GENERIC LIMITATIONS IN THE HOFMEISTERIA COMPLEX (Compositae - Eupatorieae) [1]

R. M. King [2] and H. Robinson [3]

The genus Hofmeisteria (Compositae-Eupatorieae-Eupatoriinae) was established by Walpers in 1847 to include two species, H. fasciculata, and H. (Phania) urenifolia. Of these, H. urenifolia was shortly removed to the genus Fleischmannia on the basis of differences in the pappus (Schultz Bipontinus, 1850). Again on the basis of pappus the genus Malperia S. Watson (1889) has been reduced to synonymy under Hofmeisteria by Johnston (1924). Podophania Baillon (1880) a genus closely resembling Hofmeisteria has been maintained in the subtribe Piquerinae on the basis of supposedly unappendaged anthers.

The present study is an attempt to redefine the limits of these various genera and evaluate the various characters by which they have been distinguished. Monographic studies of the genera are intended to appear separately.

In addition to the regular observations, detailed examinations of the dissected floral parts were made under the compound microscope. Semi-permanent slides were made using Hoyer's Solution (Anderson, 1954). This mounting medium has the advantage of being both water miscible and a clearing agent.

The genus Hofmeisteria is usually distinguished by the pappus consisting of intermixed aristate and squamate bristles. Hofmeisteria, as typified by H. fasciculata (Benth.) Walp., has the following characters: woody sub-shrub. Leaves in 2/5 phyllotaxy (congested at flowering nodes, appearing whorled), petiolate, mostly pinnately to bipinnately dissected; somewhat fleshy. Peduncles rather long, bearing a few minute leaves, becoming lateral by innovation. Heads solitary, massive. Phyllaries numerous, multiseriate, densely imbricated, narrowly lanceolate. Florets 100-150. Corolla narrowly tubular glabrous, with short lobes. Anther sacs long and slender with large erect appendages, exothecial cells often longer than wide. Pollen tricolpate, surface nearly smooth. Style branches elongate, blunt; slightly enlarged

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at the tips, cells of the surface only slightly bulging, basal node of style glabrous. Pappus in a single series, 2-3 long scabrate setae and 3-4 short squamae with lacerate margins. Achenes 5 ribbed, ribs setose, sub-cuticular cells of ribs and lateral walls with many minute punctations; carpopodium somewhat flaring, with many rows of short or transversely elongate cells; basal foramen prominent, with an even margin.

There are seven species which agree in most of these characters with Hofmeisteria fasciculata. These fall into three groups. The first group consists of the species H. crassifolia S. Wats. and H. filifolia Johnston. These are characterized by rather fleshy leaves with narrow to filiform segments. In both species the pappus is differentiated into 3-5 long setose members and intervening groups of short setae. The intervening setae of H. filifolia tend to be very short. These setae, though separate to the base, are the equivalent of the squamose members of H. fasciculata.

Hofmeisteria filifolia is unlike any of the other seven species of Hofmeisteria recognized here in the variation of phyllotaxy and inflorescence. Clustering of the leaves at the flowering nodes tends to be less evident and the peduncles tend to be apical and often bear larger leaves than are typical for the genus. In spite of these differences, the species closely agree with others of Hofmeisteria in the basic characters: pollen, glabrous corolla tube; and the cellular structure of the acene.

The second group of species can be characterized by the thin lamina of the leaves and appendages of the anthers being folded over and superficially appearing absent. Podophania dissecta has been placed in the subtribe Piquerinae because of the supposed lack of appendages on the anthers. Microscopic examination reveals appendages as large as those of other species of Hofmeisteria. The appendages, however, are folded over to form a hood on the end of the anther. Podophania also differs from typical Hofmeisteria by the possession of about 12-15 setose pappus bristles of rather uniform length. In view of the variations in pappus structure already evident in the genus Hofmeisteria, we propose the following new combination:

Hofmeisteria dissecta (Hook. and Arn.) R. M. King and H. Robinson Comb. nov. (Phania dissecta Hook. and Arn. Bot. Beech. Voy. 433. 1841). Hooker & Arnott compared P. dissecta with their P. (Hofmeisteria) urenifolia, and while

noting the pappus difference, state it was "doubtless a congener." Rose (1895) also remarked on the resemblance of Podophania to Hofmeisteria.

Hofmeisteria sinaloensis Gentry very closely resembles H. dissecta in the texture of its leaves. Although not mentioned in Gentry's original description, H. sinaloensis also possesses the cucullate appendage on the anther. It differs from H. dissecta clearly by the pappus which is differentiated into 5 or 6 long setae members with intervening short, very lacerate squamae.

The third group of species showing the essential characters of the genus Hofmeisteria can be characterized by the pappus consisting of 5-6 long setae with only vestigial intervening members, and leaves with thin laminae. Here may be found H. urenifolia (Hook.& Arn) Walpers which had originally been placed in the genus Hofmeisteria by Walpers. In spite of the difference in pappus structure we feel that the proper position of this species is in Hofmeisteria rather than in Fleischmannia where it has more recently resided.

Hofmeisteria schaffneri (A. Gray) R. M. King and H. Robinson, comb. nov. (Fleischmannia schaffneri A. Gray, Proc. Am. Acad. 41: 101, 1881) is closely related to H. urenifolia differing primarily by the densely glandular pubescent stem. The leaves in H. schaffneri tend to be more dissected than in H. urenifolia.

Hofmeisteria standleyi (Blake) R. M. King and H. Robinson; comb. nov. (Fleischmannia standleyi Blake, Contr. U. S. Nat. Herb. 22: 590, 1924) also differs from H. urenifolia by densely glandular pubescent stems, but has leaves only lobed and dentate, not dissected.

As thus conceived Hofmeisteria includes a great range of variation in pappus structure. When compared with the following groups with which the species of Hofmeisteria have been confused, numerous other characters are available to support the present concept.

Fleischmannia Sch. Bip. has been characterized by a pappus consisting of a reduced number of setae, usually 5 or 10. The three species remaining in the genus are F. arguta (H.B.K.) Rob. (= F. rhodostylis Sch. Bip. type species) F. microcephala

Brandg. and F. repens Rob. These are a heterogeneous assemblage of species which, however, share a number of basic characters that contrast with those of Hofmeisteria, and the three species may prove to be a natural group. In this group the leaves are all simple, spirally arranged or opposite; the flowering nodes and peduncles are not strongly differentiated; the inflorescense is polycephalic; the corolla tube bears hairs on the upper portion (these are very highly developed in F. repens); the pollen is distinctly spinose; the carpopodium is rounded to only slightly flaring and consists in part of vertically elongate cells. Within the genus as presently understood there remain such variations as pappus consisting of about 10 setae in F. microcephala as compared with 5 in the other two species; corolla much inflated in the upper portion, very narrow below in F. repens as opposed to narrowly tubular in the other two species; anther sacs very elongate in F. arguta as opposed to to shorter sacs in F. repens and very short sacs in F. microcephala; cells of the carpopodium rather thin walled in F. repens as opposed to very thick walled in the other two species.

The genus Malperia S. Wats. resembles Hofmeisteria by the presence of a pappus differentiated into long setae and short squamae. It differs most noticeably by having sessile linear sub-entire leaves. In addition to this, it can be noted that the leaves are not clustered at the flowering nodes, and the peduncles are not strongly differentiated; the inflorescense is polycephalic; the corolla tube bears glandular hairs; the pollen is distinctly spinose; the carpopodium has a very large foramen, and is often strongly asymmetric; the cells of the carpopodium are relatively short vertically. In its various characters Malperia shows much greater similarity to the genus Stevia than to Hofmeisteria.

There remain three species which have been placed in the genus Hofmeisteria which do not resemble any of the previously discussed genera. For these species we propose the following new genus:

Pleurocoronis R. M. King and H. Robinson genus novum (Compositarum-Eupatorieae-Eupatoriinae) Folia inferiora opposita; alia subopposita vel alterna, capitula homogama discoidea; flores omnes hermaphroditi, fertiles, regulares. Antherae cum appendice apicali. Achaenia 5 angulata, faciebus lateralibus dense hirsutis. Pappus mixtus interdum biseriatus.

Woody sub-shrub. Leaves simple to compound, petiolate,

serrate, opposite in lower portions of plant becoming alternate above. Peduncles not strongly differentiated, bearing alternate leaves. Inflorescence polycephalic. Heads many flowered. Phyllaries in multiple series, outer one short ovate, inner lanceolate. Corolla slender, tubular with glandular hairs on the outer surface. Anthers elongate with large erect appendages, exothecial cells iso-diametric or slightly wider than long. Pollen tricolpate, distinctly spinose. Style branches elongate, slightly enlarged at the tip, cells at the surface slightly bulging; basal node of style glabrous. Pappus of 3-6 long scrabrate setae with intervening short erosely dentate squamae, sometimes bearing numerous additional setae in a distinct inner series. Achenes 5 ribbed, lateral surfaces densely pubescent, sub-cuticular cells without minute punctations except on the ribs; carpopodium somewhat rounded, usually asymmetric, cells vertically elongate; basal foramen shallow, indistinct.

Pleurocoronis pluriseta (Gray) R. M. King and H. Robinson comb. nov. Type species (Hofmeisteria pluriseta Gray Pacif. Rail. Rep. 4: 96, 1857).

The only significant character shared by Pleurocoronis and Hofmeisteria is the similar form of the pappus. A review of numerous other characters both macroscopic and microscopic indicates there is no close relationship between these two genera. The phyllotaxy is different; Hofmeisteria is monocephalic while Pleurocoronis is polycephalic; the pubescence of the corolla is different; the pollen is different; and the structure of the achene is very different. Pleurocoronis is particularly distinct in the structure of the achene, differing from most genera of the Eupatorieae which we have seen, in the combination of dense pubescence on the lateral walls and the lack of minute punctations. These characters do occur again in the genus Brickellia. It is possible that Pleurocoronis and Brickellia are closely related, but Brickellia is easily distinguished by 10 ribbed achenes and carpopodia with shorter cells and a large even-margined foramen.[4]

[4] In Brickellia we have noticed a further possibly significant distinguishing character regarding the node which occurs at the base of the style which is often enlarged to close the lower end of the corolla tube. In Pleurocoronis and in all other genera we have seen, the stylar node is glabrous. In the species of Brickellia we have seen, the stylar node is densely covered with setae.

A second species of the genus, Pleurocoronis laphamioides (Rose) R. M. King and H. Robinson comb. nov. (Hofmeisteria laphamioides Rose, Contr. U. S. Nat. Herb. 1: 79, 1890), is distinguished from P. pluriseta by the deltoid to reniform lamina with 15 or more marginal teeth. In P. pluriseta the the lamina of the leaves is small, narrowly ovate with usually five or less teeth.

Pleurocoronis gentryi (Wiggins) R. M. King and H. Robinson, comb. nov. (Hofmeisteria gentryi Wiggins, Contr. Dudley Herb. 4: 25. 1950) is easily distinguished from the other two species by its dissected leaves.

The genera of the Hofmeisteria complex as presently recognized can be distinguished by the following key:

1. a. Inflorescence monocephalic; corolla glabrous; pollen nearly smooth; leaves usually clustered at flowering nodes----------Hofmeisteria.

   b. Inflorescence polycephalic; corolla with hairs or glands externally, at least on the lobes; pollen spinose; leaves not clustered at flowering nodes----------2.

2. a. Pappus of 5-10 setose members in a single series, without squamose members, corolla with nonglandular hairs in the upper part----------Fleischmannia.

   b. Pappus in one or two series, of three or more setose members with intervening or subtending squamose members; corolla with numerous glandular hairs---3.

3. a. Lateral surfaces of the achene covered with dense pubescence; pappus in one or two series, squamose members often subtending some of the setose members; leaves petiolate, often opposite in the lower portions of the plant----------Pleurocoronis.

   b. Setae restricted to the ridges of the achene; pappus members in a single series, squamae only overlapping the setose members; leaves sessile, rarely opposite----------Malperia.

Since some of the characters involved in this study have not been previously used in delimiting Composite genera, and since

some of the traditional characters seem misleading, the following comments are offered. These comments are admittedly often based on limited observations of other tribes of the Compositae.

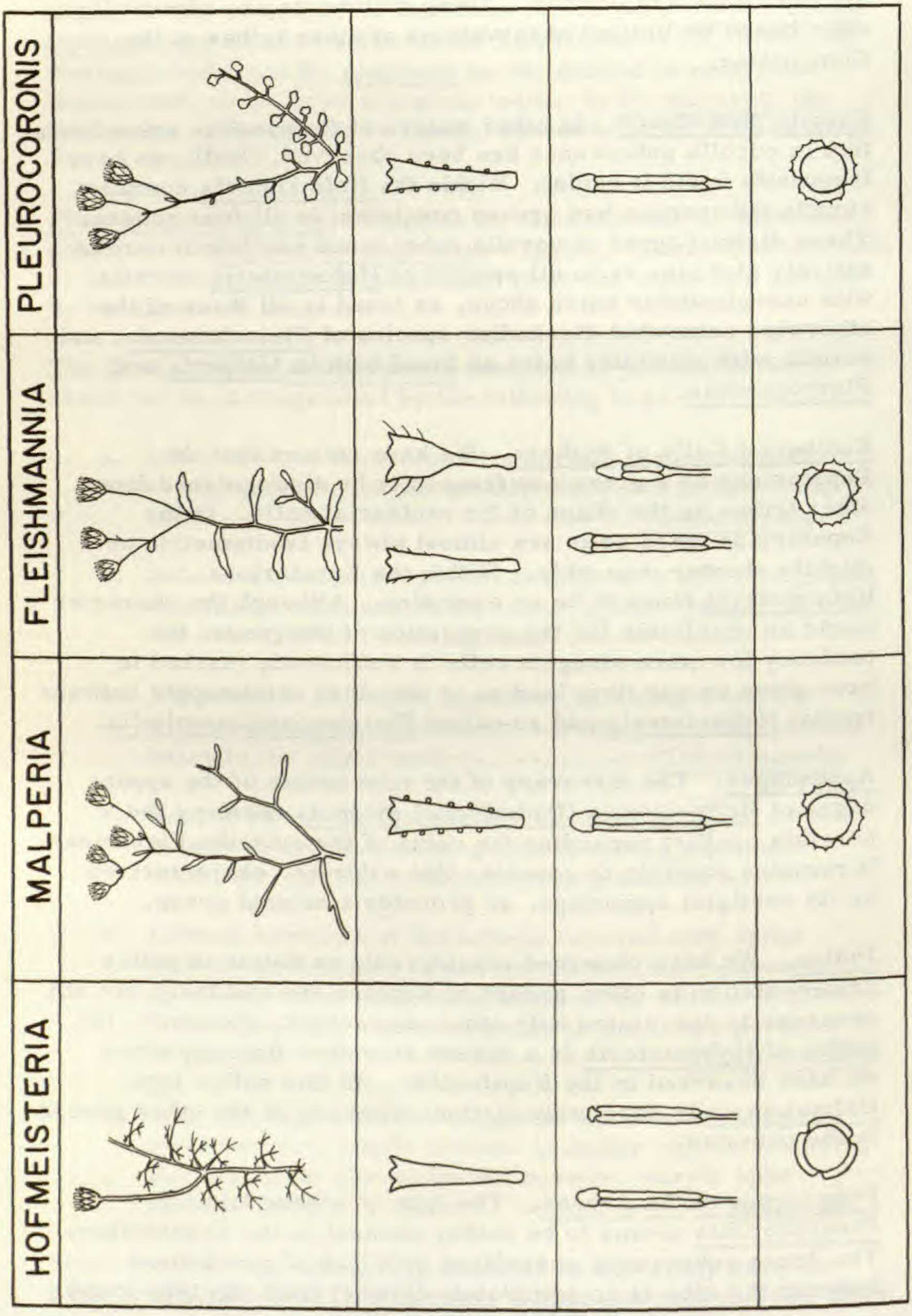
Corolla pubescence. In other genera of Compositae some variation in corolla pubescence has been observed. Still, we have frequently found it useful. Within the Hofmeisteria complex, corolla pubescence has proven consistent in all four genera. Three distinct types of corolla pubescence are found; corolla entirely glabrous as in all species of Hofmeisteria; corolla with non-glandular hairs above, as found in all three of the otherwise somewhat dissimilar species of Fleischmannia; and corolla with glandular hairs as found both in Malperia and Pleurocoronis.

Exothecial Cells of Anthers. We have noticed that the Eupatorieae as a group can frequently be distinguished from other tribes by the shape of the exothecial cells. In the Eupatorieae these cells are almost always isodiametric or slightly shorter than wide. Within the Eupatorieae, Hofmeisteria tends to be an exception. Although the character would be unreliable for the separation of the genus, the tendency for more elongate cells is sufficiently marked to have given us our first lead as to the close relationship between typical Hofmeisteria and so-called Fleishmannia urenifolia.

Appendages. The discovery of the true nature of the appendages of Hofmeisteria (Podophania) dissecta resolves the possible conflict regarding the value of the subtribe Piquerinae. It remains possible to consider this subtribe, characterized by its vestigial appendage, as probably a natural group.

Pollen. We have observed considerable variation in pollen ornamentation in other groups of Eupatorieae and these are not necessarily correlated with other characters. However, the pollen of Hofmeisteria is a degree smoother than any other we have observed in the Eupatorieae. In this pollen type Hofmeisteria is absolutely distinct from any of the other genera in the complex.

Pubescence of the Achene. The type of achene found in Pleurocoronis seems to be rather unusual in the Eupatorieae. The dense pubescence correlated with lack of punctations between the ribs is so completely distinct from the type found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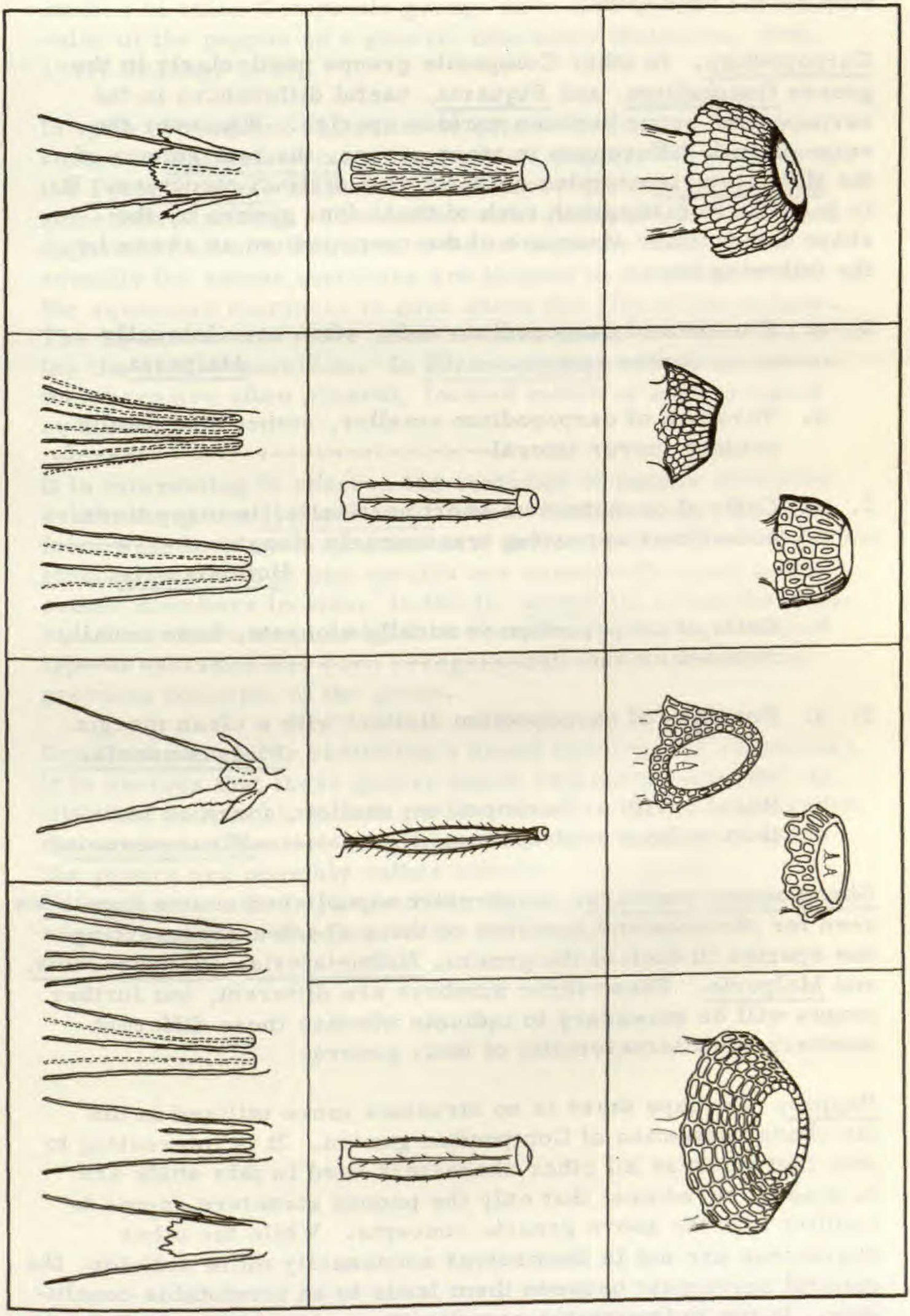
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in the other three genera of the complex that close relationship seems impossible.

Carpopodium. In other Composite groups particularly in the genera Gnaphalium, and Piqueria, useful differences in the carpopodium occur between various species. Whatever the value of such differences in other groups, the four genera of the Hofmeisteria complex each shows a distinct structure. It is possible to distinguish each of these four genera by the shape and cellular structure of the carpopodium as shown by the following key:

1. a. Foramen of carpopodium wide, often born laterally Malperia.

   b. Foramen of carpopodium smaller, sometimes hardly evident, never lateral----------2.

2. a. Cells of carpopodium short vertically, in many tiers, sometimes appearing transversely elongate---------- Hofmeisteria.

   b. Cells of carpopodium vertically elongate, base usually rounded or bud-like----------3.

3. a. Foramen of carpopodium distinct with a clean margin Fleischmannia.

   b. Basal cavity or carpopodium shallow, foramen indistinct without evident margin----------Pleurocoronis.

Chromosome numbers. Apparently unpublished counts have been seen for chromosome numbers of three species representing one species in each of the genera, Hofmeisteria, Pleurocoronis, and Malperia. These three numbers are different, but further counts will be necessary to indicate whether these different numbers are characteristic of their genera.

Pappus. Perhaps there is no structure more utilized in the the characterization of Compositae genera. It is interesting to note that whereas all other characters used in this study are in general agreement that only the pappus structure seems to conflict with the above generic concepts. While the other characters are not in themselves necessarily more reliable, the general agreement between them leads to an irrefutable conclusion. In the Hofmeisteria complex the pappus structure is

totally unreliable above the species level. A number of recent studies in other Composite groups have also questioned the value of the pappus as a generic character (Shinners, 1946, 1947; DeJong, 1965).

In spite of frequent reference to pappus consisting of two series in Hofmeisteria, this situation actually occurs only in the Pleurocoronis element. Even here, the inner series is sometimes lacking. The setose and squamose members are apparently often considered to be in separate rows, but actually the setose members are located in the same series as the squamose members in gaps above the ribs of the achene. The squamose members often broaden above the base and overlap the setose members. In Pleurocoronis additional setose members are often present, located inside of uninterrupted squamae.

It is interesting to observe the variation of pappus structure within the genus Hofmeisteria. Here variation may be seen from well developed squamae to a series of distinct filamentous structures which in one species are essentially equal to the setose members in size. In the H. urenifolia group the squamose members are vestigial or completely lacking. This type of variation has been recognized to some extent in the previous concepts of the genus.

Conclusions: After reviewing a broad spectrum of characters, it is obvious that these genera which resemble each other in little but pappus structure are not closely related. In view of the number of consistent differences, relationships between the genera are possibly rather remote. The genus Hofmeisteria seems particularly distinctive and perhaps future reorganization of the Eupatoriae will reflect this.

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