water storage tissue   0

Foliage fronds
45. Maturing of fronds
simultaneously, in undetermined number   1
simultaneously, in pairs   2
single   3

46. Development of fertile and sterile parts
simultaneous   1
in succession   2

47. Position
erect   1
pendulous   2
spreading   3
both pendulous and spreading   4
all forms present   5

48. Central meristeles of stipe
present, well developed   1
present, poorly developed   2
absent   3

49. Ring of dark fiber like cells
present   1
absent   2

50. Number of stomata lower epidermis
14-50/mm2   1
78-88/mm2   2

51. Palisade parenchyma
present   1
absent   2

52. Distinctness of palisade parenchyma
distinct   1
gradual integration into spongy mesophyll   2
poorly defined   3

53. Symmetry
symmetrical   1
asymmetrical   2
both forms present   3

54. Forkings
present   1
absent   2
both forms present   3

55. Transition from first to second order
forkings
gradual   1
abrupt   2
no transition   0

56. Lateral appendages
present   1
absent   2

57. Length (cm)
only forms   40 present   1
forms   40 and between 40-80 present   2
between 40-120   3
    120   4
    80   5
    40   6

58. Texture
pergamentaceous   1
leathery   2

Soral patches
59. Dependence relation between numbers of
forkings and soral patches
present   1
absent   2

60. Placement
away from the plant   1
facing the plant   2
horizontally   3
both horizontally and facing the plant   4
all forms present   5

61. Position
on ultimate segments and often around
ultimate sinus   1
in sub-apical zone   2
apical part   3
both state 1 and 3 possible   4
specialized lobe   5
in main sinus   6
on (pen-)ultimate segments, usually reaching
below first sinus   7
both state 3 and 7   8

62. Shape of soral patches
wedge-like   1
linear or elongate   2
both wedge-like and linear forms present   3
spoon- or kidney-like   4

Sporangia

63. Sporangial development
graduate   1
mixed   2
mixed, weakly   3
mixed, strongly   4
simple   5
gradate, weakly   6

64. Shape of stalk
(2-)3-seriate   1
l-seriate   2

65. Length (μm)
260   1
300   2
300-340   3
300-340   3
260-340   4
340   5
300   6
all forms present   7

66. Index
1.3   1
1.3-1.8   2
1.8   3
1.8   4

67. Number of indurated cells
13   1
13-16   2
17-20   3
13-20   4
17   5

68. Number of epistomium cells
4   1
4   2
4 or 4   3
4 or 5   4
4, 4 or 5   5
4-6   6
5   7
4   8

69. Number of hypostomium cells
1   1
1 or 2   2
3   3
2 or 3   4
3 or more   5

70. Number of annulus cells
22   1
22-25   2
25   3
26-29   4
22-29   5
29   6
26   7

71. Length of stalk (μm)
0.3   1
0.5   2
0.5   3

72. Number of spores
8   1
64   2

73. Length (μm)
60-70   1
70-80   2
60-80   3
70-90   4
60-90   5
80-100   6
90   7

74. Width (μm)
30-40   1
40-50   2
30-50   3
50-60   4
40-60   5
30-60   6
60   7
50   8

75. Height (μm)
30-40   1
40-50   2
50-60   3
40-60   4
30-60   5
60   6
50   7

76. Periscope
distinct   1
indistinct   2

77. Dehiscence of sporangia and paraphyses
present   1
absent   2

Indument

78. Stellate hairs, number of rays
7,8   1
9,10   2
7-10   3
1-10   4
10   5
8   6
6   7
all numbers present   8

79. Length (μm)
150   1
150-250   2
250   3

250-350	4	83. Shape	
350	5	flat or convex	1
250-450	6	involute to canaliculate	2
150-450	7	state 1 or 2	3
350	8	short clavate	4
450	9	spine-like	5
		no shape as above	0
80. Paraphyses, stalk			
long	1	84. Length (μm)	
short	2	150	1
		150-250	2
81. Insertion of rays		250	3
terminally only	1	150-350	4
terminally and sub-terminally	2	450	5
		250	6
82. Number of rays			
11	1	85. Width (μm)	
11-13	2	30	1
13	3	30-50	2
11-16	4	50	3
16	5	30.70	4
11	6	70	5
		50	6

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PTERIDOPHYTES OF THE STATE OF VERACRUZ, MEXICO: NEW RECORDS

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ABSTRACT

The following Pteridophyte species are reported for the first time for the state of Veracruz, México: *Adiantum capillus-veneris, Asplenium heterochroum, Ceratopteris pteridoides, Ctenitis sloanei, Diplazium induratum, Elaphoglossum monicae, Elaphoglossum revolutum, Huperzia cuernavacensis, Nephrolepis falcata f. furcans, Phlebodium araneosum, Polypodium hispidulum, Polypodium polypodioides var. michauxianum, Polypodium subpetiolatum, Selgainella estrellensis, Thelypteris (Goniopteris) ghiesbreghtii,* and *Trichomanes bucinatum.*

INTRODUCTION

During the last phase of research for the preparation of the Annotated Checklist of the Pteridophytes of Veracruz, México (Palacios-Rios, 1992a 1992b), I found 16 species that had not been reported, for this state. I consider them new records for Veracruz because they have not been mentioned in previous accounts, i.e., Conzatti, 1981, Fée, 1857; Finck, 1875, 1877, 1895; Fournier, 1869; Liebmann, 1848; Martens & Galeotti, 1842; Mickel & Beitel, 1988; Palacios-Rios, 1987, 1990; Rovirosa, 1909; Smith, 1981.

RESULTS

For each of the 16 species, I will present data from the voucher specimens examined (i.e., collecting site, data, collector, herbarium), its known distribution in México, and a brief description, when needed, to differentiate between closely related species.

Adiantum capillus-veneris L. Orizaba, Herbarium University of Chicago 354798, collector unknown (F); *M. Váquez et al. 379* (NY, XAL). Tropical rain forest, tropical dry forest, inhabiting gorges along streams, elevation 150-1300 m; terrestrial or epipetric herb. Local name "culantrillo", with ornamental and medicinal uses. It is easy to differentiate from related species by the presence of veins ending in teeth, with its strongly denticulate margins, with blades gradually reduced to the apex. This species has a wide distribution in México and had been mentioned as of possible occurrence in Veracruz by Palacios-Rios & Riba (1983); this is the first report based on herbarium specimens.

Asplenium heterochroum Kunze, Sumidero, *Copeland 67* (BM); temperate montane forest, on limestone, in coffee plantations; elevation 1100 m; terrestrial to epipetric herb. Closely related to *A. palmeri,* differing from that species in the nonflagelliform apex and lack of a terminal bud, thinner leaf texture, and segments more noticeably incised (Smith, 1981). This species was previously known for the state of Chiapas.

Ceratopteris pteridoides (Hook.) Hieron., Mpio. Pajapan, swamp near Barrillas, *Lot 1625* (MEXU); Mpio. Alvarado, Laguana en el Rancho "El Ensueño", ca. 5 km después de la caseta Puente Alvarado, carretera Alvarado-Tlacotalpan, *Palcios-Rios et al. 3232* (XAL); in swamps and road-side ponds; aquatic herb; sea level. This species has 32 spores per sporangium, basal pinnae of sterile frond opposite, stipe width 1-19 mm and sterile fronds mostly simple (palmately or pinnately lobed), sometimes pinnate. This species was previously known for the state of Tabasco (Cowan, 1983).

Ctenitis sloanel (Poeppig ex Sprengel) Morton, Mpio, Córdoba, Vallée de Córdoba, *Bourgeau 1838* (K, NY, UC); Mpio, Córdoba, Córdoba, *Orcutt 3214* (K, MO); elevation 1000 m; terrestrial herb. Closely related to *C. equestris* but differing in the scales of axils of pinnae which are tan to light reddish brown, rhizome and stipe base scales filiform, orangish (Smith, 1981). This species was previously known for the state of Chiapas.

Diplazium induratum Diels, Huatusco, 3 km al SE por la carretera para Fortin, *Calzada 7969* (XAL); near 8 km S of Misantla, *Conant 733 et al.* (GH, MEXU); Orizaba, Cuautlancillo, *Copeland 45* (MEXU, UC); Córdoba, *Finck 26* (MEXU); Rancho El Durazno adelante de Chocamán, cerca del Puente sobre el Río Jamapa, *Herrera et al. JB-1225* (MEXU); Córdoba, *Hutchinson (Finck 453)* (UC); Huatusco, *F. Ventura 16740* (ENCB); temperate montane forest, oak forest, inhabiting gorges along streams; elevation 750-1500 m; terrestrial herb. This species has lamina glabrous beneath; costae and rachis with scattered, lax, catenate hairs (0.8-1.0 mm long) and fibrillose scales (0.5-1.5 mm) at axils of segment midribs and costae; it is closely related to *D. lindbergii* (Mettenius) Christ of Brazil, which has smaller indusia and smaller blade scales (Mickel & Beitel, 1988). This species was previously known from the states of Guerrero, Puebla, Oaxaca, and Chiapas.

Elaphoglossum monicae Mickel, Mpio. Vigas de Ramíirez, Pedregal Las Vigas, *Bohs et al. 1757, 1775* (XAL); Mpio. Xico, Ranchería Paso Panal, camino para Positos [Pocitos], *Calzada 5740* (XAL); Mpio. Vigas de Ramírez, Volcancillo Ver. 3 km SW de Las Vigas *B. Dorantes 566* (XAL); Mpio. Vigas de Ramírez, El Volcancillo, *Dorantes 5111* (XAL); Mpio. Vigas de Ramírez, Pedregal Las Vigas, carretera Xalapa-Perote, *Dorantes & M. Acosta 2390* (XALU); Mpio. Vigas de Ramírez, El Volcancillo, *R. Ortega 530* (XAL, XALU); Mpio, Vigsa de Ramírez, Pedregal Las Vigas, *Palacios-Rios 3414* (XAL); pine forest, pine-oak forest; elevation 2200-2350(2925) m; epiphytic herb. This species was recently described for the Flora of Nueva Galicia (Mickel, 1992), and it is closely related to *E. lindenii*, differing by the oblong blade and the larger (37-49 μm) ave. 43 μm echinate-reticulate spores.

Elaphoglossum revolutum (Liebm.) Moore, Mpio. Hidalgotitlán, a 1500 m del Campamento Hermanos Cedillo hacia La Laguna, *Valdivia 942* (XAL); tropical rain forest; elevation 156 m; epiphytic herb. It is distinguished from *E. squamipes* by the generally more elliptic blade and the much lower elevations. This species was previously known for the states of Chiapas and Oaxaca.

Huperzia cuernavacensis (Underw. & Lloyd) Jolub, Las Minas. *C. Durán 925* (XAL); temperate montane forest; elevation 1700 m; epiphytic herb. This species is very closely allied to *L. taxifolium*, its leaves generally strong coriaceous and tightly appressed and occurring at higher elevations, whereas *L. taxifolium* appears to be quite variable in its leaf texture and degree of appression (Mickel & Beitel, 1988). This species was previously known only for the states of Sinaloa, Michoacán, México, Morelos, Oaxaca, and Chiapas in México.

Nephrolepis falcata f. furcans (Moore) Proctor, Nautla, *Ortega-Torres 427* (XAL). tropical deciduous forest; elevation 50 m; terrestrial herb. This cultivated species had not been previously reported for Veracruz.

Phlebodium araneosum (Martens & Galeotti) Mickel & Beitel, Mpio. Maltrata, Cumbres de Maltrata, *R. Hernández M. & C. Orozco 1645* (MEXU, MO); oak forest; elevation 1700 m; terrestrial or epipetric herb. Closely related to *Phlebodium areolatum* (Humb. & Bonpl. ex Willd.) J. Smith (= *Phlebodium pseudoaureum* (Cav.) Lellinger), but the former often has falcate pinnae, but this is not constant, blade with linear, twisted, toothed, orange scales on the lower surface, blade margin with low teeth consistently, pinnae are wider

(16-30 mm wide), rhizome scales shorter (4-7 mm), entire with a long tip. This species was previously known only for the states of Jalisco, Michoacán, Guerrero, México, Distrito Federal, Morelos, San Luis Potosí, Hidalgo, Puebla, and Oaxaca.

Polypodium hispidulum Bartlett, Soteapan, *Riba 1148a* (UAMIZ); Soteapan, *F. Ramírez 514* (XAL); tropical rain forest, *Bursera* forest; elevation 300-600 m; epiphytic herb. Related to *P. fuscopetiolatum,* but stipe and rachis stramineous below; rhizome scales ovate, acute at tip, more or less entire, blade hairy, sporangia setose (0.1-0.3 mm) and occurs at low elevations. This species was previously known for the states of Oaxaca and Chiapas.

Polypodium polypodioides var. michauxianum Weatherby, Mpio. Pueblo Viejo, vicinity of Pueblo Veijo, 2 km south of Tampico, *Palmer 542* (K, MO, US); matorral; sea level; epiphytic herb. The variety *michauxianum* has scales of lower laminar surface lacking long, acicular tip, and the upper laminar surface is glabrous. This species was previously known for the states of Coahuila, San Luis Potosí, Tamaulipas, and Chiapas.

Polypodium subpetiolatum Hook., Mpio. Orizaba, Orizaba, *Pringle 5953* (MO); Mpio. Teocelo, La Barranca, *F Ventura 15797* (ENCB, MO); temperate montane forest, oak forest, inhabiting gorges along streams; elevation 1000 m; epiphytic herb. This species resembles *P. adelphum* in the serrulate blade margin, hairy blade, and sporangia lacking long setae, but is distinct from that species in its glabrous rhizome scales, entirely free veins, and densely hairy adaxial pinnae midvein. This species was previously known for the states of Chihuahua, Sinaloa, Jalisco, Colima, Michoacán, Guerrero, México, Distrito Federal, Morelos, San Luis Potosí, Hidalgo, Puebla, and Oaxaca.

Selaginella estrellensis Hieron., Jilotepec, Xico, *Nee & Taylor 26253* (F, NY, XAL); *R. Ortega et al. 244* (NY, XAL); *C. Munoz 29* (NY); temperate montane forest, *Liquidambar-Alnus* forest; elevation 1300-1600 m; creeping herb. This species had been collected in México but the specimens were mistaken for other species of *Selaginella.*

Thelypteris (Goniopteris) ghiesbreghtii (Hook.) Morton, Hidalgotitlán, *M. Vázquez et al. 874* (XAL); tropical rain forest (jimbal); elevation 150 m; terrestrial herb. This is one of a few species of subgenus *Goniopteris* that apparently lacks stellate or forked haris. However, on the basis of other characters and its obvious affinities with *T. poiteana,* it is clearly a member of the subgenus (Smith, 1981). This species was previously known for the states of Oaxaca, Chiapas, and Tabasco.

Trichomanes bucinatum Mickel & Beitel, Xalapa; *Pringle 10809* (XAL); temperate montane forest; elevation 1200 m; epiphytic to epipetric herb. Closely related to *T. reptans,* but the former has fronds linear with shallow lobes bearing a mixture of short and long segments, the longer segments mostly near the apex; sori strongly exserted (stalks 0.5-1.0 mm long) with wide lips (1.0 mm long); margin with both forked and multi-rayed hairs, many near pinna tips Mickel & Beitel, 1988). This species was previously known only for the states of Hidalgo and Oaxaca.

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SHORTER NOTE

CHROMOSOME COUNTS FOR TWO SPECIES OF *GLEICHENIA* SUBGENUS *MERTENSIA* FROM ECUADOR

Cytological fixations were made in the field by Benjamin Øllgaard during the course of fieldwork undertaken in April 1973 for the Flora of Ecuador project by members of the Botanical Institute, Aarhus University, Denmark. He generously gave me these fixations from which I have obtained meiotic chromosome counts for two species. Herbarium vouchers are held at AAU.

1. *G. bifida* (Willd.) Spreng. Colleted by L. Holm–Nielsen, J. Jeppesen, B. Løjtnant and B. Øllgaard, number 2902 from the Province of Cotopaxi. Here it formed an extensive colony on a slope by the side of the Quevedo – Latacunga road, 46 km from Quevedo on NE exposed slopes with rain forest at 600 m altitude.

This proved to be diploid with n = 34 as have other members of this species from several areas in the New World (see Walker 1990).

2. *G. revoluta* H.B.K. Coll. no. 3614 from the Province of Zamora – Chinchipe where it grew on a slope along the road from Loja to Zamora at 17 km and at an altitude of 2400 m. The roadsides and slopes were covered by montane forest.

This plant was tetraploid with n = 68 and is a new specific record.

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REVIEW

FLORA MALESIANA, Ser. II (Pteriodophyta) Vol. 2 (1): Tectaria Group by R.E. Holttum, 132 pp. 1991. Leiden University, ISBN 90-71236-11-0. Price Dfl. 50–.

This is Eric Holttum's last major work, submitted to the editor shortly before Holttum died aged 95. It says something of this remarkable man that this substantial account maintains the very high standard that Holttum had set many years before for this Pteridophyte series of *Flora Malesiana*. The accompanying line drawings are by Peter Edwards and SEM pictures of spores of selected species give some idea of the variation seen.

Eleven genera are described: *Aenigmopteris* (5 spp.), *Chlamydogramme* (2 spp.), *Ctenitis* (28 spp.), *Cyclopeltis* (5 spp.), *Heterogonium* (17 spp.), *Lastreopsis* (4 spp.), *Pleocnemia* (17 spp.), *Psomiocarpa* (1 sp.), *Pteridrys* (6 spp.), *Tectaria* (105 spp.) *Tectaridium* (1 sp). The first two genera above are named by Holttum as a result of this revision. One hybrid in *Pleocnemia* is included, and I noted one new combination (*Pleocnemia dahlii* (Hieron). Holttum which could slip by as it was not highlighted in bold type in the index.

A C JERMY

REVIEW

THE PTERIDOPHYTES OF FRANCE AND THEIR AFFINITIES: SYSTEMATICS, CHOROLOGY, BIOLOGY, ECOLOGY. Bulletin de la Société Botanique de France vol. 138. Actualités botaniques (2) 103-237. Edited by S. Muller and M. Boudrie. 140 Ff.

This publication came from a conference in Paris on November 9th 1990 which was organised to bring together amateur and professional botanists. It was the first conference to be held in France entirely on French pteridophytes. The papers in the volume follow the different themes of the conference and given an insight into the range of work currently underway in France.

Some explore the geographical ranges of pteridophytes and discuss conservation needs. Parent describes how the Atlas of pteridophytes in Lorraine and the Vosges Mountains is progressing. Then, in another paper, he shows how the distribution of three species of *Equisetum* can be used as markers for the underlying rock strata. Lazare and Vivant, with the collaboration of Sastre, present an interesting synthesis of current knowledge and conservation status of the more than 300 taxa of pteridophytes in Guadeloupe and its dependencies. Botineau, Boudrie, Prelli and Vilks outline the official protective measures for pteridophytes in the "centre-ouest" part of France, while Muller shows that *Botrychium matricarifolium* is under threat in the Vosges Mountains due to changing patterns of land use and how appropriate land management could ensure the survival of the species.

There are papers on hybrids. Prelli uses *Asplenium* to discuss hybridization in ferns, while Bennert, Boudrie and Rasbach report on the cytology of *Asplenium* x *sarneiense* and confirm the autotetraploidy of *Asplenium billotii.* Boudrie discusses three apogamous *Dryopteris* found in France and a focusses on problem shared by pteridologists in Britain: the recognition of the sub-species of *Dryopteris affinis.* Hopefully the discussion and the table of characters will lead to a greater understanding of their distribution in France.

Other papers concentrate more on the overall morphology or developmental biology of a species. Loiseau and Felzines discuss the pioneering habit of *Equisetum* x *moorei* in the Loire valley and relate this to the mode of growth of its underground rhizome. Vindt-Balguerie outlines the development of young plants of *Huperzia selago* from bulbils. Bordonneau and Tourte discuss the embryonic development of heterosporous ferns. Then Le Coq, Guervin, Laroche and Robert briefly outline the mode of excretion of silica in *Selaginella kraussiana* and *Equisetum maximum.*

There are in addition two papers on RNA in the gametes of *Phyllitis scolopendrium* by Bajon, Blaize, Robert and Roland and in *Marsilea vestita* by Kuligowski, Ferrand and Chenou. Also a paper by Carnat, Lamaison and Boudrie on the use of thin layer chromatography in studying *Equisetum* hybrids.

Overall the papers are a good mix and contain some very useful and readable material. It is to be hoped that it will stimulate further interest in pteridophytes in France and indeed throughout Europe.

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