

A Redefinition of the Genus *Hemionitis*¹

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In the summer of 1971 during field work on the ferns of the state of Oaxaca, Mexico, I collected four species of the genus *Hemionitis*, only one of which had previously been reported from that state. A broader examination of the genus was undertaken in order to determine the species' limits and relationships. Spore studies showed that certain species of *Hemionitis* had spores that closely resembled those of some species of the closely allied *Gymnopteris*, and so the study was broadened to include the species of both genera.

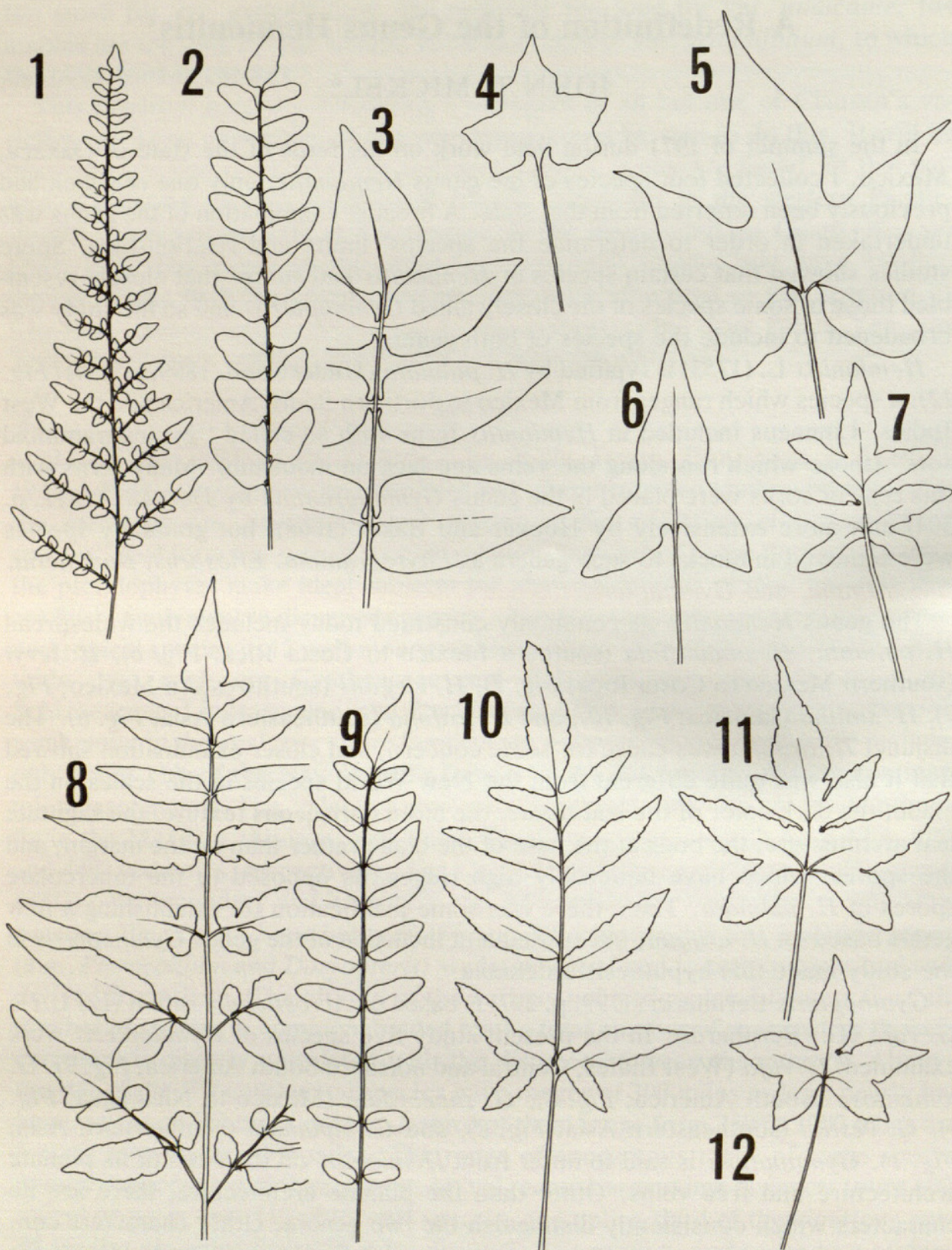
Hemionitis L. (1753) is typified by *H. palmata* (Underwood, 1899, p. 254) (Fig. 12), a species which ranges from Mexico to northern South America and the West Indies. Linnaeus included in *Hemionitis* ferns with so-called "gymnogrammoid sori" (those which run along the veins and lack an indusium). Many ferns with this type of sorus were placed in the genus *Gymnogramma* by Desvaux (1811, p. 304) and more extensively by Hooker and Baker (1868), but gradually species were removed in blocks to such genera as *Pityrogramma*, *Eriosorus*, *Bommeria*, *Anogramma*, and *Gymnopteris*.

The genus *Hemionitis* as commonly construed today includes the widespread *H. palmata*, *H. pinnatifida* (southern Mexico to Costa Rica; Fig. 6), *H. levyi* (southern Mexico to Costa Rica; Fig. 7), *H. elegans* (southwestern Mexico; Fig. 5), *H. smithii* (Jamaica; Fig. 10), and *H. arifolia* (southeastern Asia; Fig. 6). The disjunct *H. arifolia* was cause for some concern, and closer examination showed that it also was quite different from the New World species in the scales on the blade, the dark color of the leaf tissue, the more coriaceous texture, the sagittate leaf architecture, the buds at the base of the blade rather than on the margin, and the spores, which have noticeably high ridges, as opposed to the tuberculate spores of *H. palmata*. Thus, there was some justification for establishing a new genus based on *H. arifolia*, but subsequent inclusion of the genus *Gymnopteris* in the study made this hypothesis untenable.

Gymnopteris Bernhardt (1799, p. 297) is based on *Acrostichum rufum* (L.) L. (= *G. rufa* (L.) Bernhardt). In the present study five species of *Gymnopteris* were examined: *G. rufa* (West Indies, Central and northern South America; Fig. 9), *G. tomentosa* (South America; Fig. 8), *G. subcordata* (Mexico to Nicaragua; Fig. 3), *G. vestita* (southeastern Asia; Fig. 2), and *G. bipinnata* (southeastern Asia; Fig. 1). *Gymnopteris* is said to differ from *Hemionitis* on the basis of its pinnate architecture and free veins. Other than the pinnate architecture, there are no characters which consistently distinguish the two genera. Other characters contradict the separation of these two genera, and I find a stronger argument for combining the two genera.

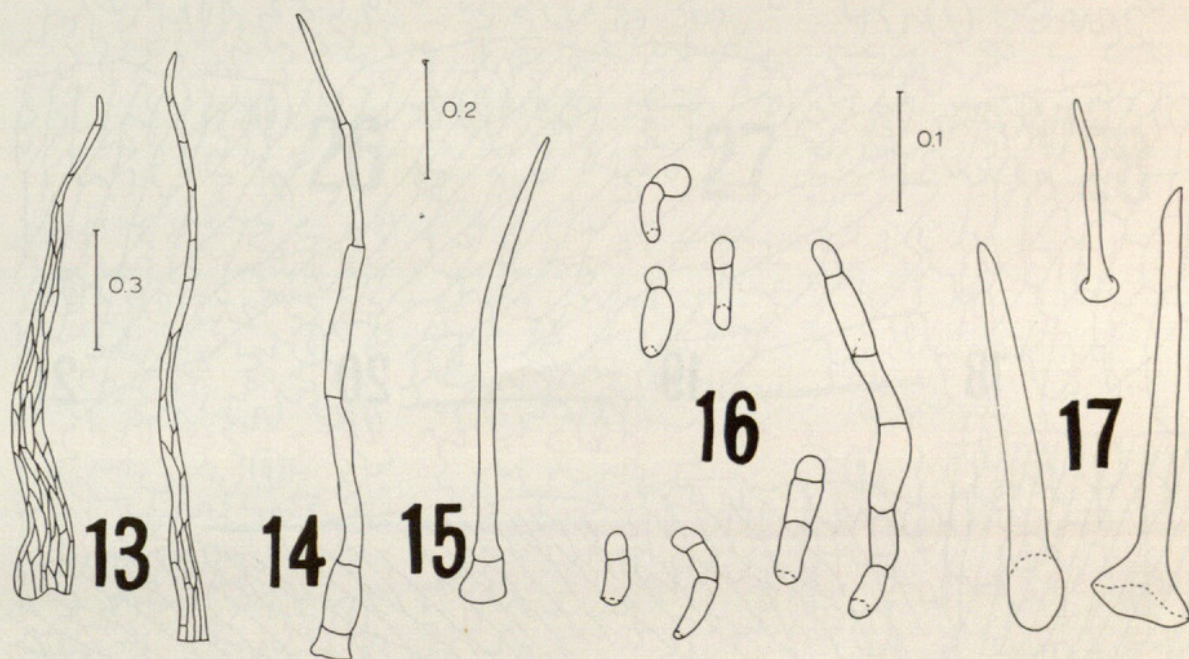
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Frond outlines of *Hemionitis* and *Gymnopteris*. FIG. 1. *G. bipinnata*. FIG. 2. *G. vestita*. FIG. 3. *G. subcordata*. FIG. 4. *H. pinnatifida*. FIG. 5. *H. elegans*. FIG. 6. *H. arifolia*. FIG. 7. *H. levyi*. FIG. 8. *G. tomentosa*. FIG. 9. *G. rufa*. FIG. 10. *H. × smithii*. FIG. 11. *H. palmata* × *pinnatifida*. FIG. 12. *H. palmata*.

Frond architecture.—Basically this character seems to keep the two genera, as commonly defined, apart. *Gymnopteris* has blades that are fully pinnate to bipinnate; those of *Hemionitis* are sagittate, palmate, or pinnatifid. *Hemionitis smithii* (Fig. 10) is pinnate with some pinnae broadly adnate and with the basal pinnae basiscopically auricled; it was postulated by Underwood (on the basis of an herbarium specimen) to be a hybrid between *H. palmata* and *Gymnopteris rufa*. This hypothesis is supported by gross and spore morphology.



Trichomes of *Hemionitis* and *Gymnopteris*. FIG. 13. *H. arifolia*. FIG. 14. *H. palmata*. FIG. 15. *H. levyi*. FIG. 16. *G. subcordata*. FIG. 17. *H. elegans*.

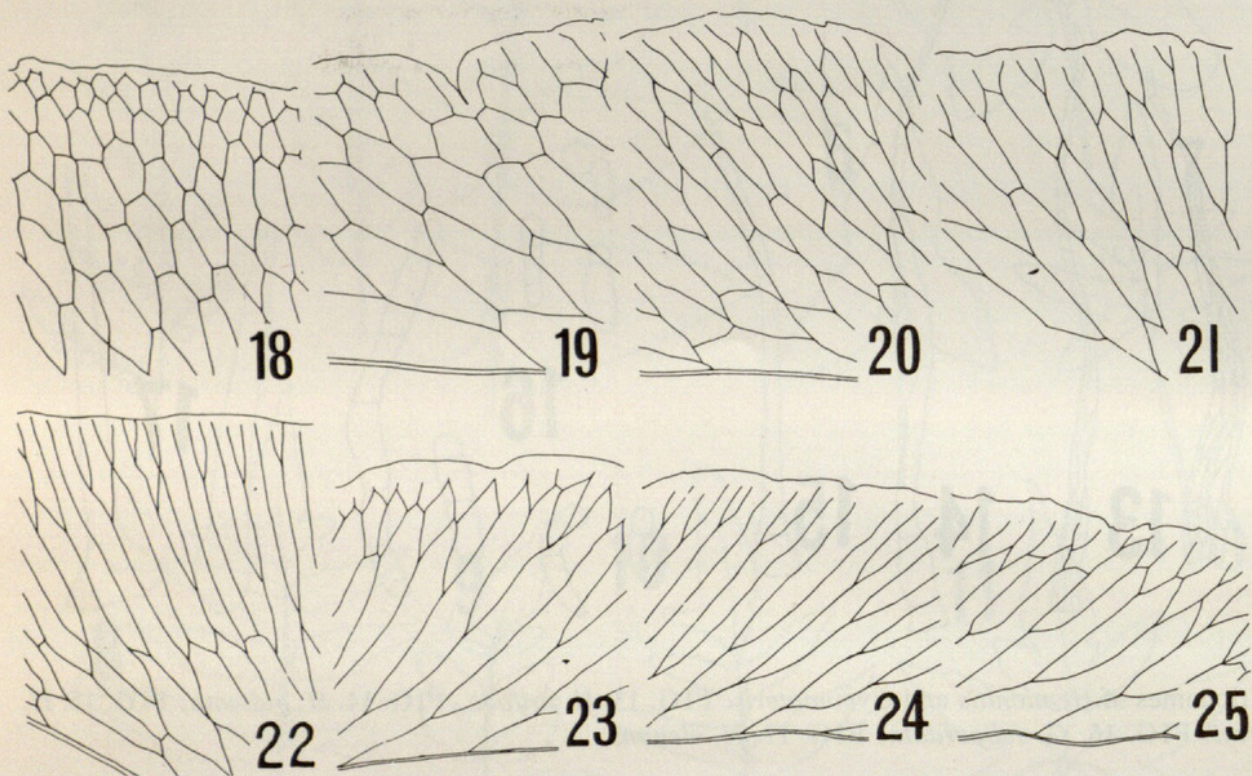
Geographic range.—Both *Gymnopteris* and *Hemionitis* contain species in both the New and Old Worlds, but no characters were found to correlate with geographic range. The Old World *H. arifolia* is quite distinct within *Hemionitis sensu stricto* in the characters mentioned above. Other than the spore ridges, these characters are not shared by the Asian species of *Gymnopteris*.

Indument.—In both genera the rhizome has scales and the blade is clothed with hairs. The hairs are generally more than one cell broad in *H. arifolia* (Fig. 13), making them technically scales, although this point is generally not cited in the literature. Copeland (1947, p. 73) states that all *Hemionitis* species have laminar hairs, but the scales are illustrated in Hooker (1842, t. 74B). This transition from hairs to scales, often on the same frond, can also be seen in *Mohria*, and no great significance should be attached to it.

In most species of both genera the hairs are several cells long (Fig. 14). Those of *H. elegans* are mostly very short, only one cell long, and sharp-pointed (Fig. 17); those of *H. levyi* (Fig. 15) are also pointed, but often are two or three cells long. *Hemionitis subcordata* is nearly glabrous, but has scattered, short, multicel-

lular hairs whose cells are nearly equal in length (Fig. 16), in contrast to the larger hairs of most species. These hairs have also been seen sparingly in *H. levyi* and *H. palmata* and are probably to be found as aberrant hairs in other species. These hair types can be seen with a hand lens.

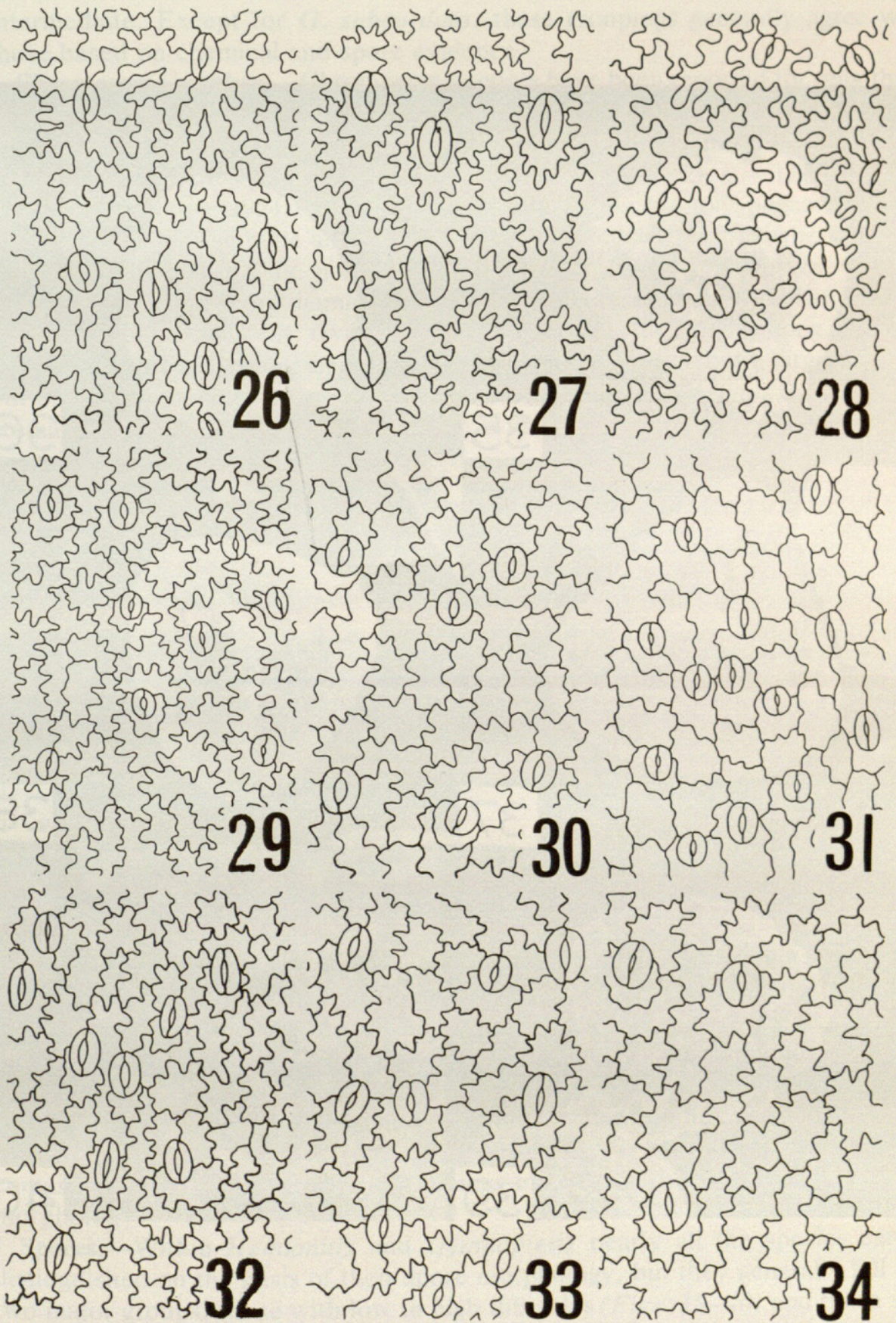
Venation.—The distinction between net and free venation as a character to distinguish *Hemionitis* from *Gymnopteris* is not valid. Although some species of *Gymnopteris* do indeed have entirely free veins (Fig. 24), and some species of *Hemionitis* have entirely net veins (Fig. 18), this character does not hold consis-



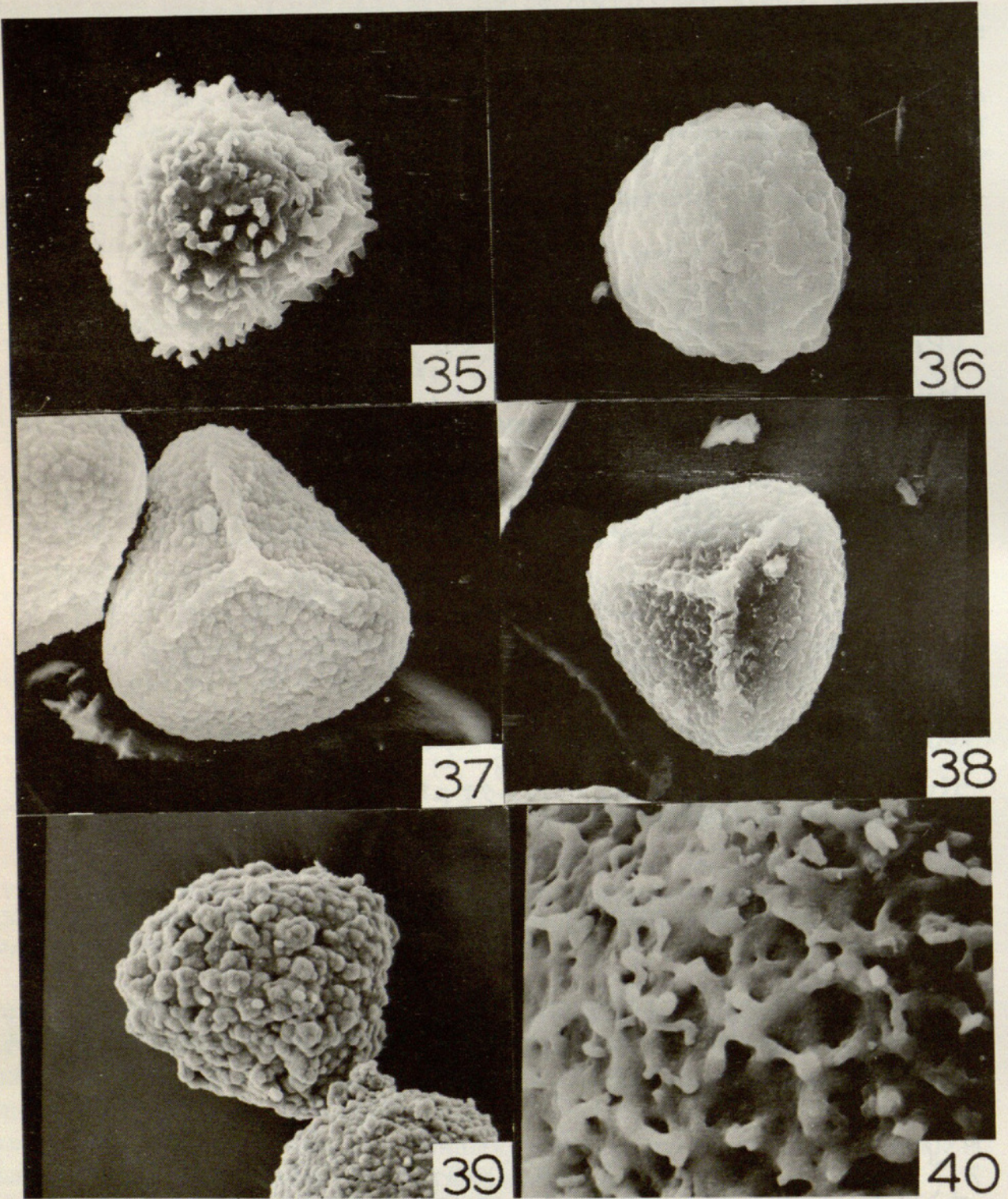
Venation patterns of *Hemionitis* and *Gymnopteris*, FIG. 18. *H. arifolia*. FIG. 19. *H. palmata*. FIG. 20. *H. elegans*. FIG. 21. *H. levyi*. FIG. 22. *G. subcordata*. FIG. 23. *H. × smithii*. FIG. 24. *G. tomentosa*. FIG. 25. *G. vestita*.

tently. Lellinger (1969) has pointed out that *G. subcordata* has largely net veins (Fig. 22). There is a tendency for some species of *Hemionitis* to have rather extensive free veins near the margin (Figs. 19–21). *Gymnopteris vestita* has mostly free veins with a few anastomoses near the margin (Fig. 25). *Hemionitis × smithii*, the hybrid between *H. palmata* (net veins) and *G. rufa* (free veins), is largely free-veined near the midvein and netted near the margin (Fig. 23).

Epidermal pattern.—Leaf clearings showed some variation in epidermal patterns. Although there are no sharp distinctions between the species of *Gymnopteris* and *Hemionitis*, the patterns do seem to fall into two rough categories. *Hemionitis elegans* (Fig. 26), *H. arifolia* (Fig. 27), and *G. vestita* (Fig. 28) have highly contorted epidermal cells, whereas *H. palmata* (Fig. 30), *G. subcordata* (Fig. 31), *H. levyi* (Fig. 33), and *H. pinnatifida × palmata* (Fig. 34) have more blocky cells. *Gymnopteris vestita* and *G. tomentosa* are somewhat



Patterns of the lower epidermis of *Hemionitis* and *Gymnopteris*, FIG. 26. *H. elegans*. FIG. 27. *H. arifolia*. FIG. 28. *G. vestita*. FIG. 29. *G. tomentosa*. FIG. 30. *H. palmata*. FIG. 31. *G. subcordata*. FIG. 32. *G. rufa*. FIG. 33. *H. levyi*. FIG. 34. *H. palmata* \times *pinnatifida*.



Spores of *Hemionitis* and *Gymnopteris*. FIG. 35. *H. palmata*, distal view, $\times 1200$. FIG. 36. *G. rufa*, distal view, $\times 1200$. FIG. 37. *H. levyi*, proximal view, $\times 1200$. FIG. 38. *H. pinnatifida*, proximal view, $\times 1200$. FIG. 39. *H. palmata* \times *pinnatifida*, distal view, $\times 1200$. FIG. 40. *H. smithii*, distal view, $\times 3000$.

intermediate. Except for *G. subcordata*, these groupings generally agree with those based on chemical and spore evidence.

Chromosome number.—Chromosome counts have been reported for only three of the ten species: *Gymnopteris rufa*, $n = 30$ (Manton, 1958; Walker, 1966), *H. palmata*, $n = 30$ (Manton & Sledge, 1954; Wagner, 1963; Walker, 1966), and *H. arifolia*, $n = 90$, $2n = 90$ (Abraham, Ninan & Mathew, 1962), $n = 120$, $2n = 120$ (Manton & Sledge, 1954). Both reports for *H. arifolia* are for apogamous polyploids. A study of stomate and spore sizes was made to determine whether other species might possibly be polyploids. The results are not conclusive. In both stomate length and spore diameter *H. arifolia* is among the largest. Other species, however, are inconsistent. *Gymnopteris rufa*, a known diploid, has long stomates but small spores. *Gymnopteris vestita* and *G. bipinnata* have the largest spores but only medium-sized stomates. The hybrid *H. palmata* \times *pinnatifida* has large stomates but small spores. Thus, there is no apparent basis for extrapolating probable ploidy levels at this time.

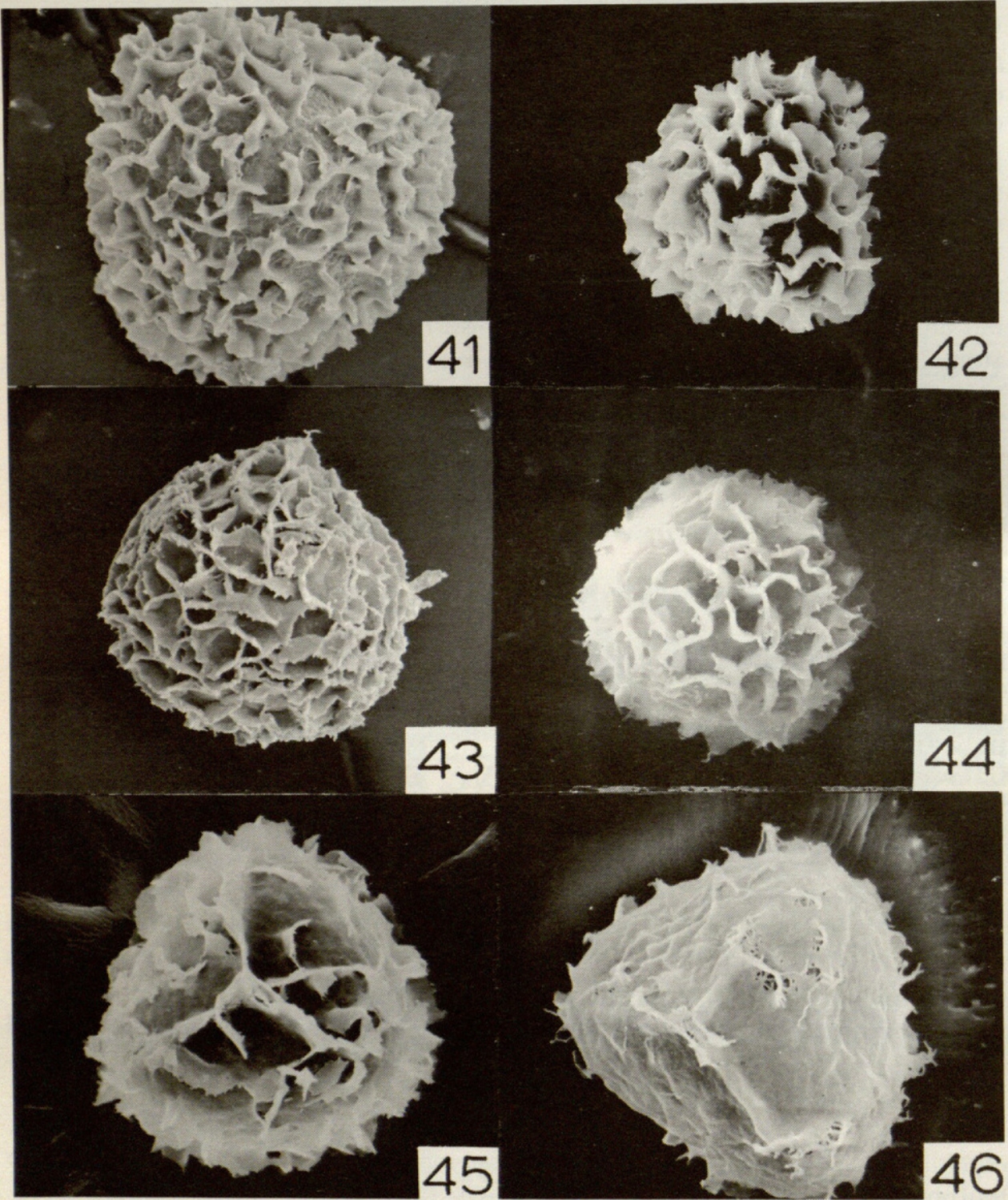
TABLE 1. STOMATE AND SPORE SIZES IN *HEMIONITIS* AND *GYMNOPTERIS*¹

	Stomate length in μm	Spore diameter in μm
<i>H. arifolia</i>	62.5	44.5
<i>G. bipinnata</i>	36.8	54.1
<i>H. elegans</i>	47.6	37.3
<i>H. levyi</i>	48.1	36.7
<i>H. palmata</i>	45.5	32.0
<i>H. palmata</i> \times <i>pinnatifida</i>	61.6	36.4
<i>H. pinnatifida</i>	48.3	37.1
<i>G. rufa</i>	55.5	31.7
<i>H. </i> \times <i>smithii</i>	51.5	34.8
<i>G. subcordata</i>	47.6	31.8
<i>G. tomentosa</i>	38.2	32.6
<i>G. vestita</i>	43.1	57.0

¹Figures represent averages of 20 measurements of representative specimens.

Chemical evidence.—Dr. David Giannasi, in a study of the phenolic compounds in the species of *Hemionitis* and *Gymnopteris* (1974), has shown that according to their compounds, the species fall into two distinct groups that cut across traditional generic boundaries. Each group has several distinct compounds not found in the other. One group, including *H. pinnatifida*, *H. levyi*, *H. palmata*, and *G. rufa*, has flavones and methylated flavonols, whereas the other species, *H. elegans*, *H. arifolia*, *G. subcordata*, *G. tomentosa*, *G. vestita*, and *G. bipinnata*, contain regular flavonols. These groupings match exactly those based on spore morphology.

Spores.—Within *Hemionitis* and *Gymnopteris* nearly all the species can be distinguished on the basis of their spore morphology, but they generally fall into two major groups: those with low to high tubercles (Figs. 35–40) and those with ridges (Figs. 41–46). Of the tuberculate species, *H. palmata* (Fig. 35) stands out with the longest projections. Spores of *H. pinnatifida* (Fig. 37), *H. levyi*, and *G. rufa* are very much alike with broad, low bumps. Among the species with ridges



Spores of *Hemionitis* and *Gymnopteris*. FIG. 41. *H. arifolia*, distal view, $\times 1200$. FIG. 42. *G. tomentosa*, distal view, $\times 1200$. FIG. 43. *G. bipinnata*, distal view, $\times 900$. FIG. 44. *G. vestita*, distal view, $\times 900$. FIG. 45. *G. subcordata*, proximal view, $\times 1200$. FIG. 46. *H. elegans*, proximal view, $\times 1200$.

on the spores, *G. subcordata* (Fig. 45) has the most slender and highest ridges. *Hemionitis elegans* (Fig. 46) has the least developed ridges and has peculiar, small caverns and small, slender projections about them. *Gymnopteris bipinnata* and *G. vestita* have numerous, fine, fingerlike projections on the ridges.

It is interesting to note that the two hybrids known in the genus both occur between species with tuberculate spores: *H. palmata* \times *pinnatifida* (Fig. 39) and *H. palmata* \times *rufa*. The hybrids show some abortion and some large, round spores with tubercles of length intermediate between those of the parents.

CONCLUSIONS

From these data we can see the generic boundaries between *Hemionitis* and *Gymnopteris* as traditionally held are not tenable. Leaf architecture is the only character separating the two. On the other hand, at least two lines of evidence point to two groups of species that cross the generic lines. Results from phenolic chemistry and spore morphology agree perfectly and epidermal patterns fall into roughly the same groupings, those with crested spores and regular flavanols generally having the most contorted epidermal patterns. Without any gross morphological differences, however, it does not seem reasonable to give these groups generic rank.

The relationship of *Hemionitis* to other genera is not entirely clear. *Hemionitis* in the strict sense was placed by Copeland (1947) closest to *Bommeria* (rather than *Gymnopteris* even). Lellinger (1965) also placed it closest to *Bommeria* and not far from *Gymnopteris* and *Paraceterach*. The spores of *Bommeria* are quite different from those of *Hemionitis*. Those of the former are nearly smooth with only slight bumps on the surface, somewhat like those of certain species of *Notholaena*. On the other hand, the spores of *Trachypteris*, which bears little superficial resemblance to *Hemionitis*, are nearly identical to the crested-spored species of *Hemionitis*. This is particularly surprising on the basis of its having its blade densely covered with broad, toothed scales, quite unlike anything found in *Hemionitis*. Further study and re-evaluation of a broad array of characters in *Trachypteris*, *Saffordia*, *Paraceterach*, *Bommeria*, and perhaps other genera are needed.

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