

the non-homologous chromosomes of the genome. Ring formation in *T. dubius* × *porrifolius* and evidence of heteromorphic pairing in *T. dubius* × *pratensis* indicate that differences in homology do exist. Around these structural differences, with the resultant interference with random chromosome recombination (because of non-viability of deficient gametes), could be built the association of distinctive genes which mark each species. If all six chromosomes of each parental genome were non-homologous for deficiencies caused by translocation or interchange of essential segments, as compared with the corresponding member of the other parental genome, only those gametes containing a reconstituted parental genome with respect to these structural differences would be viable. Disregarding crossing-over, and given random distribution of the chromosomes of each of the six pairs, one genome of each of the parental species should be reconstituted in each $2^6 =$ sixty-four gametes. In other words, approximately 3.1 per cent of the gametes should contain a parental set of chromosomes. The maximum fertility, if only reconstituted gametes were viable, would be 3.1 per cent, and the F_2 would fall into three classes, reconstituted parental species, 25 per cent for each, and reconstituted F_1 hybrids, 50 per cent. Since any deficient chromosome segments of one parental species might be compensated for by the addition through crossing-over of non-deficient segments of the other parent, the net effect of crossing-over would be an increase in the variability of the F_2 , and the genes on the cross-over segments would behave in the manner which Winge has described. Some such mechanism might explain the restored fertility in the F_2 and subsequent generations of Winge's hybrids, and the infrequency of detectable later generations in our wild populations.

The mechanism of origin of the amphiploid species, whether by somatic or gametic doubling in the F_1 is obscure. Winge's observation of tetraploid sectors in root-tip tissues would favor the former explanation, as would the absence of pollen grains exceeding the diploid size range in all of the diploid hybrids examined in the present study. Supporting the latter explanation would be the presence of spore triads in some of our hybrids, which suggests that diploid pollen grains might be produced, and the lack of extended vegetative growth. It should be noted that positive evidence favoring either of these mechanisms was observed only in the one of the three hybrid combinations for which no amphiploid is known, that between *T. porrifolius* and *T. pratensis*.

Whatever the mechanism of origin, it is apparent that the amphiploids do not originate with great frequency. The four known colonies probably represent four independent instances of chromosome doubling, and the subsequent establishment of the resultant tetraploid. Considering the frequency of all three F_1 hybrid combinations, however, chromosome doubling must be an exceedingly rare event.

For theoretical reasons, its frequent occurrence in species hybrids with essentially regular meiotic pairing is not to be expected, and amphiploids derived from such should be unsuccessful.

In spite of these theoretical handicaps, the amphiploids of *Tragopogon* have appeared, and have attained a degree of success. Although the populations are still small and precarious, fertility is good, and these species are competing successfully with their parents. Crossing-over has not led to deterioration, presumably because each chromosome usually pairs with its exact homologue, and the consequences of crossing-over, therefore, are not deleterious. Fertility ought to improve with succeeding generations, since any genetic factor which will increase fertility—and there is wide variation in this respect—will enjoy a real selective advantage.

The ecological characteristics of the new amphiploids are not yet apparent. In all instances, they occur within the ecological amplitude of the most restricted parental species. The ecological requirements of natural amphiploids are often such that they have achieved an ecological and geographical distribution somewhat different from the species from which they are presumed to have been derived (Clausen *et al.*, 1945). Since, in both instances, the present amphiploids combine genomes from species with significantly different ecological requirements, it will be interesting to follow their ecological development. At the present time, it is apparent that they have not spread far from their point of origin.

TAXONOMIC CONSIDERATIONS.—The two newly originated amphiploids are to be considered taxonomic species for the following reasons: (1) They are natural groups characterized by a combination of distinctive morphological features. (2) They are reproducing themselves under natural conditions. (3) Gene interchange between the amphiploids and the parental species is prevented by a genetic barrier (ploidy level), and presumably residual sterility factors—evident in the F_1 hybrids—would prevent free interbreeding between the two.

Search of the systematic literature has not revealed the existence of these amphiploid species in Europe, although it would be surprising if they do not occur there. The identification of many obscure species which have been proposed in *Tragopogon* must await a comprehensive taxonomic and cytogenetic study of the genus. Accordingly, these two amphiploids are here described as new species.

Tragopogon mirus Ownbey, sp. nov.—Herbae biennes primum obscure floccosae deinde glabrae glaucaeque. Folia lineari-lanceolata semi-amplexicauliausque ad 5 cm. lata paulatim attentuata, marginibus non crispis, apicibus non cirrosis. Capitula multiflora, pedunculis inflatis fistulosis usque ad 15 mm. crassis. Bractee involucri lineari-lanceolatae ubique virides, in plantis robustioribus plerumque 13. Ligulae bicoloratae ad apicem lilacinae ad basem flavae bracteis paulum breviores. Achenia rostratae conjuncta 25–35 mm. longa, exteriora fusca, in-

teriora straminea, rostro corpore subaequilongo, pappo cervino.

Type: Washington. Whitman County: in fertile bottom land, Pullman, June 9, 1949, *Owney 3195*, in Herbarium of the State College of Washington, Pullman.

Tragopogon miscellus Ownbey, sp. nov.—Herbae biennes primum obscure floccosae deinde glabrae viridesque. Folia lineari-lanceolata semi-amplexicaulia usque ad 3 cm. lata abrupte attenuata, marginibus crispis, apicibus cirrosis. Capitula pluriflora, pedunculis inflatis fistulosis usque ad 10 mm. crassis. Bracteae involucri lineari-lanceolatae in plantis robustioribus plerumque 13, marginibus purpureis. Ligulae flavae bractea dimidia subaequilongae. Achenia rostraque conjuncta 25-35 mm. longa, exteriora fusca, interiora straminea, rostro corpore subaequilongo vel longiore, pappo cinereo.

Type: Idaho. Latah County: in fertile bottom land, Moscow, June 10, 1949, *Owney 3196*, in Herbarium of the State College of Washington, Pullman.

SUMMARY

Three diploid ($n=6$) species of the Old World genus *Tragopogon* (Compositae), *T. dubius*, *T. porrifolius*, and *T. pratensis*, have become widely naturalized in North America. In southeastern Washington and adjacent Idaho, where all three occur, extensive natural hybridization is taking place. Each species crosses readily with both of the others, and wherever two or more grow together, easily detected F_1 hybrids are frequent. These dip-

loid hybrids for all three species combinations are highly sterile, not more than 1-2 per cent of the flowers producing fruits with embryos. They are intermediate only in the sense that they recombine certain dominant characteristics of the parental species involved. F_2 and back-cross individuals are absent or nearly so. Meiosis in the hybrids is fairly regular, although some multivalents and univalents are formed, particularly in *T. dubius* \times *T. porrifolius*. Four small amphiploid populations were discovered in 1949. These represent apparently four recent and independent instances of the doubling of the chromosome sets, two cases each for the *T. dubius* \times *T. porrifolius* and *T. dubius* \times *T. pratensis* hybrids. These two tetraploid entities ($n=12$) are fairly regular meiotically, usually forming bivalents at metaphase I in pollen mother cells. They are moderately fertile, on the average from 52-66 per cent of the flowers producing fruits with embryos. They are established and true-breeding entities, although population size is still precariously small. Morphologically, they are like the corresponding diploid hybrids except for conspicuous "gigas" features and their very evident fertility. Their cell volume, as revealed by measurement of the spherical pollen grains, is almost precisely the summation of the cell volumes of the two parental genomes. They are accorded species rank, described and named *T. mirus* (amphiploid *T. dubius* \times *T. porrifolius*) and *T. miscellus* (amphiploid *T. dubius* \times *T. pratensis*).

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