PITYROGRAMMA (INCLUDING TRISMERIA) AND ANOGRAMMA

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During studies in Pityrogramma, Trismeria and Anogramma in preparation of treatments of these genera as they may occur in Peru, various matters pertaining to other species, as well as the Peruvian ones, have been assembled. These seem better presented in a separate paper.

Pityrogramma, Trismeria and Anogramma are all closely related and have been usually maintained as distinct genera. Each of these is adequately separated from allied genera which are Coniogramme, Gymnopteris, Bommeria, Hemi-onitis and Trachypteris (Christensen\(^2\)) and, in addition, Saffordia, Paraceterach, Cerosora and Pleurosoiriopsis (Copeland\(^3\)). My conclusions are to unite Trismeria with Pityrogramma but to maintain Anogramma as distinct from it.

Throughout this paper frequent reference is made to two publications by Karel Domin: "Generis Pityrogramma (Link) species ac sectiones in clavem analyticam dispositae", Publ. Fac. Sci. Univ. Charles, no. 88. 1928 and "The hybrids and garden forms of the genus Pityrogramma (Link)", Rozpr. II. Tr. Ceské Akad. 38\(^4\). 1929. For the sake of brevity these will be referred to as Domin, 1928 and Domin, 1929 respectively.

I. THE GENUS PITYROGRAMMA

Pityrogramma proper consists of some 11 species and closely related to these are three species that evidently represent three isolated and specialized derivatives from it, or from a common ancestor. The species most "typical" of Pityrogramma are P. chrysophylla, P. chrysoconia, P. dealbata, P. "Eggersii", P. sulphurea, P. tartarea and P. calomelanos. These all have concolorous rhizome scales (or if darker and lighter areas are present there is no well defined central stripe); clustered petioles with a groove on their upper side and with two (or in large leaves more) roundish,

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\(^3\)Copeland, Gen. Fil. 1947.
oval to C-shaped vascular bundles; fertile and sterile leaves that are monomorphic or nearly so; a more than 1-pinnate lamina; stalked pinnae; ceraceous indument on the lamina (some variants of *P. tartarea*, *P. calomelanos* and *P. "Eggersii"* are pubescent or glabrous) and sometimes also on the rhizome, especially at its apex; the veins of the ultimate segments arising from a single basal vascular branch; and distinctive spores (Fig. 2c) that are tetrahedral-globose (or somewhat flattened) and have the exospore with rather broad and dark ridges on a lighter background, the ridges forming prominent rings at the equator and mostly "hieroglyphs" or dots elsewhere (one variant of *P. calomelanos* has nearly smooth spores).

To these species must be added *P. argentea*, *P. Humbertii*, *P. ferruginea* and *P. schizophylla*. These are clearly closely related to the species of the "central group" although they differ in some ways from them. *P. argentea*, for example, has spores with the whole exospore dark and with fewer ridges and somewhat tuberculate. (I have seen no material of *P. Humbertii* but it is evidently closely related to *P. argentea*). *Pityrogramma schizophylla* has the lamina glabrous and bears proliferous buds, and *P. ferruginea* has the whole lamina densely and persistently lanate. The characters by which these species depart from those of the "central group" are not striking and together they all form a relatively uniform genus.

In contrast, there are the three specialized species previously mentioned. These also have ceraceous indument on the lamina and two vascular bundles (at least in large leaves) near the base of the petiole. They each depart, however, in several characters from the species of *Pityrogramma* previously mentioned.

*Pityrogramma triangularis* has the petiole terete, the pinnae are sessile or adnate and the spores are light colored, the exospore has a low, fine and sharply reticulate surface. The rhizome scales have marked light margins beyond the dark sclerotic central stripe.

*Gymnogramma Lehmannii* has the spores, grooved petiole and rachis and two vascular bundles typical of *Pityrogramma*. However, the lamina is only pinnatisect (Fig. 6a) and the ultimate segments (pinna-segments) are furnished
with many veins arising from the costa (Fig. 6b), the petioles are spaced on the rhizome and the vascular bundles near the base of the petiole are elongate S-shaped.

*Trismeria trifoliata* has the two vascular bundles typical of *Pityrogramma*; they are, however, above the basal portion of the petiole (Fig. 3b), rather C-shaped but with the back of the C curved forward. The lamina architecture is somewhat different, the fertile and sterile leaves are subdichotomous and the spores are light colored with a nearly smooth exospore. These spores are quite similar to those present in one variety of *P. calomelanos* (var. *ochracea*). A relation of this species and *Pityrogramma* is shown by the 4 hybrids (discussed below) between them.

Comparing each of these three species, in their similarities and differences, with *Pityrogramma* it is evident that they represent close relatives of that genus. Two courses are possible for their classification: each may be placed in its own genus or they may all be placed in *Pityrogramma*. The former course would require the recognition of two new genera (one for *P. triangularis* and one for *Gymnogramma Lehmannii*) and this classification would emphasize the differences between them and *Pityrogramma*. However, the similarities must be considered equally and these are more than sufficient to place them all in *Pityrogramma*. Further, if this is done, the diversity of that genus is increased primarily in characters of the lamina architecture and venation, the attachment of the pinnae, and of the shape of the petiole and the vascular bundles. Such diversity can well be accommodated in a single genus, especially when the divergent characters are not correlated in a group of species. Accordingly, I am treating all of these species in *Pityrogramma*.

**PITYROGRAMMA** Link, Handb. Gewächse, 3:19. 1833

Type species: *P. chrysophylla* (Sw.) Link (*Acrostichum chrysophyllum* Sw.).

*Ceropteris* Link, Fil. Sp. Cult. 141. 1841, nom. superfl. illegit. Type species: the same as that of *Pityrogramma*.

= Acrostichum trifoliatum L.). Copeland’s choice\(^4\) of T. argentea Fée as the type is surely not as suitable as that of T. aurea by Maxon\(^5\), for the latter was not only more fully illustrated by Fée, but unequivocally represents the then well known Acrostichum trifoliatum L.


AMERICAN SPECIES OF PITYROGRAMMA

From the key and notes which follow it will be evident that I take a very different view of the species of Pityrogramma than did Domin.\(^6\) Specifically, I recognize, among the American species sufficiently studied, 10 species where Domin recognized 24. Some comments on the reasons for this treatment will be offered.

The species I recognize are based primarily on characters of the scales of the rhizome and petiole base, the color of the petiole and rachis, the relative development of the two sides of the pinna, the angle of the pinnules to the pinna rachis, the shape of the ultimate segments, the margin and relation of the veins ends to it and the spores. Other characters are the densely lanate lamina (in P. ferruginea) and the presence of proliferous buds on the lamina (in P. schizophylla). The complexity of the lamina is used as a supporting character in P. dealbata, as is the shape of the lamina in some species, and lack of indument in P. schizophylla. Indument color, although sometimes mentioned in the key where it may be useful, is not used to define the species. The use of these characters defines species which are consistent with our knowledge of the variability of these plants; and they have ranges (either contiguous or disjunct) which are of a pattern known in other species.

Domin used most of the kinds of characters previously mentioned (although not always the same ones) and also employed a considerable number of others, such as type of indument, color of the ceraceous indument, disposition of the pinnae and their shape, texture, size of segments and of the leaf, revolute or plane margin, spacing of pinnules,

\(^4\)Gen. Fil. 76. 1947.
\(^6\)Domin, 1928.
toothing of segments, and relative length of petiole. Some of these are subject to variation in plants of different sizes, and others to variation under different environmental conditions, correlations which may be seen in large suites of specimens. Others, while evidently more stable, nevertheless do vary in some species to an extent that they can not be relied upon.

The type of indument on the undersurface of the lamina and its color, if ceraceous, has been so overemphasized that some additional discussion of this character is desirable. The color of the ceraceous deposit on the under surface of the lamina may be of little or no taxonomic importance. It is true that some species such as *P. dealbata* and *P. sulphurea* are known in only one color form, but most others have two or more colors. That the color may easily vary is suggested by reports in the literature of a plant of one color giving rise, by spores, to plants with another color. These reports, however reasonable, must be subject to reservation because of the possibilities of contamination of a "culture" by spores of other kinds of *Pityrogramma*. There are some reports of two colors on a single plant. For example T. Smith\(^7\) discusses a plant of *P. tartarea* with leaves with white wax and one leaf with golden wax. Hooker\(^8\) reports a leaf of *P. calomelanos* with one pinna half white and half yellow. A specimen of *P. calomelanos* (Colombia, Daniel 292, US) has the indument on two leaves light yellow-orange and on one it is roseate.

Wax color forms are present but not recognized in the following species or varieties where the color is not correlated with any other character nor with geography: *P. calomelanos* var. *calomelanos* (white, lemon yellow, pale roseate), *P. tartarea* var. *tartarea* (white, cream yellow), *P. chrysoconia* (white, yellow), *P. chrysophylla* (white, bright yellow), *P. trifoliata* (white, yellow) and *P. "Eggersii"* (white, rose).

Some species that most commonly have ceraceous indument on the under surface of the lamina may be sometimes glabrous or pubescent. Species that have pubescent variants are *P. trifoliata*, *P. tartarea* and *P. calomelanos*. The latter rather rarely may be glabrous.

\(^7\)Gard. Chron. n.s. 8: 599. 1877.
\(^8\)Gard. Ferns, t. 50, f. 3. 1862.
That the presence and type of indument on the under surface of the lamina may be a "superficial" character is demonstrated by a plant of *P. calomelanos* from Peru. This plant has 10 leaves with the following characters: the three oldest leaves are glabrous, the next one is sparsely ceraceous and the next two are white ceraceous, the following two are pubescent and the youngest two are white ceraceous.

The type and color of indument, nevertheless, are used as the sole characters for the varieties of *P. calomelanos* and of *P. tartarea*. In these species the strong correlation of the character with geography seems to provide it with an importance it would otherwise not have. Even so, with further knowledge, it may not be reasonable to maintain such a treatment.

The extent to which hybridization among the species occurs in nature is not known. Hybrids between *P. trifoliata* and *P. calomelanos* and *P. ferruginea* are proposed in this paper. It is perhaps significant that hybrids have been recognized only with *P. trifoliata* which is an especially distinctive species in its lamina architecture. It is quite possible that the difficulties of definition and identification that exist between *P. calomelanos* and *P. tartarea*, and some other species, may be due to hybridization. However, the rather few “intermediate” plants may as well be ecological or genetic variants of either species. Where two species grow together or in close proximity, the presence or absence of intermediate plants should be confirmed.

**KEY TO THE SPECIES OF PITYROGRAMMA**

(Four insufficiently known taxa, discussed at the end of the next section, have not been keyed out.)

a. Petiole terete; rhizome scales with a dark, sclerotic central stripe and narrow, thinner, pale margins. (Pinnae, except sometimes the basal pair, adnate to the rachis, the basal ones enlarged.) ..........................

b. Lamina pinnatisect; pinna-segments entire, about as broad as long, broadly obtuse, with many veins arising from the costa of the lamina. ..........................

b. Lamina 1-pinnate or more complex; pinnae elongate; veins of the ultimate segments arising from a single basal vascular branch. c.

*Tingo Maria, Tryon & Tryon 5242 (GH).*
c. Vascular bundles of the petiole (at about 1/3 the distance to the lamina) C-shaped with the back of the C curved forward. ........................................ 7. *P. trifoliata* and hybrids of it.

The species has the pinnae entire, especially the apical ones, to commonly trifoliolate below, or a few to rarely many 5- (very rarely 7-) foliolate. The hybrids have the pinnae with many segments.

c. Vascular bundles of the petiole (at about 1/3rd the distance to the lamina) roundish, oval to C-shaped; pinnae with numerous, pinnately arranged lobes or segments. d.

d. Ultimate segments mostly shallowly (if at all) toothed, pinnately many veined (with a strong midvein), broadest at the base to lanceolate or elliptical; or rarely lacking a midvein (or with a poorly developed one) and obovate to oval. e.

e. Primary rachis and secondary rachises densely and persistently lanate, the petiole similar but sometimes deciduously lanate. ........................................ 6. *P. ferruginea*.

f. Petiole, primary rachis and secondary rachises glabrous, ceraceous or thinly and irregularly pubescent. f.

g. Scales of the apex of the rhizome and the base of the petiole with a long portion one cell wide below the terminal cell. (Spores prominently ridged, the ridges with sharply defined margins). g.

h. Pinnae equilateral; pinnules ascending, those on the basiscopic side more strongly so than those on the acrosopic side; scales of the apex of the rhizome and the base of the petiole with a long-conical terminal cell. (Fertile segments with a sterile costular area absent or substantially so, or if present, then a sterile marginal area present that is as broad or broader than the costular one.) ........................................

.................................................. 1. *P. calomelanos*.

h. Pinnae inequilateral; pinnules, on both sides of the pinna, at nearly right-angles to the pinna-rachis (or in large leaves the tertiary segments so disposed on the pinnule-rachis): scales of the apex of the rhizome and the base of the petiole with a spherical terminal cell. (Rachis and petiole reddish-brown to blackish, the ridges on the upper side of the rachis [or in larger leaves of the pinna-rachis] lighter in color than the rachis proper; absent from the Lesser Antilles) ........................................ 2. *P. tartarea*.

g. Small leaves rather fully bipinnate-pinnatifid, many ultimate segments obovate or oval. (Mexico to Panama). .................................................. 4. *P. dealbata*.

f. Scales of the apex of the rhizome and the base of the
petiole with only a short portion one cell wide below the spherical terminal cell. i.

i. Rachis and the upper portion of the petiole (or all of it except the base) straw colored to light brown, the ridges on the upper side of the same color; spores prominently ridged, the ridges with sharply defined margins. ........................................... 3. *P. chrysocomia.*

i. Rachis and petiole reddish-brown to blackish; spores heavily and closely ridged, the ridges with erose margins that give a granular appearance to the spore. (Fertile segments with a sterile costular area present, a sterile marginal area absent, or if present, then only half as broad as the costular one; Porto Rico and the Lesser Antilles) ........................................... 5. *P. chrysophylla.*

d. Ultimate segments usually mostly toothed to deeply laciniate, dichotomously or subdichotomously few-veined (without a midvein), broadly to narrowly flabellate-cuneate. j.

j. Ultimate segments strongly laciniate into 1-veined lobes; indument lacking on the lamina. (Lamina usually bearing proliferous buds, narrowed at the base where the basal pinnae are more or less reduced. .......... 12. *P. schizophylla.*

j. Ultimate segments entire and several-veined to deeply cleft into 2- several-veined lobes (these often strongly toothed); ceraceous indument usually present on the under surface of the lamina. l.

l. Basal pinnae reduced; apical pinnules usually strongly ascending; Greater Antilles. m.

m. Rhizome scales brown, firm but not thickened; indument yellow. ........................................... 10. *P. sulphurea.*

m. Rhizome scales atropurpureous, thickened; indument white or rose. ........................................... 11. *P. "Eggersii".*

l. Basal pinnae the largest or nearly so; apical pinnules usually spreading; Africa, Madagascar and Mascarenes. n.

n. Lamina lanceolate or deltoid-elongate with cuneate, emarginate lobes. ........................................... 13. *P. argentea.*

n. Lamina broadly deltoid or pentagonal, segments rounded, not emarginate or cleft. ...... 14. *P Humbertii.*

NOTES ON THE SPECIES OF PITYROGRAMMA

In the following notes, the distribution of the American species and varieties has been taken from the material in the Harvard University Herbarium (A and GH) and in the United States National Herbarium (US).

In some matters of taxonomy, or nomenclature, this study is incomplete or inconclusive: a discussion of these matters is included in the appropriate places. I have tried to include
all of the basionyms of species names that have been certainly or probably applied to native plants. Varietal names are given only where they are pertinent to the nomenclature. I have made no attempt to account for the names (in various categories) that have been applied to material of horticultural or presumed hybrid origin.10


A discussion of the difference between *P. calomelanos* and *P. tartarea* is presented under the latter species.

1a. *P. calomelanos* var. *calomelanos*

*Acrostichum calomelanos* L. Sp. Pl. 1072. 1753. LINN sheet 1245.19, photo A, GH, is this species; maintained over *A. ebeneum* L. by Lam. Encycl. 1:38. 1783.


*Gymnogramma bidentata* Presl, Rel. Haenk. 1:18, t. 2, f. 3. 1825, ex char. et icon.


*Pityrogramma chamaesorbus* Domin, 1928: 6. Type: British Guiana, Schomburgk 390, K!, photo GH.


*Pityrogramma distans* (Link) Domin, 1929: 49.

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10See Domin, 1929.
Lamina ceraceous beneath, the wax white to pale (lemon) yellow or pale roseate; or rarely the lamina glabrous.

Southern Florida; Greater and Lesser Antilles; Mexico to Panama; French Guiana west to Colombia, Ecuador and Galápagos Islands south to Bolivia and Argentina; Paraguay and Brazil. Widely introduced in the Old World tropics.

1b. P. calomelanos var. aureoflava (Hook.) Weath. ex Bailey, Man. Cult. Pl. 64. 1926.

Gymnogramma calomelanos var. aureoflava Hook. Gard. Ferns t. 50 text. 1862. Of the several specimens cited by Hooker, I would take Seemann 948 as the one that may best serve as a type but unfortunately I have not seen it. Other specimens may (or certainly do) represent either other species or else the pale yellow variant of P. calomelanos which I refer to var. calomelanos.

Pityrogramma austroamericana Domin, 1928: 7. (Also Kew Bull. 1929: 221.) Lectotype: Bolivia, Mandon 1549 bis, K!, photo GH; isotype, GH! (Five other collections were cited in 1928 and one additional one in 1929).


Bailey did not properly transfer Hooker’s epithet to P. calomelanos but C. A. Weatherby, then Editor of the Gray Herbarium Index, accepted the name as cited above in the Index and this may be taken as a correction of Bailey’s publication.

Lamina ceraceous beneath, the wax bright yellow to orange-yellow.


1c. Pityrogramma calomelanos var. ochracea (Presl) Tryon, comb. nov. FIG. 1.

Acrostichum caudatum Cav. Descr. 242. 1802. Type: “Panama”, Née, seen by C. Chr. at MA (Dansk Bot. Ark. 9*: 10. 1937, where it is figured, in part, t. 2, f. 4-5.). I believe that this name belongs here (much less likely it is P. tartarea var. Jamesonii), and that it was obtained in Andean South America rather than in Panama.
**Gymnogramma ochracea** Presl, Rel. Haenk. 1:17. 1825. Type: Peru, Haenke, PR (Herb. no. 24360), photo GH, US; probable isotypes, K, fragment NY!, B, fragment, NY!


**Gymnogramma Hookeri** J. Sm. ex Hook. & Bak. Syn. Fil. 381. 1868. Syntypes: Colombia, Purdie, fragment NY!; Colombia, Schlim 609; Bolivia, Mandon 1547.

**Gymnogramma Ballivianii** Rosenst. Fedde Repert. 6:314. 1909. Type: Bolivia, Buchtien 1038, S-PA! fragment ex Rosenst. US! (Steinbach 8507, Buchtien 35 and other specimens commonly so named are the same).

**Ceropteris adiantoides** var. *peruviana* Hieron. Hedwigia 48:221. 1909, ex char. & loc. Type: Peru, Stübel 1096, B. Not *P. calomelanos* var. *peruviana* (Desv.) Farw. (sub *P. tartarea*).


**Pityrogramma ochracea** (Presl) Domin, 1928: 8.

**Pityrogramma adiantoides** (Mett.) Domin, 1928: 8.

**Pityrogramma Ballivianii** (Rosenst.) Domin, 1928: 10.

**Pityrogramma perelegans** Domin, 1928: 8. Type: Tarapoto, Peru, Spruce in 1855-56, K!, photo GH.

**Pityrogramma caudata** (Cav.) C. Chr. Dansk Bot. Ark. 9°:10. 1937.

The earliest varietal name, var. *peruviana* Hieron., cannot be transferred to *P. calomelanos* because of *P. calomelanos* var. *peruviana* (Desv.) Farwell. **Gymnogramma adiantoides** Mett. was ineffectively transferred to varietal status under **Ceropteris tartarea** by C. Chr. Ind. Fil 333. Other “combinations” have also been ineffective and I believe that *ochracea* is the earliest epithet in the varietal category.

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**Fig. 1.** *Pityrogramma calomelanos* var. *ochracea*: la, pinna, X 1/2; lb, pinna, X 1; le, vascular bundles in petiole, enlarged. **Fig. 2.** *P. ferruginea*: 2a, pinnae, X 1/2; 2b, vascular bundles in petiole, enlarged; 2c, spores, left to right — commissural face, distal face, lateral view, much enlarged. **Fig. 3.** *P. trifoliata*: 3a, sterile pinna, X 1/2; 3b, sterile pinna, X 1/2; 3c, fertile pinna, X 1/2; 3d, vascular bundles in petiole, enlarged. **Fig. 4.** *P. calomelanos* var. *ochracea* X *trifoliata*: pinna, X 1/2, Peru, **Tryon & Tryon** 5440. **Fig. 5.** *P. ferruginea* X *trifoliata*: 5a, apical pinna, X 1/2; 5b, vascular bundles in petiole, enlarged; both from Peru, **Tryon & Tryon** 5449. **Fig. 6.** *P. Lehmannii*: 6a, lamina, X 1/2; 6b, venation of pinna-segment, X 1 1/2; both from Colombia, **Lehmann** 8444.
Presl’s name has been often misapplied to forms of this species, or of *P. tartarea*, with yellow wax.

Lamina pubescent beneath, not ceraceous.

The spores of some specimens of var. *ochracea* are of the typical *Pityrogramma* type with well defined dark ridges. Other specimens have spores that are more spherical than the usual type, although somewhat flattened in three planes on the commissural face, and the tan exospore is smooth or only slightly roughened. It is exceptional to find such different spores in the same species (or variety) but I have been unable to find any character that correlates with the spore type and there is every indication that the unusual spores are mature.

Some specimens of var. *ochracea* with the “normal” spore type are the following (all from Peru): HUANUCO: Macbride 1994 (US), Allard 22022 (GH). AYACUCHO: Killip & Smith 22667 (US). CUZCO: Vargas 4023 (US), Scolnik 881 (US), Bues 1715 (US). Some specimens with the smoothish spores are: PERU: (all from CUZCO), West 8013 (UC), Cook & Gilbert 1715 (US), Mexia 8089 (GH, US), Herrera 1285 (US), Tryon & Tryon 5366 (GH). BOLIVIA: R. S. Williams 1373 (GH), Krukoff 10094 (F, GH).

Honduras; Venezuela, Colombia, Ecuador, Peru and Bolivia.


More difficulty exists in the separation of this species from the previous one, *P. calomelanos*, than would be expected from an examination of the common forms of each. Some of this difficulty, it is true, is due to specimens that are single leaves, but the characters of each do vary toward the other. Both species are common, widely distributed, and grow in a variety of habitats and the extent to which their variation may be due to their own variability or to natural hybridization is not known. The following characters, in addition to those presented in the key, may be useful in the identification of material:

Lamina lanceolate to ovate-lanceolate, or in large leaves long-triangular, its apex often more or less acute or abruptly acuminate; apical pinnae strongly ascending; pinnules acute, serrate, or acutely pinnatifid; basal inferior pinnules more strongly ascending on the upper than on the lower pinnae. .................. *P. calomelanos*.

Lamina long-triangular, to deltoid in large leaves, its apex evenly long-acuminate; apical pinnae nearly or quite at right angles to
the rachis; pinnules obtusely lobed or pinnatifid; basal inferior pinnules at about the same angle to the pinna-rachis on all pinnae (or in large leaves the basal inferior tertiary segments so in relation to the pinnule-rachis). 

This species has a less extensive range than *P. calomelanos* and both the variety with yellow wax and the one with the lamina pubescent are also more restricted than their counterparts in *P. calomelanos*.

2a. *P. tartarea* var. *tartarea*


*Gymnogramma dealbata* Link, Hort. Berol. 2:52. 1833, (epithet from *Hemionitis dealbata* Willd.), nom. superfl., illegit. (= *Acrostichum tartareum* Cav.), not Presl, 1825 (sub *P. dealbata*).


*Pityrogramma Stuebelii* (Hieron.) Domin, 1928: 7.


Lamina ceraceous beneath, the wax white to pale (cream) yellow, rarely very sparse and almost colorless; rarely partly ceraceous-pubescent.

Greater Antilles; Mexico to Panama; Venezuela, Colombia, Ecuador and Galápagos Islands south to Bolivia; Brazil (Rio Grande do Sul, Paraná and vicinity of Itatiaya).

2b. *Pityrogramma tartarea* var. *aurata* (Moore) Tryon, comb. nov.

*Gymnogramma tartarea var. aurata* Moore, Gard. Chron. 1870: 493. Type: Cultivated by Veitch from a collection by *Pearce* in Peru. (The specimen of *Pearce* 218 at K!, photo
GH, Domin, 1929: t. 1, may be the type as Domin says; it does clearly represent Moore’s name).

Pityrogramma praestantissima Domin, 1928: 6. Type: Colombia, Kalbreyer 1909, K!, photo GH.

Pityrogramma Presliana Domin, 1928: 6. Type: Peru, Matthews 1823, K!, photo GH (although Domin also cited Pearce 218, he annotated that collection, K, as P. Presliana var. aurata (Moore) Domin and later11 stated it to be the type of that variety).

Lamina ceraceous beneath, the wax bright yellow. Colombia, Ecuador and Galápagos Islands to Argentina.

2c. Pityrogramma tartarea var. Jamesonii (Baker) Tryon, comb. nov.


Pityrogramma xerophila (Baker) Domin, 1928: 8.

Lamina pubescent beneath, not ceraceous. Colombia and Ecuador.

3. Pityrogramma chrysoconia (Desv.) Maxon ex Domin, 1928: 10


Gymnogramma guianensis Kl. Linnaea 20:413. 1847. Type: British Guiana, Schomburgk 1154, B!, photo GH, fragment NY!; isotype, K, fragment NY!

Gymnogramma Ornithopteris Kl. Linnaea 20:413. 1847. Type: Venezuela, Moritz 288, B!, photo GH, fragment US!; isotype, K!, photo GH.

Gymnogramma flexilis Kl. Linnaea 20:414. 1847. Type: Venezuela, Mérida, Moritz 287, B; isotype, K, fragment NY!

Cerapteris obtusa Fée, Mém. Fam. Foug. 8:80. 1857. Type: Colombia, Schlim 873; isotype, P!, photo GH.

Pityrogramma flexilis (Kl.) Domin, 1928: 5.
Pityrogramma obtusa (Fée) Domin, 1928: 10.
Pityrogramma subnivalis Domin, 1928: 5. (Also Kew Bull. 1929: 220). Type: Colombia, Santa Marta, Purdie in 1844, photo GH.
Jamaica (Blue Mt. Peak); Costa Rica to Panama; British Guiana west to Colombia and south to Bolivia; principally or wholly at the higher elevations.

4. Pityrogramma dealbata (Presl) Tryon, comb. nov.

The photograph of Presl's type is a very close match for some specimens of this species, for example, Costa Rica, Seemann 7055 (GH) and Panama, Allen 147 (GH). This species was long referred to as Gymnogramma peruviana Desv. (or Pityrogramma or Ceropteris peruviana) but in 1936 C. A. Weatherby pointed out that Desvaux's type was actually a specimen of P. tartarea.
Mexico to Panama.

5. Pityrogramma chrysophylla (Sw.) Link, Handb. Gewächse, 3:19. 1833


Ceropteris intermedia Fée, Mém. Fam. Foug. 11 (Hist. Foug. Antill.) :30. 1866. Type: Guadeloupe, L'Herminier in 1861, photo GH.


The white and yellow color forms, although especially striking in this species, do not merit recognition.

The material I have seen from Samoa, which has consistently been recognized as an endemic (C. Chr. Pterid. Samoa, Bull. Bishop Mus. 177:57-58. 1943), is surely this species. Porto Rico (rare); and the Lesser Antilles; introduced in Samoa.


Gymnogramma ferruginea Kze. Linnaea 9:34. 1834. Iso-type: Quebrada de Chinchao, Peru, Jul. 1829, Poeppig, Diar. 1160, P!, photo GH.


The material in Central America is more variable than that in Peru. The pinnae are often petiolulate there, while in Peru they are uniformly subsessile. Also the lamina may be long- triangular or deltoid in Central America while in Peru it is narrowly elliptic.

Guatemala to Panama; Peru.

7. Pityrogramma trifoliata (L.) Tryon, comb. nov. FIG. 3.

Acrostichum trifoliatum L. Sp. Pl. 1070. 1753. LINN sheet 1245.9, photo A, and Sloane, Hist. Jam. t. 45, f. 2, are both this species.


Trismeria microphylla Fée, Mém. Fam. Foug. 5 (Gen. Fil) : 165. 1852, ex char. “Habitat in Peruvia”.

Southern Florida; Greater Antilles; Mexico to Costa Rica (notably absent from Panama); Venezuela, Colombia south to Bolivia, Argentina and Chile (Arica); Paraguay, Uruguay and Brazil.

I am recognizing four putative hybrids of Pityrogramma trifoliata, one of them with P. ferruginea and the other three with the varieties of P. calomelanos. All of these have the long, narrow lamina of P. trifoliata, the strongly ascending-arching lower pinna-stalks and (at least in large leaves) the same type of vascular bundles. There is a strongly developed tendency in them toward long and entire segments. Characters of the pinnae and the vascular bundles of two of the putative hybrids, and their parents, are illustrated in Figs. 1-5. While these are of interest, I do not believe that a binomial is justified for any of them. The hybrids are all distinguished from P. trifoliata by their pinnae with numerous segments. In P. trifoliata the pinnae are entire to 3-, 5- or very rarely 7-foliolate.

The material has not been adequate to establish the degree of fertility of the hybrids. An examination of the fertile leaves available suggests that they may produce no viable spores or relatively few of them. The collections Tryon & Tryon 5440 and 5449 were both single plants.

7a. P. calomelanos var. calomelanos × trifoliata


Petiole and rachis glabrous or ceraceous, segments white ceraceous, or with nearly colorless wax, beneath.


7b. P. calomelanos var. aureoflava × trifoliata


Trismeria trifoliata var. subbipinnata Hieron. Hedwigia 48:223. 1909. Type: Ecuador, Stübel 733, B, is probably this hybrid.

Petiole and rachis glabrous or ceraceous, segments with yellow wax beneath.

This is perhaps the same as 7a, the yellow wax being derived from a yellow form of P. trifoliata rather than from P. calomelanos var. aureoflava.


7c. P. calomelanos var. ochracea × trifoliata FIG. 4


Petiole and rachis thinly pubescent to glabrous, segments pubescent beneath.


7d. P. ferruginea × trifoliata FIG. 5

Petiole and rachis closely and densely lanate, although deciduously so. The only collection has the pinnules markedly irregular in their length.

Peru: 10 km. sw. of San Ramón, Dept. Junín, Oct. 28, 1956, Tryon & Tryon 5449 (GH).

8. Pityrogramma Lehmannii (Hieron.) Tryon, comb. nov. FIG. 6


The unusual characters of this distinctive species have been mentioned in the key and in the discussion of the genus. It is known only from the original collection.

Colombia.


The four varieties of this species were treated by Weatherby12 and in spite of additional knowledge his taxa and their status are certainly still justified. The genetical and cytological study of Alt and Grant13, for example, is an im-


portant contribution to our understanding of this species but it does not furnish a basis for different taxonomic conclusions.

9a. **P. triangularis** var. **triangularis**
   *Gymnogramma triangularis* Kaulf. Enum. Fil. 73. 1824.
   Type: San Francisco Bay, California, Chamisso, probably LE; isotypes, P, (*Chamisso 1875*) photo GH, B (fide Alt & Grant).

   Baja California to sw. British Columbia, s. Nevada and sw. Utah.

9b. **P. triangularis** var. **viscosa** D. C. Eaton, Ferns N. Am. 2:16, t. 48, f. 5. 1879. Type: usually considered to be: San Diego, California, “Gymnogramme viscosa”, Nuttall, PH; but other material cited, or especially that illustrated, by Eaton might be a better lectotype.


   Maritaine: Baja California and s. California.


   Central California.


   Baja California, s. California e. to Arizona.


   *Acrostichum sulphureum* Sw. Prod. Veg. Ind. Occ. 129. 1788. Type: Jamaica, Swartz, s-PA (Herb. Swartz)!, fragment US! (the Plumier, Fil. t. 44 cited by Swartz is *P. chrysophylla*).

   Cuba, Jamaica, Hispaniola, Porto Rico.

11. **Pityrogramma “Eggersii”**

   The commonly accepted name, *Pityrogramma Eggersii* (Christ) Maxon\(^{14}\) can not be used for this species because the type specimen (Cuba, *Eggers*, comm. C. Rensch sub no. 4882a, Herb. Christ-P!) of *Gymnogramma Eggersii* Christ\(^{15}\)

\(^{15}\) Bull. Soc. Bot. Belg. 33\(\text{p}\): 92. 1894.
is a species of *Asplenium* and has been so annotated by C. V. Morton. Although this species does not have a name, I am deferring to C. V. Morton’s forthcoming work on the ferns of Cuba, where it will be described and named.

Cuba and Hispaniola.


Jamaica and Hispaniola.

13. Pityrogramma argentea (Willd.) Domin, 1928: 6

13a. P. argentea var. argentea


Tropical and south Africa; Madagascar and Mascarene Islands.

13b. P. argentea var. aurea (Willd.) Domin, 1929: 20.


*Gymnogramma argentea* var. aurea (Willd.) Mett. ex Kuhn, Fil. Afr. 59. 1868.


Madagascar and Mascarene Islands.

I have made no study of the African species and in this one and the next I have followed the treatment of Tardieu-Blot16. Christensen17, however, treats var. *aurea* as a species.


Madagascar (I do not know var. *elongata* C. Chr., op. cit. 112, from the Belgian Congo).

**DUBIOUS TAXA AND NAMES**

The four following names may represent valid taxa but the material I have seen has not been adequate to form a basis for definite conclusions:

Pityrogramma chrysophylla var. euchrysa Ekman ex C. Chr. Kungl.  

17Ibid. cit. and Dansk Bot. Ark. 7: 112, t. 43, f. 5. 1932.
This may be a variety of *P. chrysophylla*, as Christensen proposed, or perhaps a variety of *P. chrysoconia*; or it may represent an endemic species.


*Gymnogramma Pearcei* Moore, Gard. Chron. 1864: 340. Type: Cultivated by Veitch from a collection by *Pearce* in “Chile”. Two specimens at K!, photos GH, may be considered as authentic (I did not find a proper holotype): “Pinna of *Gymnogramma Pearcei*, n. sp. . . . . .” and *Pearce* 274, ex Veitch 7/84. The original collection was undoubtedly not made in Chile. Illustration: Schneider, Choice Ferns 2: f. 68.

**Gymnogramma decomposita** Baker, Gard. Chron. 1872: 1587. Type: “Andine side of South America, Hort. Kew ex Veitch”; this is probably the specimen at K!, photo GH, annotated by Baker as “*G. decomposita*” and with the original label “*Gymnogramma Pearcei*, H. Kew 10/71, from Veitch”. Illustration: Garden 6: f. on 495.


**Pityrogramma decomposita** (Baker) Domin, 1928: 7.


The three basionyms listed above all represent plants with highly dissected leaves. I strongly suspect that this material represents a single species but it is not sufficient to enable me to present the synonymy with assurance nor to place the species among the others of *Pityrogramma pulchella* (Moore) Domin, 1928: 9.

**Gymnogramma pulchella** Moore, Gard. Chron. 1856: 597, figure. Type: “*Hort.*”, presumably ex Hort. Linden, ex Venezuela. I did not find a proper holotype at Kew; a specimen, K!, in Moore’s herbarium, photo GH, “*G. pulchella*, *Hort.*”, “*Hort. Veitch, 1860*”, is probably another species.

I have associated the following material with this name on the basis of the small figure published by Moore. VENEZUELA: (probably Rancho Grande). *Tschudi* 176 (VEN); *Colonia Tovar, Fendler* 357 (YU, the specimen at K is figured in Domin, 1929: t. 6); ne. of Bergatín, Est. Anzoátegui, *Steyermark* 61327 (F, VEN).

The principal characters of this taxon are the strongly dissected juvenile leaves, the inequilateral pinnae and the definitely to strongly toothed segments of the adult leaves. However, the material is insufficient to come to a conclusion concerning its status, or its relation with the equally uncertain *P. Pearcei* discussed above.


Most of the specimens that I have seen have a marked resemblance to *P. argentea* and I strongly suspect that species may have escaped
from cultivation in Jamaica and probably hybridized to a degree with a native species there, most likely with *P. calomelanos*. *P. triangulata* has been collected only in St. Andrew Parish, Jamaica.

The deltoid to long-deltoid lamina, the rather triangular and inequilateral pinnae and the somewhat flabellate-cuneate ultimate segments of *P. triangulata* are all suggestive of *P. argentea*. Some specimens are rather intermediate between *P. argentea* and *P. calomelanos* in the relation of the vein to the margin. In *P. argentea* most of the veins end at the margin in a small sinus of an emarginate lobe, while in *P. calomelanos* they end well back of the margin in the center of a simple tooth. In *P. triangulata* they may end back of an often bifurcate tooth but there is a lighter colored extension of the vein to the margin. It should be mentioned, however, that the character of the veins and margin in *P. argentea* is not unique. It is sometimes similar in *P. "Eggersii"* and its development in *P. triangulata* may not show a relation to the African species.

The following names are probably synonyms of some of the American species but I have not been able to place them with certainty:

*Ceropteris monosticha* Fée, Mém. Fam. Foug. 7: 44, t. 22, f. 2. 1857. Type: Mexico, Schaffner 155. Perhaps = *P. tartarea* var. *tartarea*.
*Ceropteris plicata* Fée, Mém. Fam. Foug. 8: 80. 1857. Type: Mexico, Schaffner 164.
*Ceropteris serrata* Fée, Mém. Fam. Foug. 8: 81. 1857. Type: Mexico, Schaffner 162. Perhaps = *P. calomelanos* var. *calomelanos*.
*Pityrogramma subflexuosa* Domin, 1928: 7. Type: Montserrat, Holme in 1879, k!, photo GH.Probably = *P. chrysophylla*.

II. THE GENUS ANOGRAMMA

The genus *Anogramma* includes some five or six species which are clearly related to *Pityrogramma*, especially to *P. sulphurea* and others of spp. 10-13 (see above). The architecture of the lamina is similar to some of these, the axes are grooved in the same manner and the sorus is the same. The spores18 which are identical or similar (the ridges are often closer and somewhat tuberculate) to those of typical *Pityrogramma* are perhaps the strongest evidence of affinity. In addition, there is in *Pityrogramma* an approach toward the annual habit of the sporophyte found in *Anogramma*. Some species of *Pityrogramma* show a strong tendency to grow in open soil and especially in *P. sulphurea* this is correlated with a reduction in the life-span of the sporophyte which apparently lives for only a few years.

The species of *Anogramma* grow on bare (or nearly bare) soil and the sporophyte evidently lives for only one growing
season. In the smallest species (*A. Lorentzii*) the sporophyte may consist of only a few small fertile leaves (to 1 cm. long), a minute stem and a few roots. A gametophyte is often found attached to herbarium specimens of the sporophyte. This prothallus is reported to be perennating, surviving the dry season and producing another sporophyte from specially developed lobes the next growing season. This behavior of the prothallus, however, cannot well be used as a generic character because it has been reported in only two of the species (*A. leptophylla* and *A. chaerophylla*) and because even in these it is not known to be of regular occurrence in nature. In other species the gametophyte may not behave in this way and its frequent occurrence on a sporophyte may be due to the fact that the growth of the sporophyte is so rapid that even when it is mature the gametophyte is still present.

This reduced and specialized evolutionary line can be recognized as a distinct genus, or as a group within *Pityrogramma* as Domin did. Were there truly intermediate species, I would follow Domin’s classification. However, there are none and the several species can be separated, among other less constant characters, on the basis of the rhizome (and usually the lamina) indument and the annual habit of the sporophyte.

Rhizome scales atropurpureous to light brown, rigid and sclerotic to firm and subsclerotic; sporophyte living for a few to many years, the stem correspondingly well developed; lamina glandular, strongly pubescent or most often ceraceous (rarely glabrous or slightly pubescent).

Rhizome scales thin, whitish, sometimes mixed with similar trichomes or only such trichomes present; sporophyte living only one growing season, the stem correspondingly poorly developed; lamina glabrous or rarely sparingly pubescent.

**ANOGRAMMA** Link, Fil. Sp. Cult. 137. 1841. Type: *A. leptophylla* (L.) Link (*Polypodium leptophyllum* L.)

The usually accepted species of *Anogramma* are the following:

1. *A. chaerophylla* (Desv.) Link (the largest species). Tropical America.
2. *A. guatemalensis* (Domin) C. Chr. may be a variant of *A. leptophylla*. Mexico to Costa Rica.
3. *A. leptophylla* (L.) Link. Tropical America, Africa and adjacent islands, southern Europe, and eastward to New Zealand.

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21Domin, 1928: 3, 9-10.
6. A. Lorentzii (Hieron.) Diels (the smallest species). Argentina, Uruguay, Brazil. Gymnogramma Regnelliana Lindm. 1903 (not Christ, 1900) may be a species distinct from A. Lorentzii rather than a variety of it (Gymnogramma Lorentzii var. megaspora Lindm. Hedwigia 43: 309. 1904).

Other species that have been placed in Anogramma are referable to other genera (see C. Chr. Ind. Fil. and Suppls.). One, however, that has been maintained in Anogramma by Christensen (and others) clearly does not belong there. This is A. microphylla which Domin\(^{21}\) treated in a separate section, Pityrogramma section Monosorus. He was certainly correct in removing it from his section Anogramma, but it is probably not closely related either to that genus or to Pityrogramma.

Anogramma microphylla (Hook.) Diels (Gymnogramma microphylla Hook.), of the eastern Himalayas, has a creeping rhizome with blackish, thickened trichomes, one U-shaped vascular bundle in the petiole, unusual somewhat elliptical segments, and tetrahedral-globose spores that are pale yellow and have a perispore with a few prominent wings and tubercules between them. The leaf, segments and sorus are well figured in the original publication\(^{22}\). This species may represent a monotypic genus; or perhaps it is a diminutive Monachosorum; or it may possibly be congeneric with or related to Cerosora. — GRAY HERBARIUM, HARVARD UNIVERSITY.

\(^{21}\)Domin, 1928: 10.
\(^{22}\)Hook, Ic. Pl. t. 916. 1854. (Cent. Ferns, t. 16, 1854).

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