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Cytology of *Erigeron annuus* s.l. and its consequences in Europe

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Abstract

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There is considerable confusion in the literature about the taxonomic status of *Erigeron annuus* and *E. strigosus* (section *Phalacroloma*, Asteraceae). Both species are natives of North America, and it is claimed that both have been introduced into other temperate regions. While this is certainly true for *E. annuus* and for the variety *E. strigosus* var. *septentrionalis*, it may not be the case for the typical variety, *E. strigosus* var. *strigosus*. In this paper we propose that var. *septentrionalis* is not a variety of *E. strigosus* but should be included in *E. annuus*. Our conclusion is based on morphology as well as on cytology and on a review of the literature on the mating systems of the two species. *E. annuus* (including "septentrionalis") is triploid and agamospermous, whereas *E. strigosus* is sexual and mostly diploid. *E. annuus* (including "septentrionalis") is widespread in Europe, but there is no proof that *E. strigosus* occurs in Europe.

Key words: Cytology, *Erigeron annuus*, *E. "septentrionalis"*, *E. strigosus*, Europe, mating system, morphology.

Introduction

The genus *Erigeron* (Asteraceae, *Astereae*) comprises about 400 species (Nesom 2000). Its center of diversity – and therefore its supposed origin – is in North America (Cronquist 1947), a conclusion which has been supported by recent molecular evidence (Noyes 2000a). The genus is organized into several sections, some of which are rather large (e.g. *Euerigeron* or *Stenactis*), while others contain only a few species (Cronquist 1947). The section *Phalacroloma* contains only two species, *Erigeron annuus* (L.) Pers.

Tab. 1. Morphological characters of *Erigeron annuus* and *E. strigosus* as given in Cronquist 1980.

Character	*Erigeron annuus*	*Erigeron strigosus*
plants	60–150 cm	30–90 cm
pubescence of stem	mostly long and spreading (or shorter and appressed)	mostly short and appressed (or short and spreading)
foliage	ample	sparse
basal leaf-blade	coarsely toothed elliptic to suborbicular up to 10 × 7 cm more or less abruptly long-petiolate	entire or toothed oblanceolate to elliptic up to 15 × 2.5 cm tapered to the petiole

and *E. strigosus* Mühl. ex Willd. (Nesom 1989), which are the subject of this study. Both species are native to the northern United States and adjacent Canada, but it has commonly been assumed that both taxa have been introduced to many parts of the world (Holm et al. 1979) including Europe (Halliday 1976).

Considerable confusion exists about the taxonomic status and mating systems of *E. annuus* and *E. strigosus*, and about the relationship between the two species. Different taxonomic assignments based on morphology exist (Cronquist 1947, Wagenitz 1965), and distinct types of mating systems have been described for these taxa (Land 1900, Tahara 1915, Bergman 1944). Part of the taxonomic problem is that both species are very variable, and most morphological traits used to distinguish the two taxa are overlapping. The characters used by Cronquist (1980) to distinguish the two species are shown in Table 1. As the variability of *E. strigosus* is rather high, several varieties have been described, mainly on features of the indumentum and characters of the flowers and the heads (Cronquist 1991, Allison and Stevens 2001). In contrast, Cronquist (1991) does not recognise infraspecific taxa within *E. annuus*, although it is also morphologically very variable. Studies by Stratton (1988, 1991) showed that basal leaf length, width, shape, and basal petiole length are highly correlated with nutrient supply and clonal identity.

According to Cronquist (1947), a rather common variety intermediate between the two species is characterized by leaves like those of *E. strigosus* and pubescence as found in *E. annuus*. Various names of different taxonomic levels have been assigned to this intermediate taxon. Fernald and Wiegand (1913) described it as *E. ramosus* B.S.P. var. *septentrionalis* Fern. and Wieg. Later Fernald (1942) made the combination *E. strigosus* var. *septentrionalis* (Fern. and Wieg.) Fern. Wagenitz (1965) modified it as *E. annuus* ssp. *septentrionalis* (Fern. and Wieg.) Wagenitz and also gave *E. strigosus* the status of a subspecies within *E. annuus*. However, the type specimen of this taxon (in herbarium GH!) has leaves which are clearly intermediate in terms of dentation and shape between the leaves of typical *E. annuus* and *E. strigosus*.

E. annuus was probably introduced into Europe hundreds of years ago as a garden ornamental, but it soon became widespread in the wild. The first herbarium record of naturalized *E. annuus* in Switzerland was made in 1828 (Rikli 1904). Later Fritsch (1922) and Koch (1928) concluded that there were in fact two introduced species in Europe, viz. *E. annuus* and *E. strigosus*. Today three taxa are recognised in Europe: the two species of section *Phalacroloma*, viz. *E. annuus* and *E. strigosus*, as well as the intermediate taxon "septentrionalis". They are usually named as *E. annuus* ssp. *annuus*, *E. annuus* ssp. *strigosus*, and the intermediate *E. annuus* ssp. *septentrionalis* (Wagenitz 1965, Halliday 1976, Lauber and Wagner 1996, Haeupler and Muer 2000, Wagenitz 2002). This latter taxon is said to be the most frequent in Europe. As the aim of this paper is to reexamine the taxonomic position of the three taxa, we will refer to them here as "morphotypes", namely morphotype "annuus", morphotype "septentrionalis" and morphotype "strigosus".

The genus *Erigeron* belongs (with 5 other genera) to the subtribe *Conyzinae*, which has a basic chromosome number of $x=9$ (Nesom 1994). A wide range of chromosome numbers occurs in the section *Phalacroloma*. Not only are different ploidy levels known to occur, viz. $2n=2x=18$, $2n=3x=27$ and $2n=4x=36$, but various aneuploid chromosome numbers have also been reported (Tahara 1915, 1921, Ikeno 1935, Taylor 1967, Chojnacki et al. 1980, 1982). For a general survey see Goldblatt (1981, 1984, 1985, 1988), Goldblatt and Johnson (1990, 1991, 1994, 1996, 1998, 2000).

The reproductive biology of the section is also complex. *E. annuus* and *E. strigosus* are known to be agamospermous as well as sexual. Several different mechanisms for the mating system have been described including: mitotic embryogenesis (Holmgren 1919, Tahara 1921, McDonald 1927, Gustafsson 1936, Bergman 1944, Fagerlind 1947, Noyes 2000b), the generation of reduced gametes with $n=9$ (Turner and Flyr 1966, Hong and Zhang 1990, Noyes 2000b), with $n=13$, 14 (Holmgren 1919, Tahara 1921, Chojnacki et al. 1982) and probably with all numbers between 9 and 18 plus 21, 25 and 27 (Noyes 2000b), and double fertilization (Land 1900).

As can be seen from the above descriptions, there is considerable variation in the group and the status and relationships of the various taxa is far from clear. In particular, there has been no attempt to correlate the morphological differences between taxa with chromosome numbers and reproductive modes. The goals of this study are:

- to review critically the available data concerning chromosome counts (including new chromosome counts presented in this paper),
- to relate morphology, cytology and reproductive modes, and
- to clarify which taxa really occur in Europe.

Materials and Methods

Samples

The plants for cytological study were grown from seed collected in the field in Europe in 1995 (except where another year is indicated) and in the USA in 1996. Seed was collected from random sample of 12–23 plants in each population. The minimum distance between the populations sampled was 100 km. The sites at which populations were sampled and the morphotypes collected are indicated below. Accuracy of degree of latitude and longitude is 150 m. Vouchers are deposited in Z/ZT.

Europe

- Italy. Between Arsoli and Subiaco. Prov. Roma. Maria della Pace. 41°56.28'N. 13°03.28'E. alt. 400 m: *E. annuus* ssp. *annuus* (DF 14308)
- Italy. Prov. Cuneo. San Michele Mondovi. 44°22.23'N. 7°55.16'E. alt. 600 m: *E. annuus* ssp. *annuus* (DF 14314)
- France. Dép. Saône-et-Loire. Autun. 46°57.16'N. 4°17.28'E. alt. 310 m: *E. annuus* ssp. *annuus* (DF 14353)

- Germany. Hessen. Gemeinde Sinn, Lahn-Dill-Kreis. Fleisbach. 50°38.28'N. 8°18.07'E. alt. 260 m: *E. annuus* ssp. *annuus* (DF 14383)
- Romania. 100 km E of Timisoara. Dobra, on the road from Deva to Lugoj. 1997: *E. annuus* ssp. *annuus* (MB 13359, cult. MB 13786)

USA

- Florida. Polk County. Bartow. 27°54.19'N. 81°49.46'W. alt. 30 m: *E. annuus* ssp. *septentrionalis* (DF 31601)
- Florida. Lee County. Albany (Dougherty County). 31°40.07'N. 84°10.29'W. alt. 50 m: *E. annuus* ssp. *annuus* (DF 31606a), *E. strigosus* (DF 31606b)
- South Carolina. Laurens County. Clinton. 34°28.12'N. 81°56.67'W. alt. 200 m: *E. annuus* ssp. *annuus* (DF 31621a), *E. annuus* ssp. *septentrionalis* (DF 31621b)
- North Carolina. Hoke County. Antioch. 34°50.39'N. 79°10.03'W. alt 420 m: *E. annuus* ssp. *annuus* (DF 31627a), *E. annuus* ssp. *septentrionalis* (DF 31627b)
- South Carolina. Chesterfiled County. 4.6 miles N of Ashland. 34°23.20'N. 80°15.08'W. alt. 450 m: *E. annuus* ssp. annuus (DF 31628a), *E. annuus* ssp. septentrionalis (DF 31628b)
- Virginia. Lunenburg County. Burkeville. 37°04.17'N. 78°13.97'W. alt. 200 m: *E. annuus* ssp. annuus (DF 31640a), *E. annuus* ssp. septentrionalis (DF 31640b)
- Maryland. Charles County. Grayton. 38°25.13'N. 77°13.38'W. alt. 40 m: *E. annuus* ssp. annuus (DF 31657a), *E. annuus* ssp. septentrionalis (DF 31657b)

Cytology

For cytological investigations we used root tips which were pretreated with colchicine (0.05%) for 1/2 hour, then fixed in ethanol:acetic acid (3:1), and stained and squashed in lacto-propionic orcein (Dyer 1963). At least five metaphases from at least two root tips per plant were counted for the determination of chromosome numbers. Voucher specimens are deposited in Z/ZT.

Herbarium specimens

For the evaluation of previously published chromosome counts, we checked all available voucher specimens indicated in literature (or in some cases digital images or photocopies of the original specimens; Tab. 3). These specimens were classified according to the morphological characters given in Table 1, and based on Cronquist (1947, 1991).

Results

The data for chromosome numbers of plants investigated in this study are presented in Table 2, and the data for published chromosome numbers supported by herbarium specimens are in Table 3. Out of the total of 125 records of chromosome numbers (Tabs. 2 and 3), we were able to determine the morphotype (according to Tab. 1) for 99 specimens (77 from N. America and 22 from elsewhere in the world; Tab. 5). Table 4 presents a comparison of the taxa as given on the available herbarium sheets with our morphotype determinations. The data demonstrate the considerable uncertainty that exists about the identity of these taxa. We found that the majority of specimens labeled as *E. annuus* did have the characters of morphotype "annuus", though we assigned one third of the specimens to morphotype "septentrionalis". In contrast, the majority of

Tab. 2. Voucher specimens with the corresponding chromosome numbers and morphotypes (*annuus*, *septentrionalis* or *strigosus*) for our own counts. The voucher identification consists of a population number, the identity of the mother-plant, and the identity of the offspring plant; each identifier is separated by a slash.

Voucher identification	2n	Morphotype
Europe		
DF 14308/4/1	27	*annuus*
DF 14308/6/1	27	*annuus*
DF 14314/7/1	27	*annuus*
DF 14353/3/1	27	*annuus*
DF 14383/7/1	27	*annuus*
MB 13786/1	27	*annuus*
MB 13786/2	27	*annuus*
USA		
DF 31601/2/1	27	*septentrionalis*
DF 31601/5/1	27	*septentrionalis*
DF 31606/10/1	27	*annuus*
DF 31606/15/1	18	*strigosus*
DF 31606/18/1	18	*strigosus*
DF 31606/23/1	18	*strigosus*
DF 31621/1/1	27	*septentrionalis*
DF 31621/2/1	27	*annuus*
DF 31621/16/1	27	*septentrionalis*
DF 31621/27/1	27	*septentrionalis*
DF 31621/31/1	27	*annuus*
DF 31627/1/1	27	*annuus*
DF 31627/2/1	27	*annuus*
DF 31627/9/1	27	*septentrionalis*
DF 31627/13/1	27	*septentrionalis*
DF 31627/14/1	27	*septentrionalis*
DF 31628/2/1	27	*annuus*
DF 31628/6/1	27	*septentrionalis*
DF 31628/7/1	27	*annuus*
DF 31628/15/1	27	*septentrionalis*
DF 31628/27/1	27	*annuus*
DF 31640/2/1	27	*annuus*
DF 31640/9/1	27	*septentrionalis*
DF 31640/17/1	27	*annuus*
DF 31657/5/1	27	*annuus*
DF 31657/6/1	27	*septentrionalis*
DF 31657/9/1	27	*septentrionalis*
DF 31657/11/1	27	*septentrionalis*
DF 31657/18/1	27	*annuus*

herbarium specimens labeled as *E. strigosus*, were of morphotype "septentrionalis" (24 of 34 or 70%) and some were of morphotype "annuus" (17%). The sample does not provide a reliable indication of the relative abundance of the various morphotypes, but some points are worth noting. As is shown in Table 5, in North America, 55% of the

Tab. 3. Chromosome counts in literature with indication of vouchers: Voucher specimens with the corresponding chromosome numbers, origin of the plants investigated, taxon in the respective reference, and our reclassification of the checked vouchers (*annuus*, *septentrionalis* or *strigosus*). n.a.: the respective specimen was not available; *: see comment in the text.

Reference resp. voucher identification	Chrom. number 2n	Origin of plants	Published as	Our classification	Mowing effect
Anderson et al. 1974 (vouchers in DS)		USA			
Gegory 524	27		*strigosus*	*septentrionalis*	probably
Wiggins 19837	9_{II} [=18]		*ramosus*	*strigosus*	
Hill 1995 (BDWR)		?			
Hill 90299	27		*annuus*	n.a.	
Hong and Zhang 1990 (PE)		China			
PB82094	9_{II} [=18]		*annuus*	n.a.	
Hsu 1967 (TAI)		Taiwan			
3118	27		*annuus*	*annuus*	
Huber and Baltisberger 1992 (Z/ZT)		Europe			
WH13657/1	27		*annuus*	*annuus*	
WH13657/2	27		*annuus*	*annuus*	
WH13657/3	27		*annuus*	*annuus*	
WH13657/4	27		*annuus*	*annuus*	
WH13657/5	27		*annuus*	*annuus*	
WH13659/1	27		*annuus*	*septentrionalis*	
WH13659/2	27		*annuus*	*septentrionalis*	
WH13659/3	27		*annuus*	*septentrionalis*	
WH13659/4	27		*annuus*	*septentrionalis*	
WH13659/5	27		*annuus*	*septentrionalis*	
WH13660	27		*annuus*	*annuus*	
WH13661	27		*annuus*	*annuus*	
Kapoor 1972 (SMUH)		Canada			
Kapoor 71-167-1	27		*strigosus*	n.a.	
Keil et al. 1988		USA			
K 11636 (ASU)	27		*strigosus*	*septentrionalis*	yes
K 12823 (OBI)	9_{II} [=18]		*strigosus*	*septentrionalis*	
Kondo 1972 (NCU)		USA			
Kondo and Rao 732	18_{II} [=36]		*annuus*	n.a.	
Löve and Löve 1982 (WIN)		Canada			
L & L 5935	27		*septentrionalis*	*septentrionalis*	
Mehra et al. 1965 (PANJAB)		India			
Mussoorie	27		*annuus*	n.a.	
Simla	27		*annuus*	*annuus*	

Tab. 3. (continued)

Reference resp. voucher identification	Chrom. number 2n	Origin of plants	Published as	Our classification	Mowing effect
Montgomery and Yang 1960 (OAC)					
Guelph (31717)	27	Canada	*annuus*	*annuus*	
Guelph (31719)	27	Canada	*annuus*	*annuus*	
Guelph (31720)	27	Canada	*annuus*	*annuus*	
Guelph (31721)	27	Canada	*annuus*	*annuus*	
Huntsville (31722)	27	Canada	*annuus*	*annuus*	
Huntsville (31726)	27	Canada	*annuus*	*annuus*	
Pancake Bay (31727)	27	Canada	*annuus*	*annuus*	
Puslinch	27	Canada	*annuus*	n.a.	
Steeleville	27	USA	*annuus*	n.a.	
Theodosia	27	USA	*annuus*	n.a.	
Union	27	USA	*annuus*	n.a.	
Huntsville (31762)	27	Canada	*strigosus*	*septentrionalis*	
Huntsville (31764)	27	Canada	*strigosus*	*septentrionalis*	
Huntsville (31771)	27	Canada	*strigosus*	*septentrionalis*	
Huntsville (31774)	27	Canada	*strigosus*	*septentrionalis*	
Huntsville (31775)	27	Canada	*strigosus*	*septentrionalis*	
Guelph (31765)	27	Canada	*strigosus*	*annuus*	
Guelph (31767)	27	Canada	*strigosus*	*annuus*	
Guelph (31770)	27	Canada	*strigosus*	*septentrionalis*	yes
Puslinch	36	Canada	*strigosus*	n.a.	
Waterloo	27	Canada	*strigosus*	n.a.	
Alton (26877)	27	USA	*strigosus*	*septentrionalis*	
Centreville (31769)	27	USA	*strigosus*	*septentrionalis*	
Poplar Bluffs (31763)	27	USA	*strigosus*	*septentrionalis*	
Poplar Bluffs (31766)	27	USA	*strigosus*	*septentrionalis*	
Poplar Bluffs (31772)	27	USA	*strigosus*	*septentrionalis*	
Union (31768)	27	USA	*strigosus*	*annuus*	
Union (31773)	27	USA	*strigosus*	*annuus*	
West Plains (26876)	27	USA	*strigosus*	*septentrionalis*	
West Plains (26878)	27	USA	*strigosus*	*septentrionalis*	
Morton 1981 (WAT)		Canada			
Morton NA28	27		*annuus*	*annuus*	
Mulligan 1961 (DAO)		Canada			
Mulligan and Rae 2122	27		*strigosus*	*annuus*	probably
Nesom 1978 (NCU)		USA			
Nesom R319	27		*annuus*	n.a.	
Treiber 1476	27		*annuus*	*septentrionalis*	
Whetstone 3520	27		*annuus*	n.a.	
Whetstone 4091	27		*annuus*	n.a.	
Whetstone 4474	27		*annuus*	*septentrionalis*	
Whetstone 4728	27		*annuus*	*septentrionalis*	yes
Nesom R305	27		*annuus*	n.a.	
Nesom R317	27		*annuus*	*septentrionalis*	

Tab. 3. (continued)

Reference resp. voucher identification	Chrom. number 2n	Origin of plants	Published as	Our classification	Mowing effect
Nesom R324	18/27		*strigosus*	pop. voucher!*	
Nesom R325	18/27		*strigosus*	pop. voucher!*	
Whetstone 2916	27		*strigosus*	*septentrionalis*	
Whetstone 2995	27/36		*strigosus*	n.a.	
Whetstone 3218	18/27		*strigosus*	n.a.	
Whetstone 4279	18		*strigosus*	n.a.	
Whetstone 4499	27		*strigosus*	*septentrionalis*	
Whetstone 4666	18		*strigosus*	*strigosus*	
Peng and Hsu 1977, 1978 (TAI)		Taiwan			
Peng 1385	27		*annuus*	*annuus*	
Semple 1985 (WAT)		USA			
Semple and Brouillet 4397	36		*strigosus*	*strigosus*	yes
Semple and Chmielewski 1987 (WAT)		USA			
Semple and Brouillet 7355	18		*strigosus*	*strigosus*	
Semple et al. 1989 (WAT)		USA			
Semple, Brammall and Hart 3002	9_{II} [=18]		*strigosus*	*annuus*	
Solbrig et al. 1964 (GH)		USA			
Anderson 2201	27		*annuus*	n.a.	
Porter 950	27		*annuus*	n.a.	
Porter and Svenson 911	27		*annuus*	n.a.	
Porter and Svenson 869	27		*strigosus*	*septentrionalis*	
Porter and Svenson 916	27		*strigosus*	*septentrionalis*	
Solbrig et al. 1969 (DS)		USA			
Raven 19484	27		*annuus*	*annuus*	
Raven 19439	27		*strigosus*	*septentrionalis*	
Raven 19446	27		*strigosus*	*septentrionalis*	
Raven 19480	27		*strigosus*	*septentrionalis*	
Taylor 1967 (DAO)		Canada		not from sect.	
Taylor and Sherk 4865	n = 35-36		*strigosus*	*Phalacroloma*!	
Turner and Flyr 1966 (TEX)		USA			
Turner 4924	9II [=18]		*strigosus*	*strigosus*	
Vachova and Ferakova 1980 (SLO)		Europe			
Ferakova	27		*strigosus*	n.a.*	
Vahidy et al. 1987 (MO or KUH)	USA				
Vahidy and Davidse 21	n = 18		*strigosus*	n.a.	

Tab. 4. Comparison of taxonomic determinations of 66 available herbarium specimens (see Tab. 3) of *Erigeron* spp. according the herbarium label, and the morphotype according to the characters listed in Table 1.

Morphotype	Herbarium label			
	Erigeron annuus	*Erigeron ramosus*	*Erigeron septentrionalis*	*Erigeron strigosus*
annuus	19	0	0	6
septentrionalis	8	0	1	24
strigosus	0	1	0	4
population voucher	0	0	0	2
other	0	0	0	1

plants investigated were of morphotype "septentrionalis", whereas in the samples from other parts of the world (mainly Europe) morphotype "annuus" was more abundant (77%). There were only eight plants of morphotype "strigosus" (i.e. 8% of the sample), all of which were from North America.

A clear association between morphotype and chromosome number is evident, both for our own counts (Tab. 2) and for those previously published counts for which voucher specimens were available (Tab. 3). No specimens of morphotype "strigosus" were triploid. Plants of morphotypes "annuus" and "septentrionalis" were mostly triploid (Tab. 5), though there was a single record of diploid plants of both morphotypes "annuus" and "septentrionalis". All records of these morphotypes from Europe proved to be triploid. There are also a few records of diploid and tetraploid plants in Table 3 for which we were unable to determine the morphotype. Two vouchers are "population vouchers" representing populations with more than one chromosome number, and we can therefore not correlate the morphotype with any of these chromosome numbers (Tab. 3*).

Discussion

Morphology

A general problem of the two main taxa within section *Phalacroloma* (Cronquist 1947), *E. annuus* and *E. strigosus*, is that they are only weakly delimited and the characters are broadly overlapping. The infraspecific taxon "septentrionalis" was originally treated as a variety within *E. strigosus* but Wagenitz (1965) transferred it as a subspecies to *E. annuus*. Plants of the morphotype "septentrionalis" tend to have narrower leaves with fewer teeth than those of typical *E. annuus*. The hairiness of the stem is frequently used to distinguish the taxa, but it is so variable that it is hardly a good morphological trait to define an intermediate form. In addition, herbarium specimens and personal observations in the field showed that there is an important effect of phenotypic plasticity: plants that have been cut back show a shift in morphological characters from *E. annuus* towards morphotype "septentrionalis". We refer to this as the "mowing effect". Indeed, even the type specimen of the taxon "*septentrionalis*" (in GH!), which consists of two individual plants which had been cut back while living, exhibits this "mowing effect". This environmental effect must be taken into account when infer-

Tab. 5. Summary of data on chromosome numbers for 99 specimens representing 3 morphotypes of *Erigeron* section *Phalacroloma* collected either in North America (NA) or elsewhere in the world (Inv.).

Morphotype		Chromosome number 18	27	36	Total
annuus	NA	1	26	0	27
	Inv.	0	17	0	17
septentrionalis	NA	1	41	0	42
	Inv.	0	5	0	5
strigosus	NA	7	0	1	8
	Inv.	0	0	0	0

ring the taxon from morphological characteristics. We therefore conclude that morphotype "septentrionalis" is part of the morphological variability of *E. annuus* and not a distinct taxon.

Cytology and its relation to the morphotypes

Different ploidy levels, viz. 2n = 2x = 18, 2n = 3x = 27, 2n = 4x = 36 and some aneuploid numbers can be found in the literature, there are no obvious groupings of taxa and ploidy levels. However, determinations of morphotypes based on a rigorous application of the charcters in Table 1 reveals some simple patterns. Firstly, all plants from Europe (Tabs. 2 and 3 as well as additional indications in the literature) proved to be triploid, and are probably apomictic. In North America di-, tri- and tetraploid plants have been recorded, suggesting that sexual reproduction may also occur in all taxa. Secondly, specimens of our own counts (Tab. 2) and most of the available voucher specimens cited in literature (Tab. 3) revealed that morphotype "strigosus" is diploid or tetraploid, while morphotypes "annuus" and "septentrionalis" are mainly triploid. The main reason for this clear grouping is the fact that plants published as triploid *E. strigosus* mostly correspond to morphotype "septentrionalis" (i.e. narrow leaved forms of *E. annuus*). Some of the plants identified on herbarium labels as *E. strigosus* also show a "mowing effect".

Although the association between morphotype and chromosome number proposed here seems to be robust, a few apparently anomalous records require comment. Vachova and Ferakova (1980) give 2n = 27 for *E. strigosus* from Slovakia. The corresponding specimen (deposited in SLO) could not be found, and the plants investigated by Vachova and Ferakova could therefore not be checked. This is because "most probably only the achenes were kept..." (Ferakova, in litt.). A herbarium specimen of comparable plants (but from another site) was sent to us; "this material [cited in Vachova and Ferakova (1980)] should be identical with the specimen I found in other locality... which we enclose" (Ferakova, in litt.). These plants are morphotype "septentrionalis" which suggests that the plants investigated by Vachova and Ferakova (1980) may not have been *E. strigosus* (Tab. 3*).

Tahara (1915, 1921) published 2n = ~26 and always explicitly mentioned that this was an approximate number. This uncertainty can be better understood if we take into account that *E. annuus* was considered at that time to be diploid, and so an even number of chromosomes would have been expected. The same interpretation can be applied to the counts of Suzuki and Taguti (in Ikeno 1935) who mainly counted 2n = 27, but rarely found 2n = 26. Ikeno (1935) interpreted the additional chromosome as the result of a chromosomal mutation, which ended up in an "unbalanced" chromosome number (2 x 13 + 1).

Bijok et al. (1972) give 2n = 27, Chojnacki et al. (1980, 1982; at the same institute as Bijok and his coworkers) give 2n = 26 as well as 27 for various specimens from Poland. Bijok et al. (1972; Fig. 2) and Chojnacki et al. (1980; Fig. 1A) each published what appears to be the same illustration of a metaphase, except that one single chromosome has been omitted in Chojnacki et al. (1980). Thus, in these studies there remains some doubt concerning the exact chromosome number of *E. annuus*.

Peng and Hsu published the number 2n = 27 for *E. annuus* in 1977 as well as in 1978. As in both papers the same voucher specimen (with the same number Peng 1385) is indicated, the same count is published twice. The result published by Hong and Zhang (1990) should be mentioned here, because it provides the first proof of a diploid plant of this section outside North America.

Mating system and morphology

The first description of double fertilization in Asteraceae (Land 1900) was given for a plant of *E. strigosus* from Chicago (USA). Clearly this plant has to be considered sexual, but Land gives no further description of its morphology. Tahara (1921) reported from Tokyo the occurrence of apogamy in *E. annuus* but did not describe the morphology of the plants investigated. Later, McDonald (1927) reinvestigated *E. annuus* and *E. strigosus* for studies of seed development. Both species turned out to be agamospermous. McDonald mentioned the "surprising similarity between the two species: the size and appearance of the ovule; time of development of the integument; lack of a nutritive layer on the inner border of the integument; character and time of disappearance of the nucellus; and absence of tetrad stage in the development of the embryo-sac – all were as has been described for the preceding plant" (*E. annuus*). The description clearly separates this specimen of *E. strigosus* from the plant investigated by Land (1900). Thus, even these early descriptions reveal that we need to take into account two major groups – one agamospermous and one sexual – and within the agamospermous group, two morphotypes that are obviously different, one of them resembling *E. strigosus*.

Several papers deal with plants originating from Hortus Bergianus (Stockholm). Holmgren (1919) described apogamy in *E. annuus* and gave a rough description of the plant, which in most respects resembled *E. annuus* except that the basal leaves were entire and lanceolate. We suspect that this plant was morphotype "septentrionalis". Gustafsson (1936) investigated plants determined as *E. annuus* and *E. ramosus* (= *E. strigosus*), respectively. Both taxa proved to be apomictic, but as no morphological indications are given we can nothing say about the morphotypes; nevertheless it seems likely that the plant referred to as *E. ramosus* was morphotype "septentrionalis". Bergman (1944) investigated one individual named as E. cfr. annuus which was also apomictic though nothing is known of its morphotype. Fagerlind (1947) investigated one plant which "presumably belongs to the same biotypes or biotype group that supplied Bergman's and parts of Holmgren's material", but again nothing can now be said about the morphology of this plant.

Recently Noyes (Noyes 2000b, Noyes and Rieseberg 2000) published an extensive study on sexual x agamospermous hybrids within *E. annuus* and *E. strigosus*.

Erigeron annuus proved to be triploid and apomictic while *E. strigosus* was diploid and sexual. Noyes showed that triploid plants are able to produce viable pollen with 9 or 18 chromosomes (haploid and diploid, respectively). Gene flow and therefore genetic variability can thus be the product of (probably rare) sexually produced offspring; these may be one of the main sources of the morphological variability within the taxa of section *Phalacroloma*.

Conclusion

Overlapping traits, combined with extensive phenotypic plasticity (Stratton 1988, 1991), suggest that morphotype "septentrionalis" should be included within *E. annuus*. This is supported by the "mowing effect" which makes it possible for leaf morphology to switch from morphotype "annuus" to morphotype "septentrionalis". Additionally *E. annuus* (including morphotype "septentrionalis") is (mostly) triploid and agamospermous, in contrast to the diploid (or tetraploid) and sexual *E. strigosus*.

It has commonly been assumed that *E. strigosus* was introduced to Europe (Wagenitz 1965, Halliday 1976). However, published cytological data as well as our own investigations provide no support for the assertion that *E. strigosus* exists in Europe.

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