THE TAXONOMIC SIGNIFICANCE OF RUST SUSCEPTIBILITY IN ASTER AND ITS ALLIES (COMPOSITAE)

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INTRODUCTION

As a contribution towards the classification of the much-confused taxonomy of ***Aster*** , ***Erigeron*** and 18 other related taxa of Compositae, we have resorted to rust susceptibility as a tool which has already proved its taxonomic worth in previous studies (e.g. Drury, 1966; El-Gazzar and Watson, 1968 and 1970; Badawi, 1970; El-Gazzar and El-Fiki 1977; El-Gazzar, 1979, 1981a and 1981b; Savile, 1979). The taxa in question are: ***Alpigenia, Biotia , Boltonia, Brachyactis, Calimeris, Conyzopsis, Doellingeria, Eucephalus, Galatella, Heterotheca, Linosyris, Leptilion, Machaeranthera, Orthomeris, Psilactis, Stenachaenium, Tripolium*** and ***Xylorrhiza.*** All or some of these taxa have been treated by some authorities as subgenera or sections of ***Aster*** , and by others as separate genera.

BASIC INFORMATION

Records of susceptibility of all 20 taxa to rust fungi (order: Uredinales) have been collected from the works and compilations of: Alexopoulos (1940), Arther (1907-1940, 1962), Bubak (1908), Cummins (1978), Dennis (1970), Dietel (1899-1905), Gaumann (1959), Henderson (1958), Hennen and Baxter (1974), Hughes (1974-1977), Hylander ***et al*** (1953), Kern ***et al*** (1933), Kuprevicr and Tranzschel (1939), Vasudeva (1960), Savulescu (1953), Seymour (1929), Wilson and Henderson (1966). These publications cover collectively all the regions where ***Aster*** and its relatives are known to grow. The chief centres of distribution of these plants are in N. America, Europe and C. Asia where the rust diseases are better surveyed and studied. The collected records of susceptibility have been analyzed as follows:

1- Index cards have been prepared so that each card carried the full name of a host plant and of the rust species (and its infra specific taxa) parasitic on that host, and a full citation of the source of these data. Synonyms of both rust and host have also been entered on the same card as far as available literature allowed. Only one card of such records has been kept in the pack

and its identicals from other sources have been discarded in order to avoid repitition.

2- The task of sorting out and updating rust nomenclature has been greatly facilitated through such excellent taxonomic works as that of Cummins and Stevenson (1956), Sydow and Sydow (1904-1924) and the Index of Fungi (1920-1978). Host nomenclature on the other hand, has proved more problematic so the names and synonyms given in the original records are merely accepted with such alterations as were possible through some local floras (e.g. Fernald, 1950), or monographic treatments (e.g. Lippert, 1973 and 1980; Rommel,1977 and 1979).

3- Information contained in the pack of cards has been transformed into tabular form where the host names are arranged into one column and a separate column is assigned to the name of each rust species or variety. Susceptibility of a given host to a certain rust has been indicated against their respective names in the table by +. It soon became apparent that the table comprises records of 21 ***Puccinia*** spp. (with 8 varieties).4 ***Coleosporium*** spp. and 2 ***Uromyces*** spp. on the following range of hosts.

Aster (91 spp.), ***Galatella*** (2 spp.), ***Machaeranthera*** (3 spp.) ***Xylorrhiza*** (3 spp.), ***Erigeron*** (32 spp.) and a single species from each of ***Boltonia***, ***Calimeris***, ***Diplostephium***, ***Doellingeria***, ***Heterotheca***, ***Psilactis*** and ***Stenachaenium***.

4- When all rust taxa infecting less than 3 host species were excluded from the reckonning, the field of hosts and rusts has been narrowed considerably to the limited number shown in Table 1. ***Puccinia stipae*** Arth. has also been omitted from the table since it infects 2 species from each of ***Aster (A.novae-angliae*** and ***A.adscendens)*** and ***Erigeron (E. flagellaris*** and ***E. pumilus)***, and would thus serve no useful purpose in the discrimination between them.

DISCUSSION AND CONCLUSIONS

The most obvious feature of Table 1 is that there is no one rust species or a set of rust species which would discriminate absolutely and unequivocally between neat and well-defined groupings among the host genera and species. Therefore, all taxonomic conclusions that can be derived from this table must be based on general tendencies in the pattern of distribution of rusts on various hosts. Such conclusions may be summarized in the following.

Table 1: Summary of available records of susceptibility of *Aster*, *Erigeron* and related genera to 7 *Puccinia* species and to *Coleosporium solidaginis*.

HOST NAME	*Puccinia asteris*	*Coleosporium solidaginis*	*Pucc. extensicola-asteris*	*Pucc. grindeliae*	*Pucc. caricis-asteris*	*P. extensicola-erigerontis*	*Pucc. cyperi*	*Pucc. dovrensis*	Sections of *Aster* (Hoffmann, 1894)
GROUP 1:									
Aster incisus Fisch. (=*Calimeris incisa* DC.)				+					*Calimeris*
A. scaber Thumb. (=*Doellingeria scabra* Nees)				+					*Orthomeris*
A. tataricus L.F.				+					
A. trinervius Roxb. v. ovata Fr. & Sav.				+					
A. alpinus L.	+			+					*Alpigena*
A. tripolium L.	+			+					*Tripolium*
A. amellus L.	+			+					*Euaster*
A. linosyris (L.) Bernh. (=*Linosyris vulgaris* Cass.)	+								*Linosyris*
A. acris L. (=*Galatella punctata* DC.)	+								*Galatella*
A. lowrieanus Porter	+	+							*Euaster*
A. acuminatus Michx.	+	+							
A. undulatus L.	+	+							*Euaster*
A. patens Ait.		+							
A. novae-angliae L.	+	+							*Euaster*
A. novi-belgii L.	+	+							*Euaster*
A. lateriflorus L.	+	+							
A. ericoides L.	+	+							
A. adscendens Lindl.	+	+							
A. divaricatus DC. (=*A. linosyris* Bernh. v. *divaricatus*)	+	+							*Linosyris*
A. divaricatus L. (=*A. corymbosus* Ait.)	+	+							*Biotia*
A. macrophyllus L.	+	+	+						*Biotia*
A. puniceus L.	+	+	+						
A. cordifolius L.	+	+	+						
A. simplex Willd. (=*A. paniculatus* Lam.)	+	+	+						*Euaster*
A. laevis L.	+	+	+						
A. prenanthoides Muhl.	+	+	+						
A. umbellatus (=*Doellingeria umbellata* Hill. & Nees)		+	+						*Orthomeris*

+ = susceptible.

Table 1: Summary of available records of susceptibility of *Aster, Erigeron* and related genera to 7 *Puccinia* species and to *Coleosporium solidaginis*.

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GROUP I (continued):									
A. frondeus (Gray) Greene (=*Brachyactis frondosus* [Nutt.] Gray)			+						*Conyzopsis*
A. andersonii Gray			+						
A. apricus (Gray) Rydb.			+						
A. canbyi Vasey (=*A. spathulatus* Lindl.)			+						
A. chilensis Nees (=*A. chamissonis* Gray)			+						
A. ciliomarginatus Rydb.			+						
A. conspicuus Lindl.			+						
A. drummondii Lindl.			+						
A. engelmannii v. *ledophyllus* Gray (=*Eucephalus ledophyllus* [Gray] Greene)			+						*Orthomeris*
A. exiguus (Fernald) Rydb.			+						
A. follaceus Lindl.			+						
A. fremontii (T. & G.) Gray			+						
A. laetivirens Greene			+						
A. longifolius Lam.			+						
A. multiflorus Ait.			+						
A. nebraskensis Britton			+						
A. sagittifolius Willd.			+						
A. salicifolius Lam.			+						
A. tradescanti L. (=*A. vimineus* Lam.)			+						*Euaster*
A. tweedyi Rydb.			+						
A. yosemitana Greene			+						
A. glaucus T. & G. (=*Eucephalus glaucus* Nutt.)					+				*Orthomeris*
Boltonia asteroides (L.) L'Her.			+						
Doellingeria sericocarpoides Small		+							*Orthomeris*
Galatella acutisquamoides Novopokr.	+								*Galatella*
Psilactis asteroides Gray	+								
Stenachaenium megapotamicum Baker	+								

+ = susceptible.

Table 1: Summary of available records of susceptibility of ***Aster, Erigeron*** and related genera to 7 ***Puccinia*** species and to ***Coleosporium solidaginis***.

HOST NAME	*Puccinia asteris*	*Coleosporium solidaginis*	*Pucc. extensicola-asteris*	*Pucc. caricis-asteris*	*Pucc. grindeliae*	*P. extensicola-erigerontis*	*Pucc. cyperi*	*Pucc. dovrensis*	Sections of Aster (Hoffmann, 1894)
GROUP II:									
Machaeranthera vesiculosa Rydb.		+							*Machaeranthera*
M. canescens (Pursh) Gray					+				*Machaeranthera*
M. tanacetifolia (HBK) Nees					+				*Machaeranthera*
Xylorhiza glabriuscula Nutt.					+				*Orthomeris*
X. passyi (Gray) Greene					+				*Orthomeris*
Heterotheca subaxillaris (Lam.) Britt. & Rusby							+		
Erigeron arenarioides Gray					+				
E. caespitosus Nutt.					+				
E. eatonii Gray					+				
E. filifolius (Hook.) Nutt.					+				
E. microlonchus Greene					+				
E. macranthus Nutt.					+	+			
E. salsuginosa (Richards.) Gray					+	+			
E. philadelphicus L.						+			
E. pulchellus Michx. (=*E. bellidifolius* Mihl.)						+			
E. speciosus DC						+			
E. annuus (L.) Pers. (=*E. heterophyllus* Mihl.)						+	+		
E. canadensis L. (=*Leptilion canadense* [L.] Britton)						+	+		
E. ramosus Walt (=*E. strigosus* Mihl.)						+	+		
E. bonariensis L.	+						+		
E. floribundum HBK							+		
E. acris L.								+	
E. alpinus L.								+	
E. alpinus v. *multicaulis*								+	
E. borealis (Vierh.) Simm.								+	
E. elluriensis Boiss.								+	
E. elongatus Ledeb (=*E. politus* Fr.)								+	
E. unalaschkensis (DC) Vierh.								+	
E. uniflorus L.								+	
E. deamu Robinson	+								
E. uliginosus Benth.	+								
E. inornatus Gray		+							
E. peregrinus (Pursh) Greene		+							

+ = susceptible.

1- The genera and species fall into two major groups, (I and II). Group I takes in all representatives of ***Aster*** s. l. (i.e. including ***Calimeris, Doellingeria, Linosyris, Galatella, Brachyactis*** and ***Eucephalus)*** except ***Machaeranthera*** and ***Xylorrhiza,*** together with ***Boltonia, Psilactis*** and ***Staenachenium.*** Group II, on the other hand, incorporates all representatives of ***Erigeron*** (including ***Leptilion, Heterotheca, Xylorrhiza*** and ***Machaeranthera).*** Hoffmann (1894) treated the latter two genera as ***Aster*** section Orthomeris p.p. and ***Aster*** section Machaeranthera respectively, but their separation from ***Aster*** seems justified in the light of data on rust susceptibility.

2- While members of Group I (i.e. ***Aster*** and relatives) are prone to attacks of 4 rust species ***(Coleosporium solidaginis*** (Schw.) Thum., ***Puccinia asteris*** Duby , ***P. extensicola-asteris*** (Thum.) Arth. and ***P. carices - asteris*** Arth.), those of Group II ***(Erigeron*** and relatives) harbour a different set of 4 rust species ***(Puccinia grindliae*** Peck, ***P. cyperi*** Arth., ***P. dovrensis*** Blytt and ***P. extensicola-erigerontis*** Arth.). This means that, with some minor realignements, ***Aster*** s.l. and ***Erigeron*** s.l. are easily separable from each other on the basis of their patterns of rust susceptibility. This is a significant conclusion for a sound understanding of the relationship between the two genera, since the discrimination between them is one of the long-standing difficulties in the taxonomy of Compositae. Cursory examination of the diagnoses given by Hoffmann (1894) for the two genera should be sufficient to show clearly how tenuous the bases for their separation are:

i) Involucral bracts mostly in more than 2 rows; ligulate flowers usually in 1 row and elongate; pappus hairs biseriate; stigmatic lobe lanceolate . . . . . ***Aster***

ii) Involucral bracts approx. in 2 rows; Ligulate flowers narrowly linear, often in several rows; stigmatic lobes often short and triangular. . . . . ***Erigeron***

Although Hoffmann's diagnoses leave much to be desired (they are not strictly comparative, the pappus of ***Aster*** is bi- and multi-seriate, and the difference in stigmatic form is decidedly ambiguous), they are far superior to anything offered so far by other classical taxonomists. However, such feable diagnoses of the two genera are strengthened considerably when taken in conjunction with evidence from rust susceptibility.

3- Within ***Aster***, the most heterogeneous section is Orthomeris. This section has been variously divided into

a number of distinct genera ***Doellingeria, Eucephalus, Machaeranthera*** and ***Xylorrhiza).*** While the latter two genera Seem better treated as distinct from ***Aster, Doellingeria*** seems perfectly compatible with other sections of ***Aster. Eucephalus*** is represented in TAble 1 by two species, one of which (***E. ledophyllus*** = ***Aster engelmanni*** v. ***ledophyllus)*** is in harmony with other ***Aster*** species, while the second (***E. glaucus*** = ***Aster glaucus)*** is the only species in Group I harbouring a rust (***Puccinia grindelias***) specialized in inflicting members of Group II (i.e. ***Erigeron*** and its allies). To this extent, it seems reasonable to assume that ***Aster*** section Orthomeris should be subjected to a separate intensive taxonomic investigation in order to resolve its apparent heterogeniety.

4- Nither the two major groups (perennials/annuals and biennials) nor any of the 15 sections of ***Aster*** in Hoffmann's treatment seem to emerge intact in Table 1, since, species from the sections represented in this table share common susceptibility to one or more rust species.

5- Some species of ***Erigeron (E. deamii, E. uliginosus, E. inornatus, E. peregrinus*** and probably ***E. bonariensis)*** seem better situated among the ***Asters*** of Group I than with the rest of ***Erigeron*** in Group II, as they share susceptibility to ***Puccinia asteris*** and ***Coleosporium solidaginis*** with members of Group I. However, membership of a species to one genus or the other cannot be decided on the evidence from common susceptibility to a single rust species; one must always allow for the possibility that this susceptibility might be based on a misidentification of the host, the parasite or both and examples of taxonomists being led astray by such one-sided evidence are not infrequent (see El-Gazzar and Badawi, 1978). However, this common susceptibility is a clear indication that the genera in question are in urgent need for a comparative and comprehensive taxonomic, investigation.

6- The removal by some authors (e.g. Rommel, 1977; De candolle, 1836) of sections: Calimeris, Amellus, Tri-Polium, Linosyris, Biotia and Galatella from ***Aster*** (Sensu Hoffmann, 1894) and treating them as distinct genera (with the same or with different names) is not corroborated by their patterns of rust susceptibility, since they form (together with the largest section of ***Aster***; Euaster) a closely - knit and interrelated assemblage in Group I in the table, and no lines can be drawn within this Group to distinguish any of these sections from the rest.

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