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New Combinations in the *Pleopeltis macrocarpa* group (Polypodiaceae: Polypodieae)

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The *Pleopeltis macrocarpa* group includes the 11 members of *Pleopeltis* with simple and undivided leaves. The group is predominately neotropical and epiphytic, and the species occur most frequently between 1500 and 2500 m in disturbed habitats of wet forested areas. They are especially common along roadsides, edges of pastures, and on cultivated trees such as coffee and citrus. In addition to their simple leaves, members of the *P. macrocarpa* group are characterized by anastomosing venation; large sori subtended by a nexus of veinlets; rhizome, leaf, and soral scales that are peltately attached and at least partially clathrate; and a chromosome base number of x=34 or 35. The peltate soral scales (paraphyses), which form a complete covering over young sori, have been the main diagnostic feature for *Pleopeltis* since its establishment in 1810. Although the genus was established for *P. angusta,* an unusual fern with irregularly pinnatifid leaves, most of the species included in the genus since 1810 have simple leaves and belong to the *P. macrocarpa* group.

The *P. macrocarpa* group has been the focus of recent morphological, cytological, and isozymic studies (Hooper, 1994), which were initiated because of controversies involving generic circumscription of *Pleopeltis*. Problems have arisen for two reasons. First, because of the reliance on peltate paraphyses as the main diagnostic feature for the genus, several species (e.g., *P. munchii* and *P. fallax*) have been included in *Pleopeltis,* despite the fact that they share little else with *P. angusta* and members of the *P. macrocarpa* group other than paraphyses. Second, hybridization between at least four members of the *P. macrocarpa* group and scaly-leafed members of *Polypodium* (subg. *Marginaria*) (Wagner and Wagner, 1975; Anthony and Schelpe, 1985; Mickel and Beitel, 1987) raised initial doubts about the integrity of the generic boundary between these two groups.

Furthermore, preliminary isozyme and chloroplast DNA surveys (Andrews and Haufler, 1990; Haufler and Ranker, in press) revealed greater genetic affinity between two scaly *Polypodium* species and members of the *P. macrocarpa* group than between the former and non-scaly polypodiums. This genetic evidence, coupled with the strong similarities in rhizome, leaf, and soral indumentum between the two (Baayen and Hennipman, 1987), led Windham (1993) to transfer four scaly *Polypodium* species into *Pleopeltis*. Whereas this new arrangement more accurately portrays the evolutionary relationships

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among these taxa, *Pleopeltis* remains a heterogeneous assemblage of species that is difficult to circumscribe.

Despite these perturbations at the generic level, the simple-leafed members of *Pleopeltis* remain a relatively cohesive and apparently monophyletic group that has received little systematic attention in the past (but see Weatherby, 1922). A revision of the *P. macrocarpa* group was initiated to explore taxonomic and evolutionary relationships among its members and to serve as a springboard for additional studies within *Pleopeltis* and the Polypodieae. The results of these studies will appear elsewhere; the purpose of this communication is to present the necessary nomenclatural changes that arose as a result of these studies.

Pleopeltis complanata (Weath.) E.A. Hooper, comb. nov.—*Polypodium lanceolatum* L. var. *complanatum* Weath., Contr. Gray Herb. 65:8. 1922. *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf. var. *complanata* (Weath.) Lellinger, Proc. Biol. Soc. Wash. 89:722. 1977.—Type: Costa Rica, Pcia. Cartago, Juan Viñas, *Pittier 1855* (US!).

Pleopeltis complanata occurs from 1200 to 2300 m in montane regions of Costa Rica and Panama. It has been maintained as a variety of *P. macrocarpa* (=*Polypodium lanceolatum* L.) since its original description by Weatherby (1922). However, morphological and genetic data (Hooper, 1994) indicate that it is sufficiently distinct from *P. macrocarpa* to be recognized as a separate species. For example, *P. complanata* differs from *P. macrocarpa* in having a flattened stipe (versus terete); narrowly lanceolate leaves (versus narrowly elliptic); slightly sinuate leaf margins (versus entire but slightly revolute); smaller leaf and soral scales (ca. 1 mm smaller in diameter on average); and two-celled spores (versus single-celled). These differences are best expressed in dried material.

Genetically, the two differ in that *P. complanata* is a diploid, whereas *P. macrocarpa* is known to contain only tetraploid, pentaploid, and hexaploid cytotypes (Manton, 1959; Jarrett et al., 1968; Walker, 1966, 1973; Wagner and Wagner, 1975; Hooper, 1994). Furthermore, isozyme comparisons of the two (Hooper, 1994) revealed that relative to most species pairs in the *P. macrocarpa* group, *P. complanata* has a relatively low genetic identity with *P. macrocarpa* (Nei's I = 0.653).

The two species occasionally grow together in southern Central America and careful observation is required to distinguish them in the field. For example, the flattened stipe of *P. complanata* is not as obvious on live plants as it is on dried specimens. Nevertheless, the combination of morphological and genetic divergence between the two support their recognition as separate species.

Pleopeltis polylepis (Roem. ex Kunze) T. Moore, Index Fil. 348. 1862.—*Polypodium polylepis* Roem. ex Kunze, Linnaea 13:131. 1839.—Syntypes: Mexico, Mineral del Monte, *Ehrenberg s.n.*; without locality, *Hegewisch s.n.* (Herb. Roemer); *Karwinsky s.n.* (probably all LZ, destroyed; teste Mickel and Beitel, 1988).

Polypodium peltatum Cav., Descr. Pl. 244 (No. 597). 1802.—Lectotype: "Marianas Islands", *Née* s.n.; there are two sheets in the type collection,

and for reasons discussed below, the specimen above the lower right-hand label of sheet no. 476120 in the Herb. Cavanilles (Fig. 1A) has been chosen as lectotype [MA, photo (to be deposited at UC)!].

Drynaria vestita Fée, Mém. Fam. Foug. 5 (Gen. Fil.):271. 1852.—Type: Mexico, *Galeotti s.n.* (P; not found by Mickel and Beitel, 1988).

This species was first described by Cavanilles as *Polypodium peltatum* in 1802. However, his name was not universally adopted by later pteridologists, many of whom accepted the later name, *Polypodium polylepis* Roem. ex Kunze (exceptions include Christensen, 1938; Weatherby, 1944; Knobloch and Correll, 1962; and Stolze, 1981). Although the epithet *peltatum* is available and has priority within the genus *Polypodium,* its transfer to *Pleopeltis* is precluded by the existence of an Old World taxon, *P. peltata* Scort. ex Alderw. (1909, Bull. Dép. Agric. Indes Néerl.27:4), a synonym of *Microsorium sarawakense* (Baker) Ching (Holttum, 1968). At first glance, van Alderwerelt van Rosenburgh's name appears to be a nomen nudum, but as pointed out to me by David Lellinger (pers. comm.), the names published in this paper were validated by indirect reference on p. 1 to the author's earlier book on Malayan ferns (Alderwerelt van Rosenburgh, 1908).

Given that the epithet *peltata* is unavailable in the genus *Pleopeltis,* I have adopted the name *P. polylepis* for this predominantly Mexican taxon. The typification of the basionym *Polypodium polylepis* Roemer ex Kunze is complicated, however, by the fact that apparently none of the three syntypes (see above) cited in the original description has survived. Neotypification may prove necessary, but only after further study and searches for extant, original material have been completed. This will be addressed in a future paper.

A second issue concerns the lectotypification of the name *Polypodium peltatum* Cav. According to the original description, the type material (two sheets in the Cavanilles collection in Madrid; Fig. 1) was collected in the Marianas Islands (now Guam) by Luis Née. Née was one of two botanists who accompanied the 1789–1794 Malaspina expedition to Peru and Ecuador, Mexico, California, and finally to the Marianas (S. Pajarón, pers. comm.). The plants were sent periodically to the port of Cádiz in southern Spain before eventual transport to Madrid.

The type material of *Polypodium peltatum* is problematic for two reasons. First, no member of the *Pleopeltis macrocarpa* group currently occurs in Guam, the type locality indicated by Cavanilles. Second, photographs of the type material and detailed measurements of the specimens (provided by Santiago Pajarón, Universidad Complutense, Madrid), revealed that the type material contains at least two species. Each sheet contains several plants and, unfortunately, few of the labels can be reliably associated with any particular plant. The localities indicated on the labels of sheet 476120 (Fig. 1A) are Guam (ex insulis marianas) and Ecuador (monte San Antonio, Quito), whereas the localities on sheet 476121 (Fig. 1B) are both in Ecuador (San Antonio and Guaranda). Inspection of the specimens on both sheets revealed that most plants are indeed the Mexican *Pleopeltis polylepis,* whereas a few are apparently *P. macrocarpa.* The latter is one of only two members of the *P. macro-*

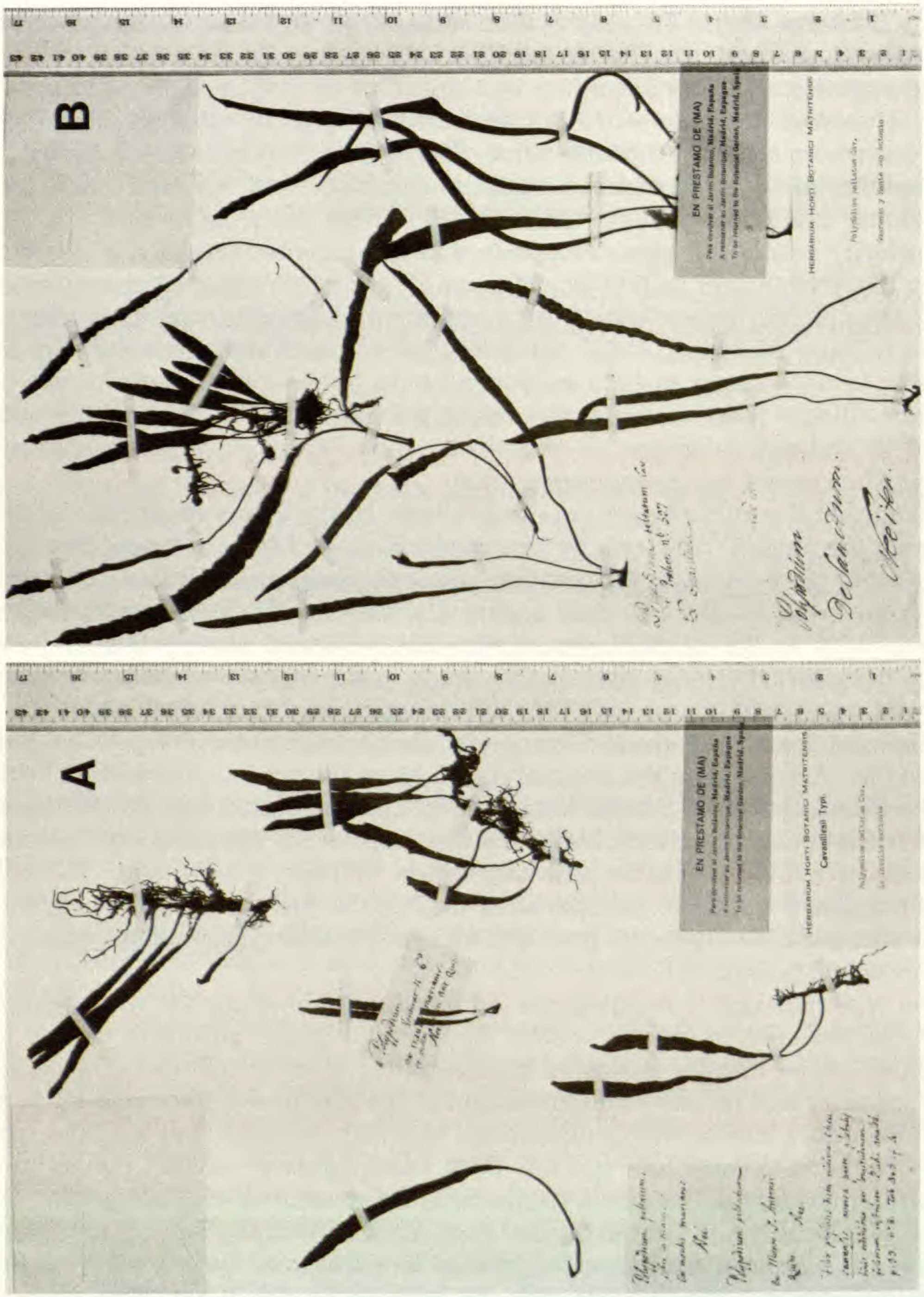

FIG. 1. The type material of *Polypodium peltatum*. A) sheet #476120, the as lectotype; B) sheet #476121. Both specimens from MA.

specimen above the label in the lower right-hand corner has been chosen

carpa group that are common in Ecuador, and thus was most likely collected there as the labels indicate. *Pleopeltis polylepis,* on the other hand, was probably not collected in Ecuador because it has never, to my knowledge, been collected south of Mexico. Thus, most of the type material was apparently collected during the nine-month period the Malaspina expedition was in Mexico. It is most reasonable to assume that the specimens and labels likely became mixed between the time of collection and the time of description in 1802. Nevertheless, Née's material must be taken as type; therefore, one of the fertile specimens from sheet 476120 (the one above the lower right-hand label in Fig. 1A) has been chosen as lectotype.

As presently circumscribed (Hooper, 1994), *P. polylepis* consists of three varieties, one of which requires a new combination. In addition to var. *polylepis,* the nomenclature of the other two varieties is summarized as follows:

Pleopeltis polylepis var. **erythrolepis** (Weath.) Wendt, Amer. Fern. J. 70:9. 1980.—*Polypodium erythrolepis* Weath., Contr. Gray Herb. 65:11. 1922. *Phlebodium erythrolepis* (Weath.) Conz., Fl. Tax. Mex. 1:95. 1946. *Pleopeltis erythrolepis* (Weath.) Pic. Serm., Webbia 23:189. 1968.—Type: Mexico, Chihuahua, Portrero [Potrero] Peak, Cold Cliffs, *Pringle 825* (holotype, GH!; isotypes, GH!, LL, NY!, UC!, US!).

Pleopeltis polylepis var. **interjecta** (Weath.) E.A. Hooper, comb. nov.—*Polypodium peltatum* Cav. var. *interjectum* Weath., Amer. Fern J. 34:17. 1944. *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf. var. *interjecta* (Weath.) A.R. Smith, Amer. Fern J. 70:26. 1980; *P. interjecta* (Weath.) Mickel & Beitel, Mem. New York Bot. Gard. 46:287–288. 1988.—Type: Guatemala, Chimaltenango, Cerro de Tecpam near Santa Elena, 2700 m, *Standley 60957* (F!).

This variety occurs in northern Central America (mainly Guatemala) and southern Mexico (mainly Oaxaca and Chiapas). It was originally described as a variety of *Polypodium peltatum* by Weatherby (1944), then transferred to *Pleopeltis* as a variety of *P. macrocarpa* (Smith, 1980), and finally elevated to species rank by Mickel and Beitel (1988). Most authors commented on its resemblance to *P. polylepis* on the one hand and to *P. macrocarpa* on the other, but each emphasized different characteristics used to separate these taxa. For example, in the original description, Weatherby (1944) differentiated his new variety from *P. macrocarpa* because it has entire (vs. erose-serrulate) laminar scales and rhizome scales with occluded cell luminae. In contrast, Smith (1980) classified *interjecta* as a variety of *P. macrocarpa,* because he considered the similarity in scale size and number between the two (small and sparse relative to *P. polylepis*) to be more consistent than the differences in scale margin used by Weatherby. Finally, Mickel and Beitel (1988) apparently considered the taxon distinct enough from both *P. polylepis* and *P. macrocarpa* to be recognized as a separate species, and stated that its affinity was with *P. macrocarpa.* Despite a recent morphometric survey of the *P. macrocarpa* group (Hooper, 1994), morphological data alone failed to resolve which of these three

taxonomic treatments is correct, because there are morphological features that support each one.

A survey of isozyme variability within the *P. macrocarpa* group (Hooper, 1994) revealed very high levels of allelic similarity between population samples of *interjecta* and *P. polylepis.* The average genetic identity value (Nei's I) among *interjecta, P. polylepis* var. *polylepis,* and *P. polylepis* var. *erythrolepis* was 0.97, a value more typical of conspecific plant populations than of congeneric species (Soltis and Soltis, 1990). Conversely, the genetic identities between *interjecta* and other members of the group, including *P. macrocarpa,* were nearly all 0.81. Electrophoretic analysis of isozymes using starch gel electrophoresis therefore provided strong evidence that *interjecta* should be treated as a variety of *P. polylepis,* rather than as a separate species or as a variety of *P. macrocarpa.*

Biogeographical data lend further support to this alignment. Within the *P. macrocarpa* group, all but one species are restricted to one of two centers of species diversity for the group, one based in southern Mexico and northern Central America and the other in southern Central America. *Pleopeltis macrocarpa* occurs in the southern region (and also extends to the Greater Antilles, South America, and parts of the Old World); whereas, *interjecta* and *P. polylepis* both occur in the northern region. Moreover, within the northern region, the ranges of *interjecta* (northern Central America and southern Mexico), *P. polylepis* var. *polylepis* (central and northeastern Mexico), and *P. polylepis* var. *erythrolepis* (northwestern Mexico) are somewhat distinct. There are, however, regions of overlap within which it can be difficult to assign an individual to one or another variety with certainty (e.g., see Wendt, 1980). Such a geographical pattern is more typical of plant varieties (or subspecies) than plant species.

Given the inconsistency of the morphological features and the correspondence of genetic and geographical data, *P. polylepis* is here described as a species with three varieties distributed throughout Mexico and northern Central America. The most distinctive of the three is *P. polylepis* var. *interjecta,* which is differentiated from the others by its narrowly elliptic leaves (vs. narrowly oblanceolate); smaller abaxial laminar scales (0.5 mm in diameter on average vs. 0.6 mm); non-overlapping abaxial laminar scales (vs. overlapping); conspicuously blackened abaxial costae [vs. green (var. *erythrolepis*) or occasionally blackened (var. *polylepis*)]; and conspicuously black-centered soral scales with occluded cell luminae (vs. brown- or black-centered with clear cell luminae).

The other two varieties of *P. polylepis* are more difficult to differentiate from one another. A morphometric analysis of representative members of each (Hooper, 1994) revealed that, on average, var. *erythrolepis* has longer stipes (about equal to the blade length vs. <¼ the blade length in var. *polylepis*); wider leaves (about one-fifth the blade length vs. one-tenth in var. *polylepis*); larger spores (55 μm on average vs. 51 μm in var. *polylepis*); and an abaxial costa that is green (vs. occasionally blackened in var. *polylepis*). Also, as pointed out by Wendt (1980), the abaxial laminar scales of mature var. *erythrolepis*

tend to be more densely imbricate, more ovate-lanceolate and acuminate (vs. roundish), and with margins that are more dissected than in var. *polylepis*.

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