TONESTUS KINGII AND T. ABERRANS ARE RELATED TO EURYBIA AND THE MACHAERANTHERINAE (ASTERACEAE: ASTEREAE) BASED ON NRDNA (ITS AND ETS) DATA: REINSTATEMENT OF HERRICKIA AND A NEW GENUS, TRINITEURYBIA

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ABSTRACT

Phylogenetic analysis of nrDNA (ETS and ITS) sequence data for 50 species of Astereae (Asteraceae) belonging to the *Eurybia-Machaerantherinae* clade show that *Tonestus kingii* and *T. aberrans* belong to this group. The genus *Herrickia* is reinstated and expanded to include *H. kingii* as well as members of *Eurybia* section *Herrickia* sensu Nesom (1994). A new genus, *Triniteurybia*, is established for *T. aberrans*, which is sister to the *Machaerantherinae*.

RESUMEN

El análisis filogenético de secuencia de bases de nrDNA (ETS y ITS) de 50 especies de Astereae (Asteraceae) pertenecientes al clado *Eurybia-Machaerantherinae* muestra que *Tonestus kingii* y *T. aberrans* pertenecen a este grupo. El género *Herrickia* se reinstaura y expande para incluir a *H. kingii* así como a miembros de *Eurybia* sección *Herrickia* sensu Nesom (1994). Se establece un nuevo género, *Triniteurybia*, para *T. aberrans*, que es "sister group" de *Machaerantherinae*.

INTRODUCTION

Several species of tribe Astereae in North America have proven difficult to assign taxonomically to genera or groups. Molecular phylogenetic studies, notably following the seminal paper of Noyes and Rieseberg (1999), have helped to solve the relationships of many of these taxa. Nevertheless, the disposition of

some species still remain controversial, notably species recently included in Tonestus by Nesom and Morgan (1990), T. aberrans (A. Nelson) G.L. Nesom & Morgan (basionym Macronema aberrans A. Nelson), and by Nesom (1991), T. kingii (D.C. Eaton) G.L. Nesom (basionym Aster kingii D.C. Eaton). The basis for inclusion of these species in *Tonestus* were the woody caudices, leaf shape and anatomy, eglandular (or sparsely short-stipitate-glandular) herbage, mostly single-headed capitulescences and foliaceous outer phyllaries (not in *T. aberrans* however). Nesom and Morgan (1990) did not discuss the specific reasons for the inclusion of Macronema aberrans in Tonestus, but pointed out its similarities to T. graniticus. Nesom (1991) reviewed the detailed taxonomic history of Aster kingii, which has also been named Machaeranthera kingii (D.C. Eaton) Cronquist & Keck, and he pointed out that various authors had seen relationships of this species with genus Asters.l., notably western members of Eurybia and Oreostemma. The similarities invoked to link this species to Tonestus are those cited above. The only discordant feature in the group would be its white rays in a yellow-rayed group. All species placed in Tonestus are n=9, a primitive and frequent number in the tribe.

A recent molecular phylogeny of Chrysothamnus and related Solidagininae (Roberts & Urbatsch 2004) suggests, however, that Tonestus sensu Nesom is polyphyletic. Further investigations by Urbatsch and colleagues (unpublished) suggested that T. aberrans and T. kingii might better be placed near Eurybia. Likewise, a study of the position of the North American asters within tribe Astereae had suggested that T. kingii was better placed with Eurybia and Oreostemma, two North American segregates of Asters.l. (see summarized phylogeny in Semple et al. 2002) that will be called henceforth the eurybioid lineage. Therefore, in preparation for the treatment of Eurybia and relatives (Asteraceae, Astereae) for the Flora of North America, we are using ITS and 3'ETS molecular phylogenetic data to investigate the taxonomic position of T. aberrans and T. kingii within the Astereae. These molecular markers have proved useful in determining the position of taxa in tribe Astereae (e.g., Noyes & Rieseberg 1999; Roberts & Urbatsch 2004). We show that these species belong to the eurybioid grade within the North American clade and are presenting the necessary combinations to reflect this phylogenetic position. Genus Herrickia is reinstated and T. kingii transferred to it as H. kingii (along with congeners H. glauca and H. wasatchensis), and a new monotypic genus is described to accommodate T. aberrans, Triniteurybia. These names are subsequently used in the paper.

MATERIAL AND METHODS

Samples were preserved either as frozen leaf material, in silica gel, or taken from herbarium specimens. Data for the Machaerantherinae were taken from Markos

and Baldwin (2001). Extraction and molecular methods used here are as described in Roberts and Urbatsch (2004) (Urbatsch laboratory) and in Fougère-Danezan et al. (2003) (ITS, Brouillet laboratory). For ETS (Brouillet laboratory), the primers Ast-8 (Markos & Baldwin 2001) and 18S-2L (Linder et al. 2000) were used, with PCR conditions similar to ITS (above); this resulted in longer ETS sequences than those produced in the Urbatsch laboratory (*T. kingii* and *T. aberrans*).

Sequences were input into already aligned matrices of ITS and ETS for the Astereae and manually adjusted. All new sequences used in this study are deposited in GenBank under the accession numbers provided in Table 1. Sources for already published sequences are provided also.

Preliminary parsimony analyses were done on the full ITS (more than 500 taxa in Astereae) and ETS (106 taxa) matrices, using PAUP* 4.0b10 (Swofford 2002). Resulting trees (not shown) clearly indicate that T. kingii and T. aberrans are members of the Eurybia complex (eurybioids) at the base of the Machaerantherinae (see Semple et al. 2002), but the trees were unresolved (polytomy) in the current region of interest. Given that the trees were not in conflict, data were combined for 50 taxa for which both sets were available, in an attempt to better define the position of these species within the Eurybia complex. The total number of characters in the combined ETS + ITS matrix is 1149, of which 195 are parsimony informative; few phylogenetically informative indels are found in the reduced taxon matrix (mostly in the ITS portion) and they were not coded as distinct characters. The matrix was subjected to parsimony analysis using PAUP* 4.0b10 (TBR, characters unordered, unweighted, gaps as missing, random addition, Multrees in effect), and to Bayesian analysis using Mr.Bayes3 (Ronquist and Huelsenbeck, 2003). For the latter, the following parameters were applied: 4 chains, 1,000,000 generations, burn in 100.000, every 10.000th tree saved, model GTR+ gamma+gamma inv, nst=6. Analyses were run to completion. Bootstrap and jacknife supports were calculated for the parsimony analysis (5000 replicates, TBR, random addition); for the jacknife, 50% of characters were deleted in each run. Strict and 50% majority rule consensus trees were drawn for the parsimony analysis, and posterior probabilities were input onto the 50% majority rule tree for the Bayesian analysis. Trees were rooted using Chloracantha spinosa and Canadanthus modestus.

RESULTS

Parsimony analysis of the ETS + ITS matrix yielded 6910 trees of length 687, CI 0.662, RI 0.812 and RC 0.538. In the strict consensus tree (not shown) the eurybioids + *Machaerantherinae* form a clade, within which *Oreostemma*, *Eurybia* and *Eurybia* sect. *Herrickia* form a polytomy sister to a *T. aberrans-Machaerantherinae* clade. The parsimony 50% majority rule tree is similar to that shown for the Bayesian analysis (Fig. 1), which resulted in 9002

TABLE 1. List of voucher specimens for the sequences generated for the current study, and sources of previously published data. Current species names (e.g., Morgan & Hartman 2003){ Sida 20:1403} are used and original published names are provided in parentheses when differing (as deposited in GenBank; Markos & Baldwin 2001). For eurybioids, names proposed here are used and formerly used ones are in parentheses.

Species	Source (collectors, number,	GenBank accession number	
	Herbarium or citation)	ITS	ETS
Canadanthus modestus (Lindl.) G.L. Nesom	Semple 10639 (WAT)	AY772432	AY772446
Chloracantha spinosa (Bentham) G.L.Nesom	Spellenberg 13101 (MT)	AY772431	AY772445
Oreostemma alpigenum (Torr.& A.Gray) Greene var. haydenii (T.C.Porter) G.L.Nesom	Semple 10419 (WAT)	AY772430	AY772444
Triniteurybia aberrans (A. Nelson) Brouillet, Urbatsch & R.P.Roberts clone 1 (Tonestus aberrans (A. Nelson) G.L.Nesom & D.R. Morgan)	Urbatsch 7812 (LSU)	AY772426	AY772440
Triniteurybia aberrans (A. Nelson) Brouillet, G.L.Nesom & D.R.Morgan) clone 2 (Tonestus aberrans (A. Nelson)	Urbatsch 7812 (LSU)	AY772427	AY772441
Herrickia kingii (D.C.Eaton) Brouillet, Urbatsch & R.P.Roberts clone 1 (Tonestus kingii (D.C.Eaton) G.L.Nesom)	Garrett 1576 (US)	AY772428	AY772442
Herrickia kingii (D.C.Eaton) Brouillet, Urbatsch & R.P.Roberts clone 2 (Tonestus kingii (D.C.Eaton) G.L.Nesom)	GS. Goodrich 16357 (UT)	AY77242	AY772443
Herrickia horrida Wooten & Standl.	Spellenberg & Fletcher 6027 (NMC)	AY772425	AY772439
Herrickia glauca (Nutt.) Brouillet (Eurybia glauca (Nutt.) G.L.Nesom)	Semple 5758 (WAT)	AY772424	AY772438
Eurybia divaricata (L.) G.L.Nesom	Semple 10710 (WAT)	AY772423	AY772437
Eurybia surculosa (Michx.) G.L.Nesom	Semple 10527 (WAT)	AY772422	AY772436
Eurybia sibirica (L.) G.L.Nesom	Semple 10627 (WAT)	AY772421	AY772435
Eurybia eryngiifolia (Torr. & A.Gray) G.L.Nesom	Semple 10557 (WAT)	AY772420	AY772434
Dieteria bigelovii (A. Gray) D.R.Morgan & R.L. Hartman (Machaeranthera bigelovii (A.Gray) Greene)	Semple 10468 (WAT)	AY772419	AY772433

TABLE 1. continued			
Species	Source (collectors, number,	GenBank accession number	
	Herbarium or citation)	ITS	ETS
Benitoa occidentalis (H.M.Hall) D.D.Keck (Lessingia occidentalis (H.M.Hall) M.Lane)	Markos & Baldwin (2001)	AF251585	AF251643
Haplopappus foliosus DC.	Markos & Baldwin (2001)	AF251577	AF251635
Haplopappus glutinosus Cass.	Markos & Baldwin (2001)	AF251578	AF251636
Haplopappus macrocephalus (Less.) DC.	Markos & Baldwin (2001)	AF251579	AF251637
Haplopappus marginalis Phil.	Markos & Baldwin (2001)	AF251580	AF251638
Haplopappus paucidentatus Phil.	Markos & Baldwin (2001)	AF251581	AF251639
Hazardia detonsa (Greene) Greene	Markos & Baldwin (2001)	AF251582	AF251640
Hazardia squarrosa (Hook. & Arn.) Greene var. grindelioides (DC.) W.D.Clark	Markos & Baldwin (2001)	AF251583	AF251641
Hazardia whytnei (A.Gray) Greene	Markos & Baldwin (2001)	AF251584	AF251642
Isocoma acradenia (Greene) Greene subsp. eremophila (Greene) G.L.Nesom	Markos & Baldwin (2001)	AF251572	AF251630
Isocoma menziesii (Hook. & Arn.) G.L.Nesom var. vernonioides (Nutt.) G.L.Nesom	Markos & Baldwin (2001)	AF251571	AF251629
Lessingia arachnoidea Greene	Markos & Baldwin (2001)	AF251587	AF251645
Lessingia filaginifolia (Hook. & Arn.) M.A.Lane var. californica (DC.) M.A.Lane	Markos & Baldwin (2001)	AF251593	AF251651
Lessingia filaginifolia (Hook. & Arn.) M.A.Lane var. filaginifolia	Markos & Baldwin (2001)	AF251589	AF251647
Lessingia germanorum Cham.	Markos & Baldwin (2001)	AF251596	AF251654
Lessingia glandulifera A.Gray var. glandulifera	Markos & Baldwin (2001)	AF251599	AF251657
Lessingia glandulifera A.Gray var. pectinata (Greene) Jepson	Markos & Baldwin (2001)	AF251597	AF251655
Lessingia glandulifera A.Gray var. tomentosa (Greene) Ferris	Markos & Baldwin (2001)	AF251603	AF251661
Lessingia hololeuca Greene	Markos & Baldwin (2001)	AF251604	AF251663
Lessingia lemmonii A.Gray var. lemmonii	Markos & Baldwin (2001)	AF251606	AF251664

	GonBank accossion num	hor
Source (conectors, number,	Herbarium or citation)	ITS ETS
Markos & Baldwin (2001)	AF251608	AF251666
Markos & Baldwin (2001)	AF251610	AF251668
Markos & Baldwin (2001)	AF251612	AF251670
Markos & Baldwin (2001)	AF251614	AF251672
Markos & Baldwin (2001)	AF251615	AF251673
Markos & Baldwin (2001)	AF251616	AF251674
Markos & Baldwin (2001)	AF251618	AF251676
Markos & Baldwin (2001)	AF251620	AF251678
Markos & Baldwin (2001)	AF251622	AF251680
Markos & Baldwin (2001)	AF251624	AF251682
Markos & Baldwin (2001)	AF251568	AF251626
Markos & Baldwin (2001)	AF251567	AF251625
Markos & Baldwin (2001)	AF251574	AF251632
Markos & Baldwin (2001)	AF251569	AF251627
Markos & Baldwin (2001)	AF251575	AF251633
Markos & Baldwin (2001)	AF251570	AF251628
	Markos & Baldwin (2001) Markos & Baldwin (2001)	Herbarium or citation) Markos & Baldwin (2001) AF251608 Markos & Baldwin (2001) AF251610 Markos & Baldwin (2001) AF251612 Markos & Baldwin (2001) AF251614 Markos & Baldwin (2001) AF251615 Markos & Baldwin (2001) AF251616 Markos & Baldwin (2001) AF251616 Markos & Baldwin (2001) AF251620 Markos & Baldwin (2001) AF251622 Markos & Baldwin (2001) AF251622 Markos & Baldwin (2001) AF251624 Markos & Baldwin (2001) AF251568 Markos & Baldwin (2001) AF251567 Markos & Baldwin (2001) AF251569 Markos & Baldwin (2001) AF251569 Markos & Baldwin (2001) AF251569 Markos & Baldwin (2001) AF251575 Markos & Baldwin (2001) AF251575 Markos & Baldwin (2001) AF251575 Markos & Baldwin (2001) AF251570



FIG. 1. 50% majority rule consensus tree of the Byaseian analysis of the eurybioids-*Machaerantherinae* (Asteraceae: Astereae); *T. aberrans* and *H. kingii* are in bold; dash lines indicate branches with less than 50% posterior probabilities, thick ones those that have 100% posterior probability, 100% parsimony bootstrap and 100% jacknife support. Posterior probabilities are indicated above the lines, bootstrap and jacknife (second figure) below.

trees. Posterior probabilities are shown on Figure 1, as well as the bootstrap and jacknife support values from the parsimony analysis.

DISCUSSION

Both the preliminary separate ITS and ETS parsimony analyses and the reduced combined analyses (Fig. 1) show that *Herrickia kingii* and *Triniteurybia aberrans* belong to the eurybioid-*Machaerantherinae* lineage of the Astereae. The basal branch of the eurybioid-*Machaerantherinae* receives strong support (posterior probabilities 89%, bootstrap 90%, jacknife 89%), a fact further reinforced by the possession of a non-homoplasic, synapomorphic 1-bp deletion at

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position 124 (ITS1). Such a relationship had been foreseen for H. kingii when described as a species of Aster s. l. (e.g., Welsh 1983) or when transferred to Machaeranthera section Xylorhiza (Cronquist and Keck 1957). Watson (1977), however, later excluded it from Xylorhiza when he segregated the section from Machaeranthera, pointing out instead similarities to Aster s.l. species (Oreostemma alpigena, Eurybia conspicua and E. integrifolia). Hartman (1990) likewise excluded H. kingii from Machaeranthera. Nesom (1991) mentioned that A.G. Jones (in pers. comm.) thought the species was associated with Aster sect. Oreostemma (Oreostemma), a basal group in the eurybioids. Nesom (1994), however, did not consider this possibility in his review of North American asters, though he did discuss Tonestus and the species studied here, noting that this (possibly polyphyletic) genus stood clearly outside Machaerantherinae. In transferring H. kingii to Tonestus, Nesom (1991) stressed its similarities to T. aberrans. A relationship to Aster s.l. was never envisioned for T. aberrans. However, the species was treated in Macronema, Sideranthus and Haplopappus, before its transfer to Tonestus, a yellow-rayed member of the Solidagininae, by Nesom and Morgan (1990). In all these genera, T. aberrans appeared unusual and aptly named.

The combined ETS + ITS analyses (Fig. 1) allow us to determine the position of *T. aberrans* and *H. kingii* within the eurybioid grade. In the parsimony strict consensus tree (not shown), the eurybioids are mostly polytomous, but *T. aberrans* emerges as sister taxon to the *Machaerantherinae*. This relationship is seen clearly in Figure 1 and receives high posterior probabilities (99%), as well as good bootstrap (73%) and jacknife (70%) support in the parsimony analysis (Fig. 1). In no analysis (Brouillet, unpublished data) is *T. aberrans* associated with *Eurybia* species. It occupies an isolated position between *Eurybia* and the *Machaerantherinae* and deserves recognition as a new monotypic genus, described below. Identification of this taxon as sister to the *Machaerantherinae* does not affect relationships previously determined within the subtribe (e.g., Morgan 2003; Markos & Baldwin 2001), and may shed light on the early evolution of this complex of mostly xeric, western species that have undergone a rapid diversification in ecology, morphology and karyology.

The position of *T. kingii* also appears resolved, but in a less striking manner. In all analyses (including a larger ITS study using different sequences for the species than those used here; Brouillet et al., in preparation), the species is sister to *Herrickia* (*Eurybia* sect. *Herrickia* of Nesom 1994; see below) (Fig. 1); it groups here with *H. glauca* and *H. horrida*, two of the three members of the genus. Support for this relationship, however, is not strong (posterior probabilities, 60%; bootstrap 74%, jacknife 67%), and is based on a single synapomorphy (in ETS) that is homoplasic due to parallel changes in the *Machaeranthera* complex. In all analyses done so far (including the large ITS parsimony study), *Herrickia* appears either in a polytomy or basal within *Eurybia* sensu Nesom

(1994). Its distinction from Eurybia receives 97% posterior probability, but this branch receives no support in parsimony analyses. Yet, it is defined by two synapomorphies (both from ITS1) without reversal or homoplasy. Another observation reinforces the conclusion that *Herrickia* may be best segregated from *Eurybia*, coming from cpDNA trnL-F sequence data (Brouillet, unpublished): while species of *Eurybia* s. str. have a 4-bp synapomorphic deletion, Oreostemma, Herrickia, T. aberrans and the Machaerantherinae all have the standard sequence, which suggests that Eurybia s. str. is a distinct clade. Despite this observation, one could advocate separating *E. surculosa* from other Eurybia on the basis of its position in Figure 1. The branch leading to this species is long, however. Furthermore, in analyses of ITS data using a larger set of eurybioids, E. surculosa groups with other Euribia species, though Eurybia and other eurybioidds globally are polytomous. The position of *E. surculosa* in the current tree appears the result of low taxon sampling and a long branch in the combined data. At the present time, relationships within and monophyly of Eurybia s. str. (including subgenera Eurybia and Heleastrum of Nesom 1994) cannot be tested appropriately. This is not the case for Herrickia, which forms a group in these analyses. Nevertheless, Herrickia as a genus appears monophyletic and worthy of reinstatement, with a new circumscription that includes the taxa grouped within section Herrickia by Nesom (1994) (i.e., H. horrida, H. glauca and H. wasatchensis), as well as H. kingii, as sister to the clade Eurybia s. str.-Triniteurybia-Machaerantherinae.

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Herrickia kingii (D.C. Eaton) Brouillet, Urbatsch & R.P. Roberts var. kingii.

- Herrickia kingii (D.C. Eaton) Brouillet, Urbatsch & R.P. Roberts var. barnebyana (Welsh & Goodrich) Brouillet, Urbatsch & R.P. Roberts, comb. nov. BASIONYM: *Machaeranthera kingii* (D.C. Eaton) Cronquist & Keck var. barnebyana Welsh & Goodrich, Brittonia 33:299. 1981. Aster kingii D.C. Eaton var. barnebyana (Welsh & Goodrich) Welsh, Great Basin Naturalist 43:221. 1983. *Tonestus kingii* (D.C. Eaton) G.L. Nesom var. barnebyana (Welsh & Goodrich) G.L. Nesom, Phytologia 71:125. 1991.
- **Triniteurybia** Brouillet, Urbatsch & R.P. Roberts, gen. nov. Type: Macronema aberrans (A. Nelson) Brouillet, Urbatsch & R.P. Roberts

Ab *Eurybia* differt capitulae eradiatae et foliae stipitato-glandulosae. Differs from *Eurybia* by its eradiate capitula and stipitate-glandular leaves.

Herbs perennial, cespitose; caudices woody, ramified, from slender, creeping taproots. Stems erect, simple, slender, 0.5-2.5(-3) dm, stipitate-glandular. Leaves basal and cauline, alternate; basal mostly persistent, petiolate to subpetiolate, bases tapering, distal sessile; blades ascending, simple, obovate or oblong to broadly oblanceolate, distal usually gradually reduced, 1-nerved, margins sparsely serrate, apices obtuse to subacute, faces stipitate-glandular. Capitulescences of solitary heads or 2-4 in dense, ± corymbiform arrays, sessile or subsessile in axils of distalmost leaves. Heads discoid. Involucres cylindrocampanulate, 9-14 mm. Phyllaries in 3-4 series, imbricate, graduated, bases indurate, 1-nerved, green zones +/- basally truncate, occupying distal 1/2-1/3, apices acute, faces glandular-viscid (exposed parts). Receptacles slightly convex, alveolate, margins toothed, chartaceous, epaleate. Disc florets 25-60, bisexual, fertile; corollas yellow and often reddish (particularly in lobes), slenderly cylindric, barely ampliate, tubes shorter than throats, lobes 5, erect, lanceolate, ca. 0.8 mm, minutely and sparsely puberulent; style-branch 2-3 mm, moderately exserted, appendages linear-triangular, very acute, +/- equaling stigmatic portion, short-hairy. Cypselae fusiform, ca. 10-nerved, ca. 3 mm, faces sparsely strigillose, eglandular; pappi of few bristles in 1 series, unequal, soft, barbellate, barely exceeding disc corollas.

Etymology.—*Triniteurybia* is named for Trinity Lake, Idaho, the type locality, and the closely related genus *Eurybia*, to indicate its relationships.

The genus is known only from the Sawtooth Mountains of Idaho and the Bitterroot Mountains of Montana, where it is considered of conservation concern. It inhabits the crevices of cliffs and outcrops of the dry coniferous montane forest zone, sometimes at or above timberline. The chromosome number is yet unknown.

Triniteurybia aberrans (A. Nelson) Brouillet, Urbatsch & R.P. Roberts, comb. nov. BASIONYM: Macronema aberrans A. Nelson, Bot. Gaz. (Crawfordsville) 53:226. 1912. Sideranthus

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