# TRIBAL REVISIONS IN THE ASTERACEAE. IV.

## THE RELATIONSHIPS OF NEUROLAENA, SCHISTOCARPHA AND ALEPIDOCLINE.

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A number of genera placed in the Senecioneae have keeled anther appendages that mark them as relatives of the Helianthian-Helenian series. One small complex among these is further distinguished by paleaceous receptacles, having prominently graduated multiseriate involucres and having structures on the corollas that can be referred to as "Helianthian hairs". This complex includes the genera Neurolaena, Schistocarpha and Alepidocline.

Linneaus treated the first known member of the complex under the name Conyza lobata. The species was later transferred to Calea and then placed by Brown (1817) in a new genus, Neurolaena, with the following explanation, " . . . Calea lobata, which linneus, from the general appearance, I. conclude, rather than from actual examination of the plant in Clifford's Herbarium, had referred to Conyza; and having no specimen in his own Herbarium, the twofold error of supposing it to belong to Polygamia superflua, and to have a naked receptacle, remained uncorrected in all his subsequent works." Brown went on to say, "Its real structure was first pointed out by Professor Swartz, who consequently referred it to Calea, with the character of which it exactly agrees. This alteration is adopted in the first edition of Hortus Kewensis, where the generic character of Calea is modified, to admit those species that are without pappus; and by Gaertner, who limits the genus to C. lobata and C. jamaicensis, as the only species that correspond with the Linnean character. But as C. jamaicensis, the original species of Calea has been shown to have a pappus of a very different kind, it becomes necessary to give a new name to Calea lobata; . . ."

Cassini (1825) gave an admittedly poor disposition for the genus with the following statement, "Ce n'est gu'avec beaucoup d'hésitation que nous nous sommes décidé à comprendre ce genre dans notre tribu naturelle des Inulées, dont il s'éloigne sous plusieurs rapports, et surtout parce que le point de libération des filets des étamines se trouve précisément au sommet du tube de la corolle, tandis qu'il est beaucoup plus bas chez les autres Inulées. Ajoutons que les appendices basilaires de anthères sont nuls ou presque nuls; que le fruit et son aigrette sant très-analogues à ceux des Eupatoriées; que les stigmatophores, quo ique privés de glandes, ressemblent à ceux des

Adénostylées. Le Neurolaena semble avoir aussi quelques points de contact avec les Tagétinées et avec les Astérées. Le principal motif qui nous a déterminé à ranger le Neurolaena. parmi les Inulées, c'est que les deux espèces de Cassinia que nous avons observées, nous ont offert quelques-unes des anomalies du Neurolaena, qu'il y a des rapports notables entre ces deux genres, et que l'un d'eux, le Cassinia, étant évidemment attiré par ses affinités naturelles dans la Inulées, semble devoir y entrainer l'autre." Cassini went on to say, "On remarquera surtout que le Cassinia doit nécessairement être placé parmi les Inulées - Gnaphaliées, et que pourtant les filets de ses étamines sont greffés à la corolle jusqu'au sommet du tube, comme dans le Neurolaena. La forme du fruit, celle de la corolle, celle des éstamines, offrent aussi quelques analogies avec le Neurolaena.

Neurolaena was apparently first placed close to Senecio by DeCandolle (1836) in his conspectus tribus Senecionideae. The two relevant subtribes were characteristzed as follows: "Heliantheae. Capitula saepius heterogama radiata aut homogama discoidea. Recept. totum aut marginw plaeaceum. Cor. fl. herm. lobi crassi. Pappus nullus coroniformis aut aristatus. Antherae nigricantes ecaudatae.— Folia saepius opposita" versus "Senecioneae. Capitula homo- aut heterogama, discoidea aut radiata. Antherae ecaudatae. Achaenio pappo piloso aut setaceo coronata, exteriora rarissimè calva.— Folia alterna." On the basis of the pappus and alternate leaves Neurolaena was placed in the Senecioneae. Such a disposition has apparantly been followed by all more recent workers including Bentham (1873) who offerred no explanation but only said "two species, admitted on all sides to be a Senecionid".

The second genus, Schistocarpha, was described by Lessing in 1831 with the brief comment "Differt a Neurochlaena R.Br. tantummodo pappo 1-nec 2-seriali". Decandolle (1836) placed the genus in the subtribe Heliantheae as a synonym of Perymenium. All other authors have kept Schistocarpha with Neurolaena in the Senecioneae.

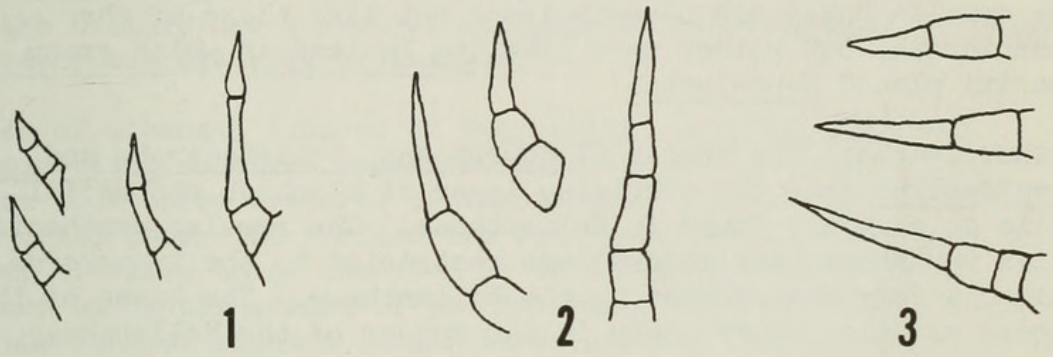
The third genus, Alepidocline, was placed by Blake (1934) as a relative of Schistocarpha but with the remark, "In its general appearance, Alepidocline is suggestive of the tribe Heliantheae".

Critical review of a number of features of the three genera Neurolaena, Schistocarpha and Alepidocline indicate that they should be placed in the Heliantheae. The conclusion is derived from improved understanding of the distribution of the following characters in the Asteraceae.

Receptacles: Neurolaena and Schistocarpha both have distinctly paleaceous receptacles. Alepidocline has paleae present toward the edge of the receptacle. Other genera with paleaceous receptacles that have been placed in the Senecioneae are Liabum

(Bentham, 1873) and Dyscritothamnus (Rzedowski, unpublished) neither of which really belongs to the tribe. On the basis of present knowledge the receptacles of the true Senecioneae never have paleae. Receptacles with paleae are most characteristic of the Heliantheae but occur also in many other tribes. The reduced number of paleae in Alepidocline might raise questions as to placement in the Heliantheae if all other characters were not so like Schistocarpha.

Phyllaries: Neurolaena, Schistocarpha and Alepidocline all show multiseriate graduated involucral bracts. These phyllaries are usually rather papery and distinctly multinerved. The appearance has often resulted in misidentification of specimens as




Figures 1-3. Helianthian hairs. 1. Neurolaena. 2. Schistocarpha. 3. Alepidocline.

Eupatorieae where such phyllaries are common. The Heliantheae have few genera with such phyllaries but some species of Calea are close. The Senecioneae do not have such involucres. Dr. Jose Cuatrecasas, who has worked extensively in the tribe has spoken often of the characteristic uni- or biseriate involucre of the Senecioneae where it occurs within a well developed imbricated calyculus in some species of Senecio.

Corolla hairs: Neurolaena, Schistocarpha and Alepidocline all show a type of trichome on the corolla which might be referred to as "Helianthian hairs" (Figures 1-3). These sharply pointed usually multicellular hairs are found on the corollas of most genera of Heliantheae. Such hairs are not found in any supposedly related tribes and do not occur in some groups within the Heliantheae such as the Coreopsinae. The presence of such hairs seems to be sufficient evidence for placement of a genus in the tribe. The genus, Raillardella, also shows such hairs on some species and on the basis of this, nectaries, and anther appendages seems to be a member of the Heliantheae though paleae are lacking in the genus and exact relationship is not known.

In contrast, corollas of the true Senecioneae seem to

usually have no pubescence at all. Ray corollas of some species have been seen with hairs or glands near the base but most rays and all disk flowers seen have been glabrous. Such a concept excludes from the tribe not only genera with helianthian hairs but also those with more lax or blunt corolla hairs such as Peucephyllum, Psathyrotes and Bartlettia.

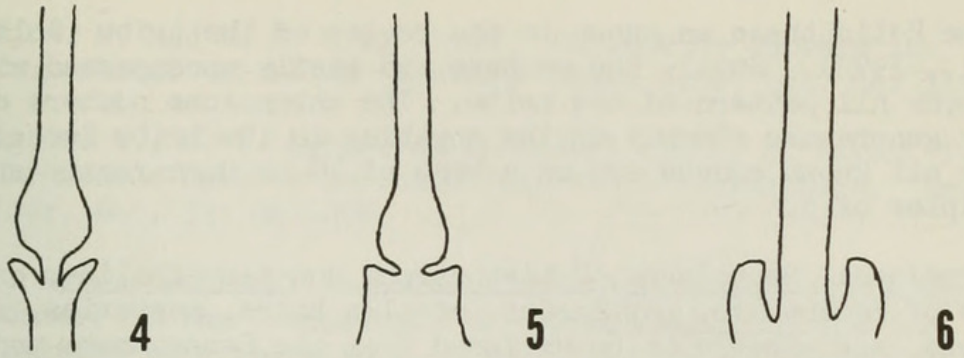
Corolla base: The long rather indistinct corolla bases of Neurolaena, Schistocarpha and Alepidocline are one of the two reasons the genera have not been placed in the Heliantheae by most authors. The corollas of the Heliantheae characteristically have shorter and very sharply demarcated basal tubes. The cells of the basal tubes also usually contain raphids but no raphids have been seen in Neurolaena, Schistocarpha or Alepidocline. The corolla bases are neverthelesss not like those of the Senecioneae, but rather more like the Inuleae in which group Cassini placed Neurolaena.

Anther thecae: The thecae of Neurolaena, Schistocarpha and Alepidocline show the overlying layer of blackish exothecial cells so commonly found in Heliantheae. The regular exothecial cells are short with thickenings restricted to the transverse walls, a form most common in the Heliantheae. The bases of the thecae are also short-acute in the manner of the Heliantheae.

Anther appendages: The appendages of Neurolaena, Schistocarpha and Alepidocline show the concave or keeled structure that is characteristic of the Heliantheae and Helenieae. With a few dubious exceptions such appendages are not known in the Senecioneae. Such genera as Tussilago have appendaegs broad and inflexed but not truly concave. Crocidium seems to have the most nearly helianthian appendage of any genus that might be retained in the Senecioneae. Genera besides Neurolaena, Schistocarpha and Alepidocline that should be rejected from the Senecioneae on the basis of the anther appendage are Dyscritothamnus, Peucephyllum, Bartlettia, Psathyrotes and Raillardella.

In Neurolaena the anther appendage often bears a gland. Such glandular appendages are most common in the Heliantheae, and are found in the Helenieae, Inuleae and Vernonieae, but are not known in the Senecioneae.

Nectaries: The style bases of Neurolaena, Schistocarpha and Alepidocline are partially immersed in the nectaries (Fig. 4) as is characteristic of certain tribes including the Heliantheae. In contrast, the styles of the Senecioneae and Astereae along with some other compositae are borne on top of the nectaries or are completely fused with the nectary below the node (Fig. 5). The degree of fusion seems to be of considerable significance in distinguishing major trends in the family Asteraceae. Other genera that should be excluded from the Senecioneae on the basis




Figures 4-6. Nectaries and style bases. 4. Neurolaena. 5. Senecioneae. 6. Eupatorieae.

of the nectary are a dubious assemblage including Raillardella, Peucephyllum and Dyscritothamnus.

Walls of achene: Achenes of Neurolaena, Schistocarpha and Alepidocline observed under the microscope with transmitted light show three features of importance. Minute punctations on the cells under the surface are very pronounced. Such punctations are like those observed in most Eupatorieae and they are common among the genera of the Heliantheae. The second feature is the lack of raphids in all three genera. Raphids are mostly lacking when the minute punctations are present. The Senecioneae usually lack the punctations and have raphids. In the third feature of the achene wall the three genera in the complex are not alike. Schistocarpha and Alepidocline show the numerous narrow longitudinal plae lines in the walls that are common in many genera of the Heliantheae and that are found in some Helenieae. Neurolaena has no such lines and shows only the five differentiated costae as in some other Heliantheae and in most Eupatorieae.

Pappus: Neurolaena, Schistocarpha and Alepidocline have been excluded from the Heliantheae in the past primarily on the basis of their simple polysetose pappus. The pappus and the achenes in general were quite properly noted by Cassini for their resemblance to the Eupatorieae. Still, the previous delimitation of the Heliantheae on the basis of pappus seems particularly artificial considering the recognition of plumose and even short-setose forms of pappus in the tribe.

Cytology: Neurolaena has been reported twice with a chromosome number n = 11 (Turner, Powell & King, 1962; Powell & King, 1969). Schistocarpha has been reported on the basis of ten counts and two species with n = 8 (Turner, Ellis & King, 1961; Turner, Powell & King, 1962; Turner, Powell & Cuatrecasas, 1967; and Powell & King, 1969). The numbers are not particularly common

in the Heliantheae as shown in the review of the tribe (Solbrig, et al., 1972). Still, the numbers are easily encompassed within the over all pattern of the tribe. The chromosome numbers of the three genera are clearly unlike anything in the tribe Senecioneae where all known counts are on a base of 10 or more rarely are multiples of 5.

Conclusions: Neurolaena, Schistocarpha and Alepidocline, on the basis of receptacle, phyllaries, corolla hairs, nectaries, and anthers, are clearly to be excluded from the Senecioneae and included in the Heliantheae. The relationship to the Heliantheae is evident in spite of rather exceptional structure of the pappus and corolla base. The disposition confirms the impressions of Swartz and Brown regarding Neurolaena, the general impression of DeCandolle regarding Schistocarpha, and the impression of Blake regarding the habit of Alepidocline.

The three genera might be placed in a large Helianthian complex consisting of the Lagascinae - Verbesininae - Galinsoginae, being technically most like the Galinsoginae. Actually the three genera might better be accomodated in a broader more natural subtribal concept that included all three of the listed subtribes. A narrower concept might well result in a new subtribe. Such a separate subtribe would show some diversity since Neurolaena differs in many characters from Schistocarpha, including phyllotaxy, achene wall, corolla shape, gland on the anther appendage, and chromosome number.

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