The Origin of Bread Wheats.

By Prof. R. RUGGLES GATES.

AN immense amount of work has been done in recent years in crossing species of cereals and investigating the chromosome behaviour of the hybrids. These crosses include not only many cultivated and wild species of wheat, rye, oats and *Ægilops*, but also intergeneric crosses between these four genera, *Triticum*, *Secale*, *Avena*, and *Ægilops*. The results have thrown much light on the phylogeny of the bread wheats and their relation to other genera.

In all these genera the basal haploid chromosome number is 7, and each genus except rye contains species with $2n$, $4n$, and $6n$ chromosomes. It therefore seemed not unlikely that in all three genera the hexaploid condition had been independently reached, through parallel evolution, and that the bread wheats had therefore been derived from crosses between tetraploid and diploid species of wheats, forming triploid sterile hybrids in which chromosome doubling then gave rise to fertile hexaploid forms. The recent work has, however, brought much evidence to show that the genera *Ægilops* and *Triticum* are very closely related as regards some of their species, and that *Ægilops cylindrica* is directly or indirectly one of the ancestors of the hexaploid bread wheats or soft wheats. This latter view was first put forward by Percival in 1921 on taxonomic grounds, and has now been strongly substantiated by genetical and cytological work, confirmed by various other investigators. Various workers now approximate to the view that the *A* and *B* sets (of 7 chromosomes each) in *T. vulgare* came from the emmer ($4n$) wheats, while the *C* set has been derived from *Ægilops cylindrica* or its diploid ancestor, and a fourth (*D*) set from *Æ. ovata*.

Popova (1923) found that much natural crossing took place in Turkestan, near Tashkent, where the hills were covered with wild *Ægilops cylindrica*, *Æ. squarrosa*, and *Æ. crassa*, which crossed freely with wheat in the neighbouring fields. *Ægilops* species showed numerous parallel variations, as indicated by the variety names, *flavescens*, *rubiginosa*, *albescens*, *ferruginea*, *brunnea*, etc., in different species. The wheats also show parallel variations, awned or awnless, smooth or pubescent, ears white, red, brown, etc. Also *Æ. triuncialis* ($4n$), like the hard ($4n$) wheats, is resistant to rust and has a solid straw, while the other three species of *Ægilops* mentioned are affected by rust and have a hollow stem, like the soft ($6n$) wheats.

The chromosome numbers in more than twenty species of *Ægilops* have now been counted, chiefly by Schiemann (1928) and Sorokina (1928). Among the diploid species ($2n = 14$) are *Æ. squarrosa*, *Æ. speltoides* and *Æ. caudata*, while *Æ. triuncialis*, *Æ. cylindrica*, and *Æ. ventricosa* are tetraploid, and *Æ. crassa* and *Æ. turcomanica* are hexaploid. *Æ. crassa* from Turkestan is, however, tetraploid. Zhukovsky divided the genus into nine sections. In each of these sections the chromosome number is uniform, but the sections do not coincide with chromosome numbers, as is the case in *Triticum*. Asia Minor appears to be the centre of distribution of the genus, but evidently the classification of the species into sections has not yet reached a definitive state.

Crosses have been made between three subspecies of *Æ. triuncialis* ($n = 14$) and two of rye ($n = 7$), by Karpechenko and Sorokina (1929), using the rye as male parent. The F_1 grains were mostly shrivelled and the hybrid plants resembled *Ægilops* in the majority of their characters, but the fragility of rachis in rye was dominant. The 21 chromosomes

in meiosis showed 5-7 bivalents, with the members of each pair end to end. Occasionally a trivalent of three chromosomes arranged tandem was seen.

Philipchenko (1930) made a study of the development of the ear in different species of wheat, *Ægilops*, and rye. He was so impressed with the fact that in *Triticum monococcum* ($n = 7$) the development is different from that of the $4n$ and $6n$ wheats and more like rye, that he proposed to regard it as representing a separate genus, *Monococcum*. The systematist's view has been that *T. monococcum* (and the wild form *T. ægilopoides*) stands apart from other species of *Triticum*. To place it in a genus by itself seems, however, rather an extreme action. Philipchenko found that the ear development in the hard ($4n$) and soft ($6n$) wheats was very similar, while the differences between *Monococcum*, *Triticum*, and *Secale* appear very early. On the contrary, in *Ægilops squarrosa* ($n = 7$), *Æ. ovata* ($n = 14$) and *Æ. crassa* ($n = 21$) he found no important differences in ear development, from which it is concluded that polyploidy has no influence on ear development in either *Triticum* or *Ægilops*.

Vavilov and Jakushkina (1925) reported on a study of *T. persicum* Vav. and its hybrids with other species of wheat, with *Ægilops* species, and with rye. This 'Persian wheat' was obtained at Moscow in 1902 from Haage and Schmidt, who had it from a firm in Moscow in the 'nineties. It was a black-awned spring wheat, very resistant to mildew, and showing considerable immunity to rust. Vavilov in 1916 found in Persia a series of varieties with black ears, pubescent, bearded, of the type of soft wheats; and Zhukovsky discovered in Turkestan a great diversity of varieties of this species. *T. persicum* is tetraploid and placed by Percival in *T. dicoccum*, but Vavilov regards it as forming a link geographically between the Asiatic group, rising to *T. vulgare*, and the Afro-Mediterranean tetraploid wheats. It produces a dirty-brown flour without the yellowness of the *durum* wheats, the bread being more like that from rye in appearance but having a peculiar flavour. Although tetraploid, it shows a number of characters belonging to the soft wheats. It produces fertile hybrids with other $4n$ wheats; but markedly sterile hybrids with $6n$ wheats, and still more with *T. monococcum*, as well as in crosses with *Ægilops triuncialis* and rye.

In 1914 Tschermak (1929) found in the Greek Theatre at Palermo, and afterwards as a weed in the Appian Way at Rome, the wild *T. villosum* or *Secale villosum*, which Bleier showed to be diploid. It was used as male in crosses with *T. spelta* ($n = 21$), *T. durum* ($n = 14$), and especially *T. turgidum* ($n = 14$). The latter hybrids were intermediate and mostly sterile. A few stronger F_2 plants were obtained from unprotected seeds. The strain was more fertile in F_3 and F_4 , but showed no segregation. This is probably an amphidiploid with $(14 + 7) \times 2 = 42$ chromosomes, but the number has not been counted. The first observed case of this kind in wheats will be referred to later.

Some of the wheat-rye hybrids which have been investigated throw important light on the relationship of the cereals and the general manner in which the hexaploid wheats may have arisen. W. P. Thompson (1926) studied the cytology of a wheat-rye hybrid. The cross was easily made with certain varieties of *T. vulgare*, producing a very vigorous F_1 , which was not quite sterile. Its chromosomes numbered $21 + 7 = 28$. The heterotypic metaphase in meiosis was very irregular. There were often one or

two, but rarely three, bivalents. Most of the chromosomes divided in the second division, but many lagging chromosomes formed extra nuclei. It was concluded that probably none of the rye chromosomes are homologous with those of the wheats.

The experiments on rye-wheat hybrids (*S. cereale* × *T. vulgare*) which Meister was making for a number of years at the Saratov station on the Volga have yielded important results. Among the practical results has been the production of wheats with valuable rye characters, such as early ripening and winter hardiness. Meister also obtained a constant intermediate fertile hybrid in F_2 . It has since maintained its type, and the F_6 plants recently examined by Levitsky and Benetzkaia (1929) showed 56 chromosomes. It is thus an amphidiploid with $(7+21) \times 2$ chromosomes. Meister and others have shown that the F_1 probably do not pollinate themselves, hence there is probably apogamous development of certain F_1 ovules with the somatic chromosome number, this number being doubled in the first mitosis of the egg cell. It was found that in the embryo sac of the F_1 the chromosomes do not conjugate but about 28 pass to each pole, so that eggs with 28 chromosomes must be formed. The meiosis in the pollen mother cells of the amphidiploid shows 28 bivalent chromosomes, but notwithstanding this balanced condition there are many irregularities from lagging chromosomes and disintegration of certain chromosomes.

Perhaps the most striking cases of an amphidiploid hybrid, however, and the first of their kind, were obtained by Tschermak and Bleier (1926). From the crosses *Aegilops ovata* × *T. dicoccoides* and *A. ovata* × *T. durum*, constant octoploid forms were derived by chromosome doubling in the F_2 , producing plants with normal chromosome pairing in later generations. The frequency with which such forms can arise from *Aegilops-Triticum* crosses strengthens the view that the hexaploid wheats actually did arise from such a cross between tetraploid (emmer) wheats and a diploid species of *Aegilops*. In all the hybrids between *A. cylindrica* and the 6n wheats there are constantly seven close pairs of meiotic chromosomes, from which Percival concludes (1930) that seven of the chromosomes of these wheats have been derived from the tetraploid *A. cylindrica*.

Extensive studies of the chromosome behaviour in many hybrids between *Triticum* and *Aegilops* have also been made by Sax (1924), Jenkins (1929), Aase (1930), Longley and Sands (1930), Bleier (1930), and others. Bleier has recently concluded that pairing of the chromosomes in these hybrids depends partly on the varieties chosen and partly on the environment. He is less sanguine than some others that the phenomena of pairing will furnish a sufficient key to chromosome homologies in the various species. Sax supported the view that the hexaploid wheats came from crosses between emmer and *Aegilops*, based partly on chromosome pairing and partly on the fact that the characters which distinguish the hexaploid from the emmer wheats are all found in *A. ovata* and *A. cylindrica*.

Another interesting line of evidence of relationships has been obtained by Kagawa (1928, 1929). The volume of the pollen grains in the diploid *A. speltoides* was compared with that of four tetraploid species. In two of the latter (*A. squarrosa* and *A. triuncialis*) the volume was approximately double, suggesting that they might be autotetraploids, while in two others (*A. ovata* and *A. cylindrica*) it was not. In *A. cylindrica* × *T. dicoccum* during meiosis there were sometimes 1-4 end-to-end pairs, and in *A. ovata* × *T. polonicum* 1 or 2 such pairs. Occasionally the chromosomes in such a pair were of unequal size. But Kagawa's most interesting work was in carefully com-

paring the types of the somatic chromosomes in various species of *Triticum*, *Aegilops*, and *Hordeum*. The chromosome pairs in a species frequently show constant differences both in length and in the position of constrictions or spindle fibre attachments. By these methods it was found that *T. monococcum* has three long pairs of chromosomes (two of which have a single constriction and the third two constrictions), the other four pairs being progressively shorter, with characteristically placed constrictions. *T. polonicum* had four similar pairs and others that were different. By such comparisons of the chromosome sets in different species it was concluded that in *T. polonicum*, *T. dicoccum*, and *T. vulgare* most of the chromosome types were represented by a single pair in each cell, and similarly that the tetraploid *Aegilops cylindrica* could not have arisen from the doubling of the chromosomes in *A. speltoides*. While this work is doubtless subject to some revision, it seems to show that autopolyploidy has seldom occurred in these genera, but that higher chromosome numbers have usually appeared following crossing.

Watkins, in a series of papers (1928), has made an intensive study of crosses between *T. turgidum* (4n) and *T. vulgare* (6n). Among his conclusions may be mentioned that the differences between the conspicuous hexaploid types *vulgare*, *speltoid*, and *spelta* were due to three factors, *k*, *K*, and *Ks*, which were either multiple allelomorphs producing different degrees of keeled glumes (the most conspicuous difference between *turgidum* and *vulgare*) from the round-glumed *vulgare*, or more probably three groups of completely linked factors. This view is supported by the fact that these three factors or factor-groups all show the same linkage value with the factor for awns. The factor *Ks* in *dicoccum* is moreover identified with *Ks* in *spelta*, while similar factors *K'K'* are believed to be carried by the extra chromosome sets of *spelta*. Thus *turgidum* and *durum* are given the formula *KK*, and *vulgare* (*kk*)*K'K'*. By study of the cytology of reciprocal back-crosses of the F_1 *turgidum-vulgare* hybrids with both parents, it was found that 14 *turgidum* chromosomes pair with 14 of the *vulgare*. The conclusion was reached that the 14-chromosome pollen from the back-crosses carries mainly *turgidum* characters, while the pollen with 17-21 chromosomes carries mainly *vulgare* characters. The results did not disclose many factor-differences between the 14 *turgidum* chromosomes and the 14 *vulgare* chromosomes with which they pair, leading to the suggestion that a simple polyploid relationship exists between these two species.

Huskins (1930) finds irregularity in the meiosis of *T. spelta* and *T. vulgare*, and on this basis extends Winge's hypothesis of the origin of speltoid wheats through irregular distribution of certain chromosome pairs in the reduction division. Thompson and Robertson (1930) have also found in hybrids *vulgare* × *spelta* and *vulgare* × *compactum* a considerable proportion of pollen mother cells with one or a few lagging univalent chromosomes, such cells being much less frequent in the pure species. Similar results are obtained among the tetraploid wheats. Such phenomena indicate complete homology between chromosomes which fail to pair. Thompson has also shown that in various hybrids between species with different chromosome numbers there is disharmony between the embryo and the endosperm with its additional set of maternal chromosomes, thus leading to differences in reciprocal crosses.

Percival (1930) has studied 33 hybrids between four tetraploid *Aegilops* species (*ovata*, *cylindrica*, *triuncialis*, and *ventricosa*) and various 2n, 4n, and 6n wheats, as well as hybrids between the four *Aegilops* species themselves. In hybrids between *Aegilops* and

wheats he finds a certain number of bivalent chromosomes, which are all telosynaptic or end-to-end. In crosses between *Æ. cylindrica* and the $6n$ wheats, however, he always finds constantly 7 parasyndetic bivalents formed from the end-to-end arrangement by the chromosomes swinging round to lie side by side. This, as well as the characters of *cylindrica*, point to the presence of 7 *cylindrica* chromosomes in the hexaploid wheats. Hence telosynaptic pairing is regarded as evidence of a less complete homology or a more distant relationship between the members of a pair than is parasynapsis.

The hybrid *Æ. cylindrica* × *Æ. ventricosa* is sterile, but its characters show remarkable resemblance to those of *T. spelta*. In meiosis there are 5-7 bivalent chromosomes, chiefly parasyndetic but some telosyndetic, indicating that one set of chromosomes are homologous in the two species. The two types of pairing are also described in various species-hybrids by Aase. Percival also considers *T. dicoccoides* ($4n$) to be an autopolyploid of *T. ægiloides*, and concludes that the emmer wheats are probably autopolyploids from the Einkorn wheats. These conclusions, however, require further evidence.

Nishiyama (1930) has described similar conditions in crosses of *Avena* species. *A. fatua* ($n=21$) × *A.*

sativa ($n=21$) gives a hybrid with 21 parasyndetic bivalents in meiosis, leading Percival to conclude that cultivated oats was derived from the wild *fatua*, while *A. barbata* ($n=7$) × *A. sterilis* gives telosyndetic pairs.

Watkins (1930) has just published an extensive critique of all the work on wheat (*Jour. Genet.*, vol. 23, No. 2), in which he points out difficulties with the theory of cumulative factors for size-inheritance as applied to wheats, and shows that the chromosome behaviour of hybrid cereals requires further study. While the details therefore remain uncertain, there is evidence for concluding that the origin of the hexaploid wheats has involved interspecific and intergeneric crossing, with allopolyploidy and probably also autopolyploidy, combined with the occurrence of numerous parallel unit mutations.

A recent study of the related grass genus *Agropyron* by Peto (*Can. Jour. Research*, vol. 3, p. 428) again shows $2n$, $4n$, and $6n$ species ($n=7$), with evidence of natural hybridisation between species having the same or different chromosome numbers. This condition is probably very similar to that under which the wheats evolved, except that the hexaploid wheats may have arisen entirely under conditions of cultivation.

Upper Atmosphere over India.

THE inexpensive type of apparatus for obtaining readings of pressure and temperature at great heights in the upper atmosphere which was invented by the late W. H. Dines in 1907 has been employed in many countries. It has been used with one minor modification at Agra (*Gerlands Beiträge zur Geophysik*, vol. 25 (1930), pp. 266-273, by G. Chatterjee and N. K. Sur).

In Dines's apparatus the graph of each record, temperature and pressure being the ordinates and abscissæ, is traced by a sharp non-rusting steel point on a silvered copper plate little larger than a postage stamp, the motion due to variations of pressure being provided by a small aneroid box and those due to change of temperature by the expansion and contraction of a rod of German silver. Difficulty was experienced at Agra in obtaining a continuous scratch on the recording plate, especially when the sounding balloon carried the instrument into the stratosphere, which is there reached at a higher level than over the British Isles, and is in consequence much colder. It was found that the substitution of a deposit of colloidal graphite on glass, for the silver surface, overcame this tendency, and allowed very sharp records to be obtained with only slight pen pressure.

Owing to the rapidity with which rubber balloons perish in India, Vulpro tissue balloons (see NATURE, vol. 124, p. 793; 1929) were substituted for them in 1926; since then balloons have often risen as high as the stratosphere, and the number of observations obtained permits of a fairly detailed account of the seasonal changes of temperature between the level of the ground and a height of 20 km.

The monsoon season in India (June to September) was found to be decidedly the hottest up to nearly 14 km., and at this season the lapse-rate of temperature is higher between 12 km. and 15 km. than lower down, a state of affairs believed to be due to a difference of origin of the air above and below the average level of the cirrus clouds (12 km.). The base of the stratosphere (the 'tropo-pause') appears to be found at an average height of about 16 km. or 17 km. at all seasons, but its mean temperature has an annual variation with a minimum of 192° A. at about the end of the rainy season. The lowest value obtained at Agra so far is 181° A. at a height of 16.5 km. on Oct. 4, 1928, which equals the lowest yet found—at a slightly higher level—over Batavia in 1923, which for long was regarded as the lowest atmospheric temperature observed anywhere in the world.

'Sea Trout' or 'Bull Trout'?

THE brown trout and the sea trout, possibly members of one plastic species, have been the cause of much controversy. Living under widely varying conditions and possessing very different habits, they show differences in appearance which have given ground for much 'splitting' in the past. Furthermore, because they have come much under the eye of observant anglers, many without the knowledge of a trained biologist, who himself is always in difficulties when deciding where a 'species' ends and where it begins, it is natural that the popular accounts of these fish have shown very divergent opinions. That they are specifically indistinguishable is perhaps the general consensus of opinion at the present day, but there has still been a certain amount of indecision as to where exactly to place the so-called 'bull trout' of the Tweed and other rivers.

A critical examination of the sea trout of the river Tweed* comes therefore as a welcome addition to our knowledge of this interesting species. Mr. G. H. Nall, of the Scottish Fishery Board, has shown that the sea trout of the Tweed exhibit a marked difference from those of many other Scottish rivers in the great rapidity of their growth during sea life. As an example, the average weight of a fish in its third sea summer for the Tweed is 7 lb. 7 oz., as against 3 lb. 5 oz. for the Howmore, 2 lb. 13 oz. for the Ailort, 2 lb. 6 oz. for the Forth, and 2 lb. 3 oz. for the Spey. Similarly, for fish in their fifth sea summer the average weight for the Tweed is $12\frac{1}{2}$ lb. as against the highest of 6 lb. 7 oz. for the Howmore amongst the above four rivers.

* Fisheries, Scotland, Salmon Fish., 1929, No. 5: Sea Trout of the River Tweed. By G. Herbert Nall. (London: H.M. Stationery Office, 1930.) 3s. 6d. net.