

ADDITIONAL DISCUSSIONS PERTAINING TO THE CONGENERIC STATUS OF PERITYLE AND LAPHAMIA (COMPOSITAE)¹

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Various taxonomic dispositions of *Perityle*, *Laphamia*, and segregate genera have been proposed or discussed by Gray (1886), Rydberg (1914), Macbride (1918), Johnston (1941), Everly (1947), Blake (1951), Shinnars (1959), and Powell and Tsang (1966). In brief, Rydberg established or recognized several small genera (including *Pappothrix*) with his rather comprehensive treatise of the subtribe Peritylanae, but subsequent workers, especially Macbride and Blake, found it necessary to marshal 6 of the taxa into two more natural categories, *Laphamia* and *Perityle*. Even the generic status of *Laphamia* and *Perityle* has been questioned by Johnston, Shinnars, and Powell and Tsang (and others), largely because the two taxa can be distinguished consistently by a single character, the structure of the pappus. Shinnars submerged *Laphamia* into *Perityle* with the strong contention that "To uphold *Perityle* as a separate genus solely by the presence of small pappus scales with or without awns (and both structures variable in number and size) seems quite arbitrary." Studies of several Composite genera, for example *Chaetopappa* (Shinnars, 1946), *Krigia* (Shinnars, 1947), *Lygodesmia* (Shinnars, 1950), *Heterotheca* (Shinnars, 1951), *Stenocarpha* (Turner, 1965), and *Galinsoga* (Turner, 1966), has indicated that some early interpretations of the importance of pappus differences are subject to re-evaluation, especially when used as a primary criterion to delimit genera. I believe, along with Johnston (1941) and Shinnars (1959), that *Perityle* provides another case in point where pappus differences must be evaluated in proper perspective with other overall differences and similarities.

Considerable morphological studies of *Laphamia* and *Perityle* have revealed another semi-consistent character by which the taxa can be delimited. The achene margins of traditional *Laphamia* species are subglabrous to short-pubescent but do not exhibit the relatively long-ciliate condition of most *Perityle* species. The few species of *Perityle* which do not have conspicuously ciliated achene margins are recognizable by the presence of pappus squamellae. If *Laphamia* and *Perityle* are separate monophyletic groups even though closely related, and I believe they are, then their recognition as genera on arbitrary grounds would seem to be justified. However, purely arbitrary designations of taxonomic rank are not necessarily commensurate with phylogeny.

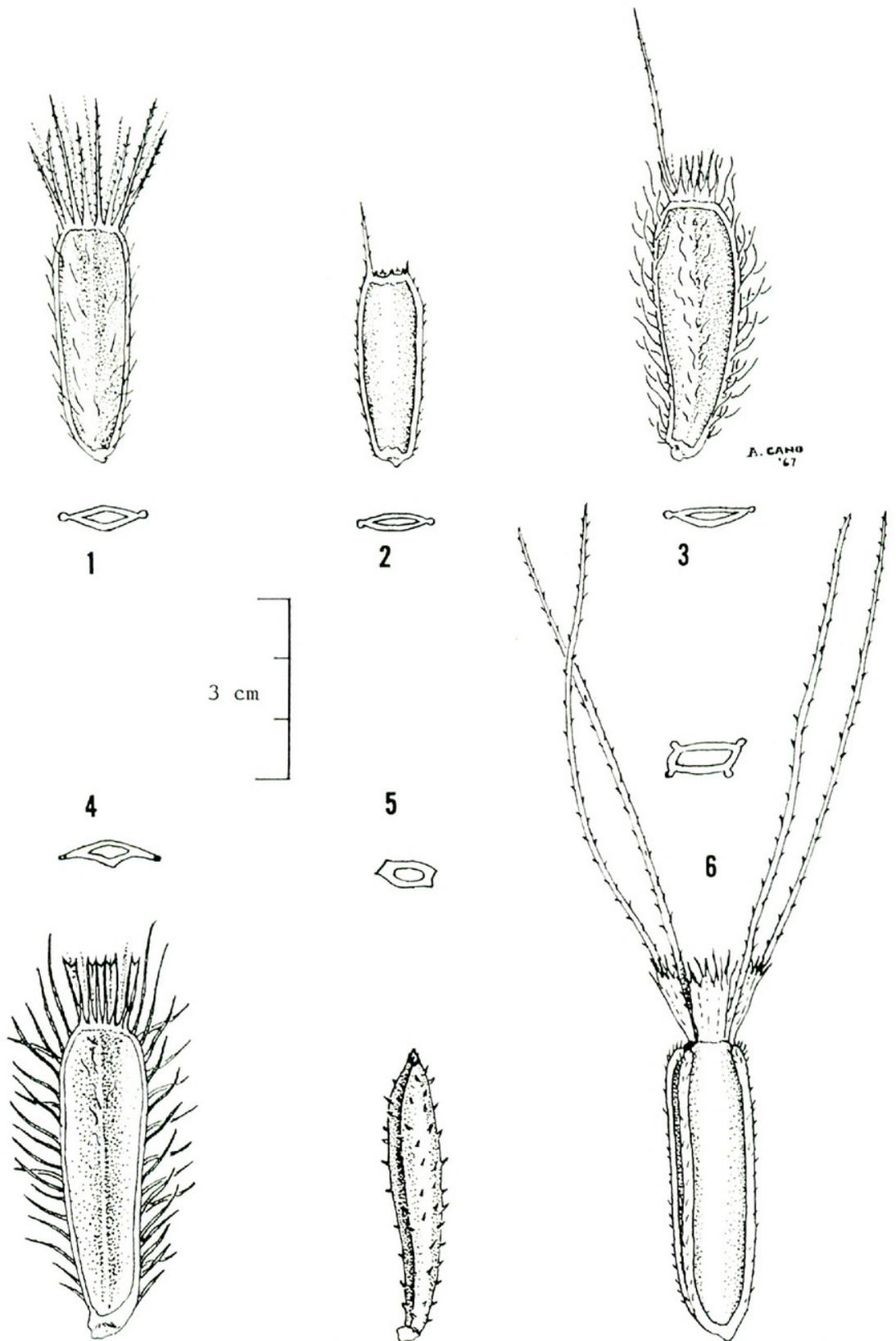
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SIDA 3 (4): 270—278. 1968.

Detailed morphological discussions are not included here since such comparisons of *Laphamia*, *Perityle*, and other taxa of this subtribe are presented adequately by most of the authors listed above. Still, morphic criteria provide the best evidence for combining *Laphamia* and *Perityle*. After studying all the *Laphamia* (*s.str.*) species and many species of *Perityle* (*s. str.*), it is abundantly clear that these traditional taxa are extremely similar. It has become evident that vestigial pappus squamellae are exhibited by most traditional *Laphamia* species and not the few (notably in *P. castillonii* and *P. dissecta*) mentioned by other authors. When the prominence of pappus squamellae is compared with the presence or absence of bristles in *Laphamia* and *Perityle*, it is very difficult to distinguish typical *Laphamia* features from those present in derived *Perityle* species. Where this situation exists usually it is possible to delimit *Perityle* from *Laphamia* by achene margin pubescence, the former typically with longer and more profuse marginal hairs than the other. However, it is significant to mention that hybrids (see below) and suspected hybrids derived from *Laphamia* and *Perityle* parental species exhibit a pappus and achene pubescence more like the *Laphamia* parent even though a combination of a few other exomorphic features might resemble the *Perityle* parent. This suggests that if much ancestral hybridization has occurred, it would be difficult to detect the origin of intermediate taxa, i.e., those with reduced squamellae. At any rate it seems evident that the use of pappus structure to separate *Laphamia* from *Perityle* is at best tenuous from a phylogenetic point of view. Additionally, it is proper to note that the *Pappothrix* pappus (10-35 bristles) is more distinctive than is that of *Laphamia* or *Perityle* (Rydberg, 1914), but numerous other features seem to prohibit the treatment of *Pappothrix* as a genus.

Also helpful in the morphological comparison of *Laphamia* and *Perityle* is an equivalent conspectus of the related genera *Pericome*, *Amauria*, and *Eutetras*. It is not possible to present an extensive morphological comparison of these genera here, albeit in summary each shows affinity with *Perityle*, but generic distinctiveness through characters of vegetative and floral habit, achene morphology, and pappus structure. By general morphic comparison, *Pericome*, *Amauria*, and *Eutetras* contrast more with each other and with *Perityle* (*sensu lato*) than does *Laphamia s. str.* with *Perityle (s. str.)*. Achene and pappus structure is compared in Figures 1-6. The likeness of *Perityle* and *Pericome* achenes belies a more distant relationship which is seen through a combination of other characters, although *Pericome* is probably closer to *Perityle* than the other genera.

Fortunately, in the case of *Laphamia* and *Perityle*, some evidence other than gross morphological and ecological similarities lends support to congeneric status. Ripley (1957) reported the spontaneous occurrence of hybrids between *P. coronopifolia* and *L. lindheimeri* in a green-



Figures 1-6. Comparative achene and pappus morphology with accompanying cross-sections. Fig. 1. *Perityle rupestris* var. *albiflora* (traditional *Pappothrix*). Fig. 2. *Perityle lindheimeri* var. *lindheimeri* (traditional *Laphamia*). Fig. 3. *Perityle vaseyi*. Fig. 4. *Pericome caudata*. Fig. 5. *Amauria rotundifolia*. Fig. 6. *Eutetras pringlei*.

house in Wappingers Falls, New York (voucher specimen, CAS, 403416). The parental species are not at all closely related, the former being native to southern Arizona-New Mexico and northern Chihuahua, Mexico, and the latter being restricted to the Edwards Plateau of Texas. I have found what appear to be natural hybrids derived from *P. parryi* × *L. rupestris* in the Chisos Mountains of Texas. The small population of putative hybrids seems to represent a fertile, moderately successful "species". Again the parental species involved are very distinct. Studies aimed toward documentation of this suspected hybridization are in progress.

Although experimental attempts to hybridize *Laphamia* and *Perityle* species are still in preliminary stages, there is considerable indication that relatively high interspecific fertility (as determined by seed-set) exists with several species (Fig. 7). While intergeneric and intersectional crosses are more pertinent to this discussion, some infrasectional crosses are presented to show relative fertility. These data are not presented as very definitive evidence at the present stage of investigation, but merely as an indication of trend.

Several limiting factors require that the significance of this inter-fertility data be interpreted with caution: 1) Fertility is measured only by apparently successful seed-set. Achenes were counted fertile when the pericarps were normally dark in color and seemingly inflated by well-developed embryos. Numerous microscopic examinations showed 100% quasi-normal embryos when achenes "looked fertile" by the above standards. 2) Achene germination, even in "pure" species, is accomplished with moderate success. Although germination of hybrid achenes is neither more nor less successful than germination of achenes taken from plants in the field, one can not be certain whether sterility of hybrid seeds is being expressed at this stage. Also, I have not managed to grow plants of pure species or putative F₁ hybrids beyond the seedling stage. It is presumed that diploid × polyploid progeny would ultimately express greater sterility than diploid × diploid progeny. 3) Several of the interfertility percentages are based on evaluation of 50 achenes or less (with a maximum of 150), and in 3 instances crosses were effected with only one head of florets on the female parent (most notably with *P. gilensis* and *Eutetras pringlei*). 4) Only a small number of species have been utilized for these hybridization tests.

Practically all species examined have shown complete self-incompatibility. Mature achenes have developed in control heads of only 3 taxa, *P. angustifolia*, *P. rupestris* var. *albiflora*, and *P. rupestris* var. *rupestris* (after examining up to 6000 florets), but the percent of apparent self-compatibility has not exceeded 0.34. No control heads were available to test the self-compatibility of *P. gilensis* and *Eutetras pringlei*.

Under natural conditions there are few places where species of *Laphamia* and *Perityle* occur sympatrically, therefore, even if general inter-

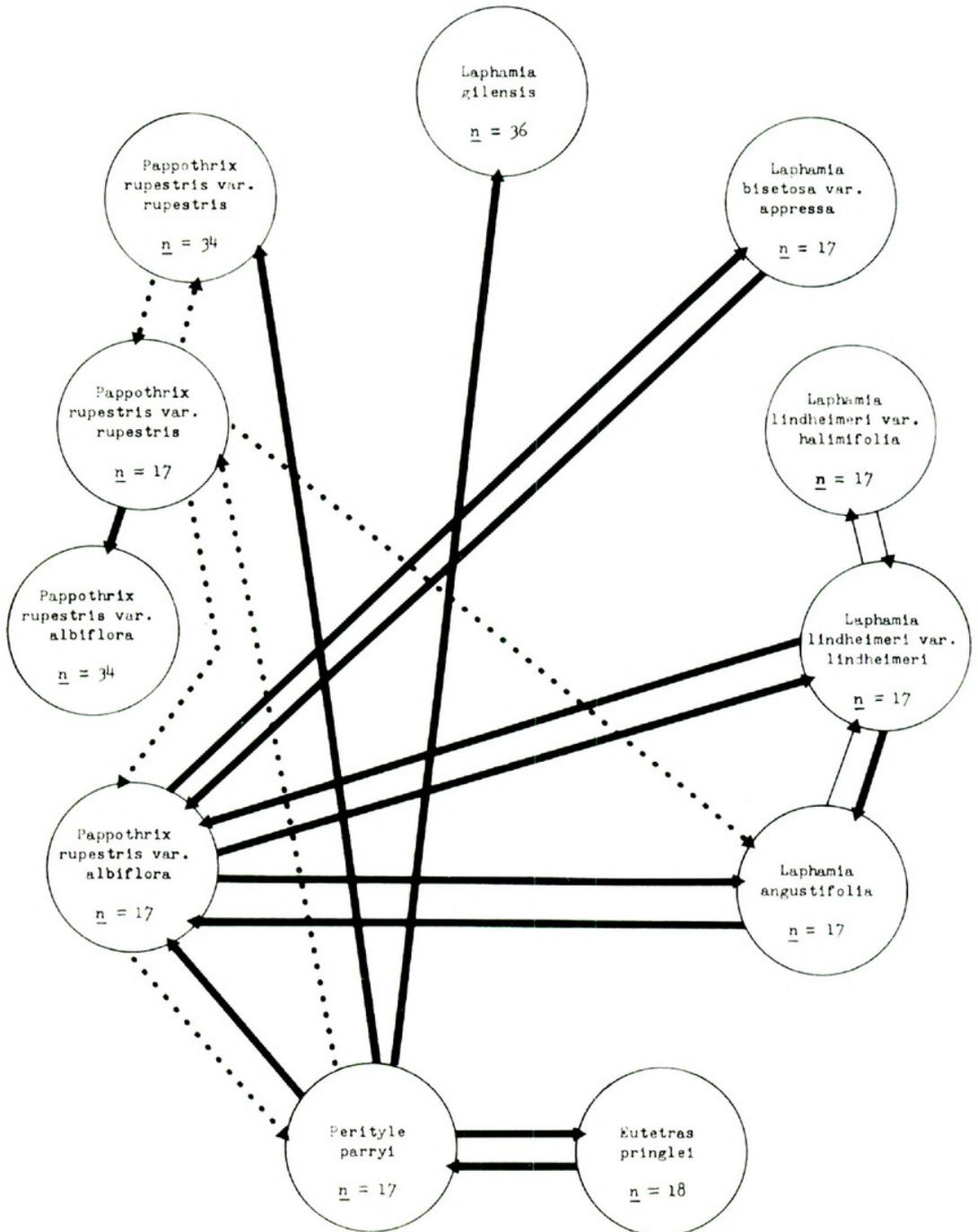


Figure 7. Results of preliminary hybridization studies in *Perityle* based on seed-set data only. The traditional generic names *Laphamia* and *Pappothrix* are utilized here to facilitate the evaluation of comparative generic and sectional interfertility. Species formerly placed in *Laphamia* and *Pappothrix* presently are regarded as comprising sections of *Perityle*. The broad lines indicate interfertility above 25 percent, narrow lines indicate very limited interfertility (.22-1.3 percent), and broken lines indicate crosses attempted with no positive results. Female parents of reciprocal and non-reciprocal crosses are designated by arrow points.

fertility exists, the taxa retain their identities in nature. I suspect that hybrids may be found whenever any two species of the taxa in question occur together, providing chromosome ploidy levels are not drastically different.

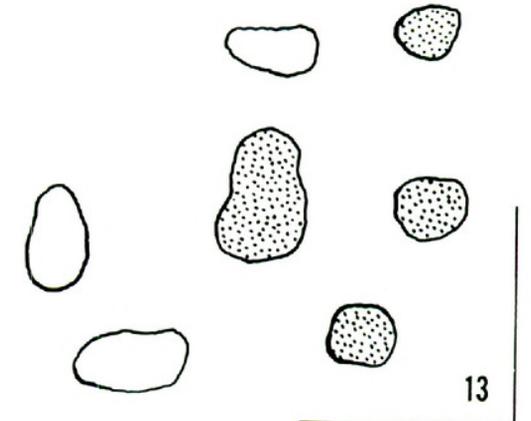
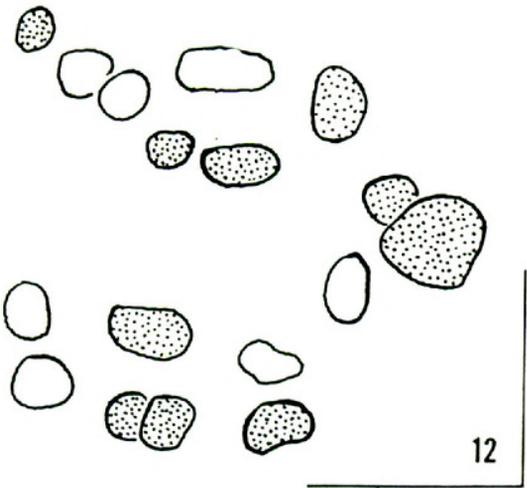
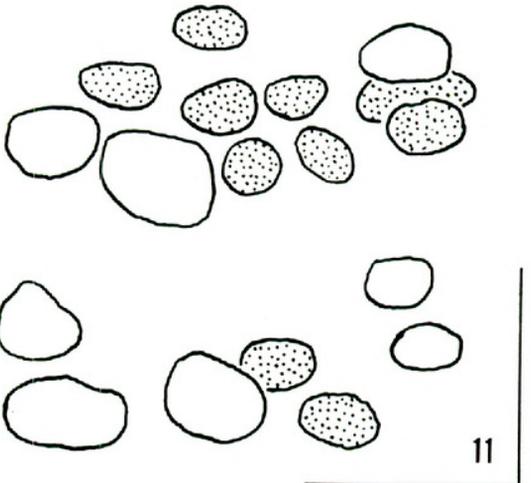
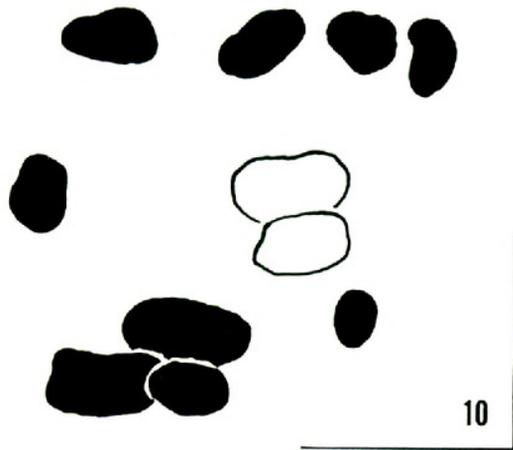
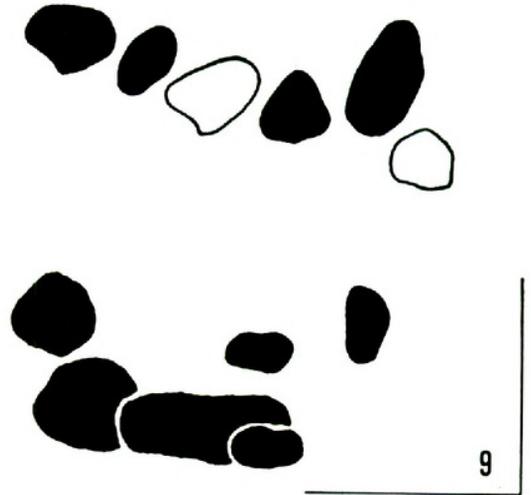
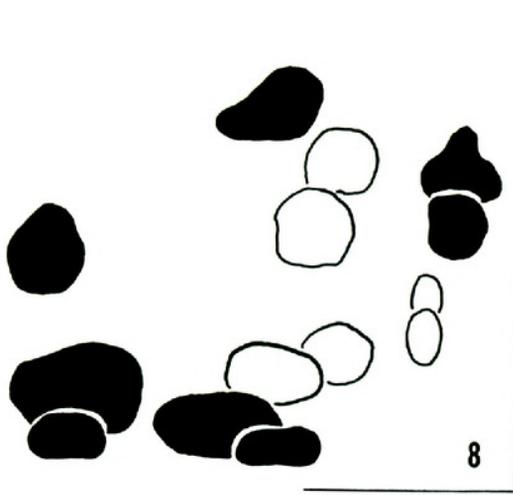
Chemical studies have shown that the 2-dimensional paper chromatographic patterns of *Laphamia* and *Perityle* species are very much alike (Powell and Tsang, 1966; Figs. 8-10). Also, it is possible to distinguish such related genera as *Pericome*, *Amauria*, and *Eutetras* by their chromatographic patterns (Figs. 11-13). Techniques for developing the chromatograms in general follow those outlined by Alston and Turner (1963).

Figures 8-13 are tracings of patterns taken from the chromatograms of species which were selected arbitrarily to represent the proposed sections of *Perityle* and the three related genera. The *Pappothrix*, *Laphamia*, and *Perityle* patterns were chosen because of the number of compounds the particular representative species share. Spots depicted here as common to each section are not necessarily shared by the species used to show representative compounds, but other species of the same section do produce the common spots. Actually all 5 species of Sect. *Pappothrix*, 17 species of Sect. *Laphamia*, and 16 species of Sect. *Perityle* have been examined chromatographically, and the chemical variability of these taxa is not at all apparent in Figs. 8-10. As indicated elsewhere (Powell and Tsang, 1966), virtually every species can be distinguished by its chromatographic pattern, although some are quite similar. Sectional or generic chemical profiles are not presented because such comprehensive assessments are possible only for Sect. *Pappothrix* at this time. Figures 8-10 emphasize what are believed to be common compounds so that close chromatographic relationship can be visualized.

For the purposes of this presentation, the evaluation of common and unique compounds has resulted from the examination of chromatograms under long wave ultra violet light, with and without the presence of ammonia vapor. Determinations were based on the relative positions of spots on chromatograms, their color, and their color changes under the above conditions. The major components have been identified as flavonoids, (Powell and Tsang, 1966) but no specific chemical characterizations have been accomplished.

Just two species are known for *Pericome*, *Amauria*, and *Eutetras*. One species of *Pericome* has been examined chromatographically. Both species of *Amauria* and *Eutetras* have been sampled, and each produces a distinctive chromatographic pattern. Figures 11-13 emphasize what are believed to be unique compounds so that generic differences of chromatographic patterns can be gauged.

The simple pattern data referred to here certainly do not represent demanding evidence for the congeneric status of *Laphamia* and *Perityle*, but the chemical similarity between these two genera does emphasize their essential unity especially as compared with related genera.



Perhaps most important is the chemical comparison of the proposed Sect. *Pappothrix* (traditional *Laphamia*) with other *Laphamia* and *Perityle* species. The cumulative chromatographic profile of *Pappothrix* is every bit as different as is that of *Perityle* from *Laphamia*, even though the chemistry of all three groups of species is similar. And, as mentioned above, in spite of the unique *Pappothrix* pappus type, the similarities of this group to other *Laphamia* are so overwhelming that one can not consider *Pappothrix* as a genus. Additional chemical evidence, with appropriate taxonomic discussions, will be presented elsewhere (Powell, unpublished).

Evidence regarding the generic relationships within subtribe Peritylanae is being accumulated, but at present it seems clear that the treatment of *Laphamia* and *Perityle* as a single genus is most desirable. Accordingly, it is necessary to make appropriate nomenclatural changes at this time in order to facilitate taxonomic preparations.

Morphological and chemical evidence suggest the recognition of three subgeneric groups within *Perityle*. These are as follows:

PERITYLE Sect. PAPPOTHRIX A. Gray, Pl. Wright. 1: 100. 1852.

TYPE: *Laphamia rupestris* A. Gray.

Pappus of (10) 20-35 bristles; achenes flattened to nearly cylindrical, but typically 2-4 angled, margins not strongly calloused, margins subglabrous to short-pubescent.

PERITYLE Sect. **Laphamia** (A. Gray) Powell, comb. nov.

Laphamia A. Gray, Pl. Wright. 1: 101. 1852.

TYPE: *Laphamia lindheimeri* A. Gray.

Pappus absent or of 1-2 (3) bristles, often with inconspicuous, vestigial squamellae; achenes flattened, margins conspicuously to inconspicuously calloused, margins subglabrous to short-pubescent.

PERITYLE Sect. PERITYLE.

TYPE: *P. californica* Benth., Bot. Sulph. 23. 1844.

Pappus a crown of lacinate, hyaline squamellae and 0-2(3) bristles; achenes flattened, margins conspicuously to inconspicuously calloused, margins typically strongly ciliate, rarely short-pubescent.

Figures 8-13. Representative chromatographic patterns of the proposed sections of *Perityle* and related genera. Fig. 8. *P. vitreomontana* (Sect. *Pappothrix*). Fig. 9. *P. congesta* (Sect. *Laphamia*). Fig. 10. *P. vaseyi* (Sect. *Perityle*). Darkened spots depict compounds which are believed to be produced in common by the various species of all 3 sections of *Perityle*. Fig. 11. *Pericome caudata*. Fig. 12. *Amauria rotundifolia*. Fig. 13. *Eutetras pringlei*. Stippled spots depict compounds which are believed to be unique for the respective genera. Numbers (8-13) which denote the respective figures are placed at the point where extracts were applied to chromatograms.

I propose the following combinations to complete the record of known species transferred to *Perityle* Benth.

PERITYLE LINDHEIMERI (A. Gray) Shinnars var. **halimifolia** (Gray) Powell, comb. nov. *Laphamia halimifolia* A. Gray, Pl. Wright. 1: 100. 1852. *P. halimifolia* (A. Gray) Shinnars, Southw. Natl. 4: 204. 1959.

PERITYLE **cinerea** (A. Gray) Powell, comb. nov. *Laphamia cinerea* A. Gray in Torr. Bot. Mex. Bound. 82. 1859. *Pappothrix cinerea* (A. Gray) Rydb. N. Amer. Fl. 34: 27. 1914.

PERITYLE **inyoensis** (Ferris) Powell, comb. nov. *Laphamia inyoensis* Ferris, Contrib. Dudley Herb. 5: 104. 1958.

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