

SUPPLEMENT TO THE SYSTEMATICS OF THE HELIANTHEAE (COMPOSITAE) ¹

Por TOD F. STUESSY ²

Since the completion of a revised subtribal classification of the tribe Heliantheae (Stuessy, in press) for the Reading Symposium on the Compositae in July of 1975, a number of new papers have been published on the systematics of the tribe. This new information falls into four general categories: (1) speculations on relationships among the newly recognized subtribes; (2) addition of a new subtribe; (3) additions of new genera; and (4) new generic transfers. The purpose of this paper is to review these new developments and comment on their significance for the systematics of the Heliantheae.

RELATIONSHIPS AMONG THE NEWLY RECOGNIZED SUBTRIBES

An important new overview of relationships among the subtribes of the Heliantheae has been provided by Baagøe (1977) by use of ligule microcharacters. This contribution is especially valuable, because the manuscript on the Heliantheae for the Reading Symposium (Stuessy, in press) was available to Dr. Baagøe during her study, and she was able to relate the new data to the subtribal classification of the tribe. Many specific comments on relationships are contained in her paper, but this review will focus only on some of the broader implications. Before these are examined, however, a few cautions need to be raised.

¹ It is a pleasure to dedicate this paper to Dr. Angel L. Cabrera, one of the outstanding synantherologists of the world, and the unqualified authority on South American Compositae. Financial support from NSF Grant DEB75-20819 is gratefully acknowledged.

² Department of Botany, The Ohio State University, Columbus, Ohio 43210, U.S.A.

The use of microcharacters of ligules to assess relationships in Compositae is essentially a new approach. When any new comparative data are used to determine systematic relationships, it is important that an understanding of their variability be obtained. This is the foremost caution. Because our knowledge of ligule microcharacters is just beginning, we must strive for increased sample sizes to put the data in proper systematic perspective. The other cautions relate to the importance of having a biological understanding of the observed *surface* structures with regard to: (1) subepidermal cellular and tissue architecture; (2) developmental patterns and relationships of the cells; and (3) functional significance (especially in UV reflectance and in physiological roles related to temperature and water stress). An appreciation of these factors is most important for distinguishing evolutionary homologies (upon which any classification must be based) from parallelisms due to similar environmental selection pressures.

With these several cautions in mind, the implications of the ligule microcharacters for the systematics of the Heliantheae can be examined. Four main topics will be considered: (1) the relationships of specific subtribes; (2) the correlation with the three main evolutionary lines of the tribe proposed by Stuessy (in press); (3) the placement of subtribes not accepted in the Heliantheae by Stuessy (in press) nor in the Senecioneae by Nordenstam (in press); and (4) the relationship of the Heliantheae to the Anthemideae.

Relationships of Specific Subtribes

Although results are given by Baagøe (1977) of ligule microcharacters on 13 of the 15 subtribes (Milleriinae and Fitchiinae have not been examined) recognized by Stuessy (in press), discussions here will be confined only to three subtribes: Coreopsidinae, Neuro-laeninae, and Verbesininae.

Based primarily on cytochrome *c* data (Ramshaw et al., 1972; Boulter, 1974; Ramshaw and Boulter, 1975) for *Guizotia abyssinica* (Coreopsidinae) and *Helianthus annuus* (Helianthinae), Turner and Powell (in press; see also Turner, 1975) suggested that the Coreopsidinae should be elevated to tribal status. On chromosomal and gross morphological grounds, Stuessy (in press) treated the Coreopsidinae and Fitchiinae as together forming a separate evolutionary line within the tribe. Emphasis was placed on the $x = 12$ base number, brown-orange longitudinal striae of the phyllaries and florets (the former often with scarious margins), black to brown anthers, etc. In terms of generalized tribal features, however, the Coreopsidinae fit clearly within the Heliantheae with their opposite leaves, large heads, paleaceous receptacles, and abaxially keeled and tailless anthers. The rationale for elevating the subtribe to the tribal

level is based primarily on the cytochrome *c* data in which the differences in amino acid sequences between *Guizotia* and *Helianthus* are greater than those separating some *families* of angiosperms.

Although these data are suggestive, they are inconclusive because of several factors. (1) Virtually nothing is known about the rates of evolution of cytochrome *c* in higher plants. In higher animals, the strong fossil record correlates well with observed changes in cytochrome *c*, and rates of evolution seem fairly constant (e. g., Wilson and Sarich, 1969; Zuckerkandl, 1976). In plants, however, the absence of a detailed fossil record makes it impossible to know if the rate of evolution (even in a particular section of the angiosperm evolutionary line) is the same as in animals. (2) The two species of Heliantheae examined are cultivated, and both have undergone artificial selection by man for many generations. The effect this may have had upon the sequence of cytochrome *c* is unknown. (3) The sample size for the tribe as well as for the family is so small as to make evaluations of relationships based upon available data premature. The results from analysis of ligule microcharacters, in which all of the seven genera of the Coreopsidinae studied have epidermis types characteristic of other Heliantheae, agree with this conclusion.

The Neurolaeninae were created as a subtribe jointly by Stuessy, Turner and Powell (in Stuessy, n press). Although the general concept of the subtribe as belonging in the Heliantheae was mutually accepted, the included genera differed. Data from ligule microcharacters on one species each of *Clappia*, *Schistocarpha*, and *Zaluzania* (all genera included in the subtribe by Stuessy, in press; the first only included by Turner and Powell, in press) support the inclusion of this subtribe in the Heliantheae. Recent studies by Olsen (1977a) on *Zaluzania* recommend a transfer of the genus back to the Verbesininae as a relative of *Viguiera*. The data from ligule microcharacters, however, suggest a closer tie to the Galinsoginae. This would be compatible with a position in the Neurolaeninae which is a close subtribal relative of the Galinsoginae (Stuessy, in press; see also comments later in this paper).

The relevance of the ligule microcharacters to the systematics of the Verbesininae is in suggesting that the evolutionary core of the subtribe centers around *Verbesina*. This is in agreement with the same idea (Stuessy, in press) based upon gross morphological considerations. The group of genera containing *Montanoa* was regarded as an evolutionary line specialized for modifications of the paleae. The derived ligule microcharacters of *Montanoa* do not contradict this interpretation.

Helpful surveys of other subtribes reveal inconsistencies with the ligule microcharacter data in some genera and their placement in the new classification, and these occur especially in the Ambrosiinae, Engelmanninae, and Melampodiinae. Because of the historical

systematic problems attending these subtribes (cf. Stuessy, 1973, for an historical review), a fuller survey of species and genera is needed before the results can be evaluated. Suffice it to mention that additional studies on the relationships of genera in these subtribes are needed.

Correlation of Ligule Microcharacters with the Main Evolutionary Lines of the Heliantheae

On of the conclusions of the morphological and chromosomal review of the Heliantheae (Stuessy, in press) is that three main evolutionary lines have existed within the Heliantheae: (1) the Verbesininoid line with chromosome numbers based on $x = 15, 16, 17$; (2) the Galinsoginoid line with $x = 8, 9$; and (3) the Coreopsidinoid line with $x = 12$. The data from ligule microcharacters support this general concept. Two principal types of epidermal ensembles are recognized (Baagøe, 1977); Group 1, characterized by ligules with thick mesophyll, stomata, and with cells with high papillae and thick and straight to slightly undulating or septate lateral walls, and containing the Ecliptinae, Helianthinae, Melampodiinae ("presumably"), Verbesininae, and Zinniinae; Group 2, characterized by ligules with mesophyll, no stomata (only rarely present), and with cells with low papillae and thin and straight to slightly undulating or sinuate lateral walls, and containing the Bahiinae, Gaillardiiinae, Galinsoginae, Neurolaeninae, and Madiinae. These groups correspond to two of the evolutionary lines proposed by Stuessy (in press), with Group 7 representing the Verbesininoid line and Group 2 the Galinsoginoid line. An exception is that the microcharacters relate the Gaillardiiinae more closely to the Galinsoginoid line than to the Verbesininoid line. The Engelmanniinae, likewise, have ligule microcharacters similar to that of Group 1 (Verbesininoid line) although they have been placed by Stuessy (in press) in the Galinsoginoid line. The problem of proper relationship of these two subtribes needs to be pursued further. The Coreopsidinae are intermediate in ligule microcharacters in that they have yellow-orange pigments and distinct UV patterns (all characteristics of Group 1), and thin cell walls and mesophyll, and sinuate (rarely septate) lateral walls (features of Group 2). This agrees with their placement in a separate evolutionary line.

Relationships of Subtribes Accepted Neither in the Heliantheae nor in the Senecioneae

During the Compositae Symposium at Reading, Turner and Powell (in press) recommended that the entire tribe Helenieae be dismantled, and that all the genera be referred to other tribes.

Many of the taxa were transferred to the Senecioneae and many to the Heliantheae. Although some of the transfers to the Senecioneae were accepted by Nordstam (in press), others were not. Likewise, although some of the transfers to the Heliantheae were accepted without reservation by Stuessy (in press), such as the Gaillardinae, others were not, and the Bahiinae were accepted only "by default". The problem of these "orphan subtribes" was discussed at some length at the Reading Symposium, and some interest for a new tribe to house these "orphans" was generated. Because *Helenium* (the type genus of the Helenieae) seems clearly to belong in the Heliantheae, a new name for such a tribe must be sought, and the "Arniceae" has been suggested (Nordenstam, in press). This tribe would probably contain the Arnicinae, Bahiinae, Chaenactidinae, Eriophyllinae, Fleveriinae, and Peritylinae. The ligule microcharacters (Baagøe, 1977) do not provide a solution to this problem, but some of the subtribes (e.g., Bahiinae, Peritylinae) have features of both the Heliantheae and the Senecioneae. Others tend more toward one tribe or the other. This problem is being given further attention by several workers (e. g., Nordenstam, Strother, Stuessy).

Relationship of the Heliantheae to the Anthemideae

The relationship between these tribes is not an obvious one, except that some of the Anthemideae do possess paleae (Heywood and Humphries, in press). Nonetheless, the Anthemideae is a close-knit unit that is under no threat of dismemberment. Data from ligule microcharacters, however, suggest some connection between the two tribes (Baagøe, 1977). The chromosomal base of the Anthemideae is clearly $x = 9$ (Heywood and Humphries, in press), as it is in at least part of the Galinsoginoid line ($x = 8, 9$) of the Heliantheae, especially in the Ambrosiinae which on morphological and chemical (Mabry and Bohlmann, in press) grounds also is somewhat similar to the Anthemideae. Another thought-provoking point is that the genus *Hippia* of the Anthemideae is morphologically very similar to *Parthenium* of the Ambrosiinae. If the similarity between these two genera is due to evolutionary parallelism instead of homology, then this leads to interesting ecological questions. Further understanding of the relationships between these two tribes is needed.

A NEWLY DESCRIBED SUBTRIBE

A significant recent contribution to the systematics of the Heliantheae is the description of a new subtribe, the Espeletiinae, by Cuatrecasas (1976). Within this new subtribe are seven genera (*Espeletia*, *Libanothamnus*, *Ruilopezia*, *Tamania*, *Carramboia*, *Espeletiop-*

sis, and *Coespeletia*), all of which were included earlier in *Espeletia*, an the last five of which are described as new in the publication. Although the recognition of seven distinct genera within *Espeletia* and their collective elevation to subtribal rank deserves careful study a convincing case has not yet been made. What must be presented is evidence for substantiation of the new genera within the context of the Melampodiinae (e.g., how do these new genera compare in degree of morphological difference with the subgeneric taxa in *Melampodium?*), as well as a similar comparison of the new subtribe with all other subtribes of the Heliantheae (especially the monotypic Fitchiinae). It will also be important to learn how *Espeletia s. lat.* and each of the segregate genera relate to *Polymnia*, which has been treated previously (Stuessy, 1973) as the closest generic relative.

NEW GENERIC ADDITIONS

Two new genera have been described recently in the Heliantheae: *Henricksonia* (Turner, 1977) and *Hybridella* (Olsen, 1977 b). *Henricksonia* belongs clearly to the subtribe Coreopsidinae and would be placed in Group 2. A feature of interest of the genus is the paleaceous pappus, which is uncommon in the Coreopsidinae. *Hybridella* has been re-established as a genus of two species near *Viguiera* in the subtribe Helianthinae (Group 1), although it previously was treated as a subgenus of *Zaluzania* (Robinson and Greenman, 1899).

GENERIC TRANSFERS

Three transfers of genera of the Heliantheae to positions in other subtribes or tribes have been suggested. *Axiniphyllum* was placed finally by Stuessy (in press) in the subtribe Verbesininae (Group 1), despite the fact that in all preliminary drafts of this same manuscript it had been positioned near *Sigesbeckia* of the subtribe Melampodiinae. The genus does have 5 outer phyllaries, stipitate-glandular stems and peduncles, and subauriculate leaf bases, which are all characteristics of *Rumfordia*, *Sigesbeckia* and *Trigonospermum* of the Melampodiinae. Discussions of the relationships of *Axiniphyllum* with B. L. Turner recently have revealed that he independently concluded that the genus belonged near *Rumfordia*, which is also of the Melampodiinae. With this supporting independent conclusion, the original viewpoint of placing *Axiniphyllum* in Group 2 of the Melampodiinae is revived and accepted. Prof. Turner also has a revision of the genus in preparation, in which the generic relationships with *Rumfordia* will be explored more fully.

Bebbia has been revised recently by Whalen (1977), in which she transfers the genus from the subtribe Neurolaeninae to the Galinsoginae. She believes that the closest generic relatives of *Bebbia* are *Dyscritothamnus* (treated by Stuessy, in press, in the Neurolaeninae) and *Tridax* (Galinsoginae). Because of these ties to genera, in different subtribes, she suggests that it might "prove taxonomically more expedient" to include the Neurolaeninae (plus the Varillinae of Turner and Powell, in press) in the Galinsoginae. The Neurolaeninae are very close to the Galinsoginae, but to include the former in the latter would enlarge the concept of the Galinsoginae beyond useful limits. A resolution of this problem must be sought by detailed revisionary studies on the other poorly known genera of both subtribes (such as *Calea*, *Schistocarpha*, etc.) followed by a review of available comparative data.

Dugesia was put in the subtribe Engelmaiinae in the treatment (Stuessy, in press) of the Heliantheae, but it was placed there by default, and its proper affinities were uncertain. A recent study of the sesquiterpenes of *Dugesia* (Bohlmann and Zdero, 1976) has revealed a new eremophilane derivative which is similar to those so far known only from the tribe Senecioneae. These data, plus the obvious difficulty of finding generic ties to *Dugesia* in the Heliantheae, suggest that the genus may belong more properly in the Senecioneae.

LITERATURE CITED

- BAAGOE, J., 1977. Taxonomical application of ligule microcharacters in Compositae. *Bot. Tidsskrift*, 71:193-223.
- BOHLMANN, F., and C. ZDERO, 1976. Ein neues sesquiterpenlacton aus *Dugesia mexicana* Gray. *Chem. Ber.*, 109:2651-2652.
- BOULTER, D., 1974. The use of amino acid sequence data in the classification of higher plants, p. 211-216. In, G. Bendz and S. Santesson (eds.), *Chemistry in Botanical Classification*. Academic Press, N. Y.
- CUATRECASAS, J., 1976. A new subtribe in the Heliantheae (Compositae): Espeletinae. *Phytologia*, 35:43-61.
- HEYWOOD, V. H., and C. J. HUMPHRIES. In press. Systematics of the Anthemideae. In, V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), *The Biology and Chemistry of the Compositae*. Academic Press, London.
- MABRY, T. J., and F. BOHLMANN. In press. Summary of the chemistry of the Compositae. In, V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), *The Biology and Chemistry of the Compositae*. Academic Press, London.
- NORDENSTAM, B. In press. Systematics of the Senecioneae. In, V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), *The Biology and Chemistry of the Compositae*. Academic Press, London.
- OLSEN, J., 1977a. Systematics and generic affinities of *Zaluzania* (Asteraceae: Heliantheae). *Bot. Soc. Aerm. Publ., misc. ser.*, 154:66.
- OLSEN, J., 1977 b. Re-establishment of the genus *Hybridella* (Asteraceae: Heliantheae). *Madroño*, 24:29-36.

- RAMSHAW, J. A. M., and D. BOULTER, 1975. The amino acid sequence of cytochrome *c* from niger-seed, *Guizotia abyssinica*. *Phytochemistry*, 14:1945-1950.
- D. L. Richardson, B. T. Meatyard, R. H. Brown, M. Richardson, E. W. Thompson, and D. Boulter, 1972. The time of origin of the flowering plants determined by using amino acid sequence data of cytochrome *c*. *New Phytol.*, 71:773-779.
- ROBINSON, B. L., and J. M. GREEMAN, 1899. Revision of the genera *Montanoa*, *Perymenium* and *Zaluzania*. *Proc. Amer. Acad. Arts*, 34:507-534.
- STUESSY, T. F., 1973. A systematic review of the subtribe Melampodiinae (Compositae, Heliantheae). *Contrib. Gray Herb.*, 203:65-80.
- In press. Systematics of the Heliantheae. In, V. H. Heywood J. B. Harborne, and B. L. Turner (eds.), *The Biology and Chemistry of the Compositae*. Academic Press, London.
- TURNER, B. L. 1975. General summary and conclusions, págs. 792-796. In, D. E. Fairbrothers, T. J. Mabry, R. L. Scogin, and B. L. Turner, *The bases of angiosperm phylogeny: chemotaxonomy*. *Ann. Mo. Bot. Gard.*, 62:765-800.
- 1977. *Henricksonia* (Asteraceae-Coreopsidinae), a newly discovered genus with a paleaceous pappus from north-central Mexico. *Amer. J. Bot.*, 64: 78-80.
- TURNER, and A. M. POWELL. In press. Systematics of the Helenieae. In, V. H. Heywood, J. B. Harborne, and B. L. Turner (eds.), *The Biology and Chemistry of the Compositae*. Academic Press, London.
- WHALEN, M., 1977. Taxonomy of *Bebbia* (Compositae: Heliantheae). *Madroño*, 24:112-123.
- WILSON, A. C., and V. M. SARICH, 1969. A molecular time scale for human evolution. *Proc. Natl. Acad. Sci. U.S.A.*, 63:1088-1093.
- ZUCKERKANDL, E., 1976. Evolutionary processes and evolutionary noise at the molecular level. II. A selectionist model for random fixations in pro-teins. *J. Mol. Evol.*, 7:269-312.