

traploids formed by hybridization between *M. lindleyi* and various taxa of section *Microseris* (Stebbins, Jenkins, and Walters, 1953; Chambers, 1955; Irmiler et al., 1982; Wallace and Jansen, 1990). Therefore, although *M. lindleyi* is morphologically well differentiated from *Microseris* and is closer phylogenetically to *Nothocalais* and *Agoseris*, the existence of reticulate evolution involving the two natural allotetraploids makes its generic classification paradoxical.

If no further taxonomic adjustments were to be made, *Microseris* would remain a paraphyletic genus, containing *M. lindleyi* and its two allotetraploid derivatives, but excluding *Nothocalais* and *Agoseris*. We have considered several ways of revising generic circumscriptions so as to improve the fit between phylogenetic information and classification. One solution, which we do not favor, would be to combine *Agoseris*, *Nothocalais*, and *M. lindleyi* into a single genus, separate from *Microseris*. *Microseris lindleyi* stands well apart from the two former genera in a number of distinctive morphological traits, including its caulescent habit and structure of its involucre, achenes, and pappus. Placing it in an expanded genus *Agoseris* would make that taxon very polymorphic and difficult to define by any coherent set of macromorphological traits. Furthermore, there are not yet cpDNA data for all the species of *Agoseris* and *Nothocalais* to clarify whether their phylogeny justifies a generic merger.

A second possibility would be to combine all three genera—*Microseris*, *Nothocalais*, and *Agoseris*—into a single genus, which would bear the name *Agoseris*. This alone would not be a complete solution, since the problem of classifying species groups within this extremely polymorphic genus would simply be pushed down to infrageneric levels of subgenera, sections, etc. Furthermore, the merger of the three genera would be highly disruptive to the nomenclature and literature of the well-studied genus *Microseris*, all of whose species would take new names in *Agoseris*.

The taxonomic solution that we favor is to revive the genus *Uropappus* for *M. lindleyi* and to erect a new genus to accommodate the two allotetraploid derivatives (*M. heterocarpa* and *M. decipiens*), leaving *Agoseris* and *Nothocalais* as separate genera. Advantages of this treatment are that it makes the fewest nomenclatural changes, leaving intact the names of most species of *Microseris*, gives generic recognition to the phylogenetic divergence of *Uropappus* from *Microseris*, and acknowledges the evolutionary origin of two species via intergeneric hybridization and polyploidy. The new

genus *Stebbinsoseris* proposed here contains two self-perpetuating, naturally evolved species and is, therefore, not a nothogenus (see Greuter, 1988, Art. H.6.2, Ex. 5).

Below we have provided a summary of the taxonomic treatment of *Microseris*, *Uropappus*, and the new genus *Stebbinsoseris*.

Microseris D. Don, Phil. Mag. 11:388. 1832
Type: *M. pygmaea* D. Don.

Subgenus *Microseris*. From the list of synonyms in Chambers (1955, p. 278) exclude: *Calais* sect. *Calocalais* DC.; *Uropappus* Nutt.; *Microseris* subgen. *Calocalais* (DC.) Sch.-Bip.

Subgenus *Scorzonella* (Nutt.) Sch.-Bip., Pollichia 22–24:309. 1866. Lectotype: *S. laciniata* (Hook.) Nutt., see Chambers (1955, p. 277). To the list of synonyms in Chambers (loc. cit.) add: *Apargidium* Torr. & Gray, Fl. N. Amer. 2:474. 1843; *Microseris* subgen. *Apargidium* (Torr. & Gray) Chamb., op. cit. 278.

Subgenus *Mosiermos* (Hook. f.) Chamb., loc. cit. Type: *Scorzonera lawrencii* Hook. f., a synonym of *Microseris scapigera* (Sol. ex A. Cunn.) Sch.-Bip.

Uropappus Nutt., Trans. Amer. Phil. Soc. II. 7:424. 1841. Corrected lectotype: *U. lindleyi* (DC.) Nutt., see Chambers (1955, p. 276). Synonyms: *Calais* sect. *Calocalais* DC., Prod. 7:85. 1838 [corrected lectotype: *C. lindleyi* DC.]; *U.* sect. *Calocalais* (DC.) Nutt., op. cit. 425, but excluding *U.* sect. *Brachycarpa* Nutt.; *Microseris* subgen. *Calocalais* (DC.) Sch.-Bip., Pollichia 22–24:308. 1866.

Stebbinsoseris Chamb., genus novum. Synonyms: *Uropappus* sect. *Brachycarpa* Nutt., Trans. Amer. Phil. Soc. II. 7:425. 1841; *Microseris* sect. *Brachycarpa* (Nutt.) Chamb., Contr. Dudley Herb. Stanford 4:286. 1955. Genus allopoloideum ex hybridis inter *Microseridem* et *Uropappum oriundum*; differt ab *Microseride* capitulis vix nutantibus involucre parum imbricato paleis pappi lanceolatis bifidis erosivis; differt ab *Uropappo* acheniis non rostratis paleis pappi sordidis persistentibus aristis crassioribus evidenter spiculatis; numero chromosomatum $n = 18$. Type: *S. heterocarpa* (Nutt.) Chamb. The name honors G. Ledyard Stebbins, Jr., who along with James Jenkins and Marta Walters first suggested the allopolyploid origin of *S. heterocarpa*.

Stebbinsoseris heterocarpa (Nutt.) Chamb., comb. nov. *Uropappus heterocarpus* Nutt., Trans. Amer. Phil. Soc. II. 7:425. 1841. Type: *T. Nuttall*, "St. Diego, N. Cal.," BM (photo!).

Stebbinsoseris decipiens (Chamb.) Chamb., comb. nov. *Microseris decipiens* Chamb., Contr. Dudley Herb. Stanford 4:290, 1955. Type: *J. H. Thomas 4094A*. "Ridge between Scott Creek and Mill Creek, Santa Cruz Mountains, California," DS.

Character evolution in the Microseridinae—

The subtribe Microseridinae has been studied extensively using a diverse array of characters, including those derived from macromorphology (Stebbins, 1953; Chambers, 1955, 1957; Jeffrey, 1966), micromorphology (Baaqoe, 1980), cytology (Stebbins, Jenkins, and Walters, 1953), palynology (Feuer and Tomb, 1977), chromosome number and morphology, secondary chemistry (Harborne, 1977), and nuclear DNA content (Price and Bachmann, 1975). In spite of these intensive efforts, there have been no attempts to construct a phylogeny or discuss the trends of character evolution within the subtribe. The availability of a cpDNA phylogeny provides us with a new and independently derived phylogenetic background upon which to discuss character evolution within the Microseridinae. To do this we have plotted the distribution of several characters on the cpDNA phylogeny; we have selected one of the two equally parsimonious Wagner trees (Fig. 5) for this purpose because this tree was slightly favored in the weighted parsimony analyses.

The extensive chromosomal investigations of Stebbins, Jenkins, and Walters (1953) make the Lactuceae one of the best studied tribes; chromosome numbers are known from 61 of the 70 currently recognized genera (reviewed in Tomb, 1977). Although there has been some debate concerning the ancestral base number for the tribe (Turner, Ellison, and King, 1961), Stebbins, Jenkins, and Walters (1953) favor $x = 9$ as the ancestral number because it is most frequent and it occurs in genera that were considered primitive. Within the Microseridinae $x = 9$ is the predominant basic chromosome number, occurring exclusively in four of the seven genera, including the basal genus *Phalacroseris* (Fig. 5). The occurrence $n = 6$ in both *Krigia* and *Pyrrhopappus* can be explained by aneuploid reduction in the common ancestor of these two genera. Basic chromosome numbers of $x = 4$ or 5 within *Krigia* may have also arisen via aneuploid reduction from $x = 6$. One species of *Krigia*, *K. wrightii*, has a chromosome number of $n = 9$; however, recent studies (Kim, 1989) have suggested that this species originated by allopolyploidy. The presence of $n = 8$ in *Stephanomeria* can be explained by aneuploidy from $x = 9$.

Several morphological characters have been important in the systematics of the Microseridinae, including habit and the morphology of the achenes, pappus, stigmas, styles, and pollen. Some of these characters provide support for the monophyletic groups in the cpDNA phylogenies, while others have evolved in parallel several times (Fig. 5). It is not surprising that the annual and perennial habits have evolved repeatedly within several genera (*Krigia*, *Pyrrhopappus*, *Stephanomeria*, *Agoseris*, and *Microseris*). The inclusion of *Stephanomeria* within the Microseridinae requires two independent origins of orange pollen and short stigmas, the characters used by Stebbins (1953) and Jeffrey (1966) to circumscribe the subtribe. Several features of the flowers and fruits have also evolved multiple times. Two of these, achene surface and corolla pubescence, were emphasized by Jeffrey (1966) in proposing informal groups within the Microseridinae. Symmetrical pollen grains with narrowed ridges, which occur in *Phalacroseris*, *Pyrrhopappus*, and *Krigia*, have originated twice. This is in agreement with Feuer and Tomb's (1977) suggestion that the pollen of *Phalacroseris* evolved independently toward the *Krigia* pollen morphology.

Surveys of flavonoid chemistry of the Microseridinae (Harborne, 1977; Kim, unpublished data) identified three major classes of compounds, chalcones, flavones, and flavanols. The production of chalcones in *Krigia* and *Pyrrhopappus* provides chemical support for the close relationship of these genera. These compounds are primarily restricted to a few generic groups in the tribe Heliantheae (Crawford and Stuessy, 1981). The other two classes of flavonoids have clearly evolved multiple times within the Microseridinae.

Rates of chloroplast DNA evolution—Several previous studies have examined relative rates of evolution of the chloroplast genome (Sytsma and Gottlieb, 1986; Schilling and Jansen, 1989; Doyle, Doyle, and Brown, 1990; Wallace and Jansen, 1990). All of these studies demonstrated substantial rate inequities in comparisons between certain lineages, while a molecular clock could not be rejected in comparisons between others. Schilling and Jansen (1989) suggested that different evolutionary rates within *Viguiera* and related genera of Asteraceae may be correlated with generation time. The role of generation time in affecting evolutionary rates has generated substantial controversy for animal mitochondrial DNA (Easteal, 1985; Wu and Li, 1985). The occurrence of both annuals and perennials in the Microseridinae allows us to test this hypothesis for cpDNA. Our results