PLANT CHIMERAS AND THEIR RELATION TO HEREDITARY PHENOMENA.[1]

(*Abstract.*)

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Vegetable chimeras, known also as graft hybrids, are plants of a hybrid nature, which, however, have not arisen through seed production, but as adventitious shoots springing from the callus formed at the juncture of stock and scion in grafting. Two classes of chimeras are recognized, sectorial and periclinal. In sectorial chimeras the tissues of the two parents or members, stock and scion, are united side by side in the growing point, so that the parts of the chimera resembling the respective parents may be separated longitudinally. A periclinal chimera is one in which the center of the plant consists of tissue of one parent overlaid by a layer of tissue of the other plant from one to two, or possibly more, cells in thickness. In the latter case the individuals may often bear the most striking resemblance to real hybrids, being complete blends between the two parents in both vegetative and reproductive parts.

Chimeras have been known for about 270 years. Probably the first on record was produced in Italy in 1644, between the citron and an orange, the fruit resembling an orange with a sector of citron. Such fruits were called Bizarrias because of this peculiar appearance. In recent years similar chimeras have been reported as originating in Florida between the orange and grapefruit. A very beautiful chimera of recent origin is that of an apple produced by Prof. W. E. Castle of the Bussey Institution by grafting a "Boston stripe" upon the "golden russet." In this case the stem end or half of the apple is russet, while the blossom end is of the "Boston stripe." Among the more famous chimeras or graft hybrids may be mentioned the much-discussed *Cytisus Adami* which originated near Paris in about 1826. This was said to have been produced as the result of a graft between *Cytisus purpurea* and the common laburnum, or golden chain, *Cytisus laburnum*. Another is the whitethorn medlar, *Crataego-Mespilus,* which is said to have originated near Metz, Germany, by grafting the whitethorn, *Crataegus monogyna,* upon the medlar, *Mespilus germanicus*. As the above-mentioned species do

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not cross, the origin of these wonderful and perplexing forms remained a matter of speculation until a few years ago, when Professor Hans Winkler produced chimeras experimentally between the common nightshade, *Solanum nigrum,* and the tomato, *Solanum lycopersicum.* Using the cleft method of union, Winkler grafted shoots of the seedling tomato upon the stem of the nightshade. As soon as union had taken place, the scion was cut near its base in such a way that the cut surface consisted partly of nightshade and partly of tomato tissue. Of the adventitious shoots arising, only those which sprang from along the line of the union of the two specifically different tissues were allowed to grow. Among a large number of adventitious shoots, about 3,000 in all, several were found which gave the desired result; i. e., they were apparently hybrid in character. Some resembled more closely the nightshade, some the tomato, while still others were intermediate as to foliage, flower, and fruit. A number of these were planted as cuttings and were grown to flower and fruition. A few set seed, while others developed fruit but no seeds. The seeds of one of them, which Winkler named *Solanum tubingense* and which more closely resembled the nightshade, developed into pure nightshades, while those of another, *Solanum proteus,* more closely resembling the tomato, gave pure tomato plants. Although Winkler had produced experimentally plants that were hybrid in appearance, inasmuch as the two plants were wholly blended, yet it was clear that they were not real hybrids. The real explanation was still to be found. This was accomplished by Professor Erwin Bower of Berlin, who discovered the key to the situation in his study of the tissues of a variegated geranium. Plants which bear green leaves with white borders are well known. Such leaves are due to the fact that the green central part of the leaf tissue is covered over by a layer of colorless tissue two or more cells in thickness, and the thin edges of such leaves being, as a consequence, made up of colorless cells exclusively. Thus the colorless tissue covers the leaf as a glove covers the hand. Now it is supposed that in the growing point from which such leaves spring, a layer of white (colorless) cells covers the green tissue beneath, and a leaf originating from such growing point will consist of green cells within and white cells without. Likewise, in the formation of a terminal bud at the juncture of the two parental tissues of the graft, the tissues of one parent, whether stock or scion, by growing a little faster, may soon cover that of the other parent, and the result will be a

shoot composed internally of cells of one parent with a covering made up of cells of the other parent. This results in a periclinal chimera. If, on the other hand, one-half or a sector of the terminal bud be formed wholly of cells of one parent, the parts of the resultant shoot resembling the respective parents can be separated longitudinally, and the result is a sectorial chimera.

Winkler's apparent hybrids were, therefore, periclinal hybrids. For example, his *Solanum tubingense* was a periclinal chimera in which the inside of the plant consisted of nightshade overlaid with one layer of tomato tissue, since the seeds produced gave pure nightshades. It will be remembered that the germ cells or spore-bearing tissues are derived from the sub-epidermal cells. On the other hand, *Solanum proteus,* resembling more closely the tomato, and whose seeds produced pure tomato plants, is a periclinal chimera in which the interior is nightshade with a covering of tomato, two cells in thickness. Two other chimeras were developed, namely *Solanum gaertnerianum,* consisting of tomato on the inside and a two-celled layer of nightshade on the outside, and *Solanum koelreuterianum* with only one layer of tomato cells on the outside.

From the foregoing, it is clear that these plants are not hybrids, inasmuch as their seeds do not give plants of a hybrid character; they are truly chimeras. However, Winkler obtained one plant which, if his observations are correct, seemed to be a real hybrid. This, the fifth produced, he called *Solanum Darwinianum.* In *Solanum Darwinianum* Winkler claims that 48 chromosomes were counted in the reproductive cells, this number representing one-half the total number of chromosomes for the two parents, namely 96 (24 in the tomato and 72 in the nightshade). If this be correct, nightshade and tomato cells, or some of them, must have actually fused in the process. *Solanum Darwinianum* seems, therefore, to be the only real graft hybrid in the world.

If it be possible to produce by the process of grafting a cross between two species that cannot be made to cross sexually, to what extent and in what manner will this fact influence current conceptions of heredity? Careful investigators, though receiving new ideas with sympathy, will, no doubt, accept Winkler's conclusions with much reserve if not with skepticism, and this they should do until his statements are verified. Every experienced cytologist knows that an accurate counting of chromosomes where they are present in large numbers is a very difficult task, and results based upon scanty material without verification cannot be regarded as strictly reliable.

If it be established beyond all doubt that real graft hybrids can be produced, the field of the florist and horticulturist will be considerably widened. The possibility of combining strains that do not cross is at once apparent, and, as vegetative propagation would naturally be easy, the new blend obtained will be easily kept pure and constant because of this mode of propagation. It is conceivable that many of the ends sought in crossing, such as increasing resistance to disease, to severe climatic conditions, etc., the improvement of quality of fruit, foliage, etc., may be reached in the development of graft hybrids. However, because of difficulties encountered, it is equally possible that little more than the production of a few interesting freaks will be the fulfillment of the experimenter's happiest dream.

As to the effect upon present conceptions of hereditary principles, little is to be expected. The discovery of parthenogenesis did not overthrow the theory of sex in plants, nor did the presence of apogamy in ferns upset the doctrine of antithetic alternation of generations in the higher plants. Far from working mischief, these singular phenomena did much toward modifying the rigidity of certain fixed conceptions, and of making more flexible principles of thought that tend to a sort of dogmatic rigidity.

In conclusion, sex hybrids which bear striking resemblances to chimeras, such as appear in plants of variegated foliage should not be confused with real chimeras. Chimeras are not hybrids at all. It would be just as proper to speak of the numerous variegated coleus varieties, which are due merely to bud variation, as chimeras, as to place sex hybrids, which owe their variegated character to crossing, in the category of chimeras.

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