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Concluding Remarks -- The Evolution of Crops and of Agriculture

R. Riley

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Concluding remarks – the evolution of crops and of agriculture

By R. Riley, F.R.S.
Plant Breeding Institute, Cambridge

The collection together at this Discussion Meeting of archaeologists and natural scientists, with a great diversity of specialist interests, emphasizes that the interpretation of evidence obtained in many different ways is necessary if we are properly to comprehend how our ancestors first took up farming and developed the many systems of agriculture that have been used from time to time. Certainly there is a need for better understanding between archaeologists and natural scientists. Without this each will not obtain full benefit from the other and the benefits are real. For example, during this Discussion Barbara Pickersgill has alluded to the new insight that has been provided to crop botany in the last 20 years by archaeology.

However, during the last two days we have had little comparison of the methodology of archaeology and of relevant natural sciences although E. M. Jope did commend to archaeology the use of protein sequencing. There was only one reference to objectives, that I can recollect. This was by M. R. Jarman who I think defined the purpose of archaeology as the description of human behaviour patterns of the past. Certainly the contributions of Heather Jarman, E. S. Higgs and M. R. Jarman fit this view. I am not sure how acceptable the definition would be to archaeologists at large, but if adequate it encapsulates the purpose of archaeology in a way that is impossible for the natural sciences. Scientists aim to describe the natural world by observation and experiment and to explain the phenomena involved in natural processes. In the field with which we are concerned here, scientists may subsequently attempt to apply the accumulated evidence to explain the evolution of crop species and domesticated animals, and the evolution of agricultural systems. The interpretation of the natural scientist may be wrong but the evidence should be reproducible. Greater skill may be demanded of archaeologists because the interpretive component is often greater and some observations cannot be repeated at will. Archaeologists and scientists need to work together more closely but this demands awareness by both of the potentialities and the weakness of the other's methods.

I am led to these thoughts by my own interest in the evolution of wheat and because I recently wrote about a conflict of archaeological and cytogenetic evidence concerning the first form of hexaploid wheat to arise (Riley 1975). During our discussions the same problem has been alluded to by Barbara Pickersgill and by W. van Zeist. The difficulty arises because there is no evidence of the occurrence of a free-threshing tetraploid such as *Triticum turgidum* ssp. *durum*, ssp. *turgidum* or ssp. *carthlicum*, before 5000 B.C. But curiously wheats that have been identified as bread wheat – *T. aestivum* ssp. *vulgare* – have been found at sites dating from 6100 B.C. at Knossos and between 5800 and 5000 B.C. in Iran, Iraq and Anatolia.

It is very difficult to account for the origin of bread wheats from the hybridization of *T. turgidum*, ssp. *dicoccum* and *A. squarrosa*, since the synthetic hexaploid derived from this hybrid most closely resembles *T. aestivum* ssp. *spelta*. But ssp. *spelta* is not found at all, even at later levels, in some locations where bread wheat has been found. Where bread wheat is found very early, and where ssp. *spelta* does occur in the archaeological record, as in Central Europe, ssp. *spelta* post-dates the first occurrence of ssp. *vulgare* by about 1000 years (Renfrew 1969).

A. squarrosa which combined with *T. turgidum* in the formation of *T. aestivum*, does not occur in nature much to the west of the Caspian Sea from where it extends eastwards into Central Asia. *A. squarrosa* is also, however, an aggressive weed in arable cultivation and in this role extends from Central Turkey to Afghanistan. Indeed, in some samples of wheat sold as chicken feed at Chalus on the southern shore of the Caspian Sea there was one spikelet of *A. squarrosa* to every four grains of wheat (Kihara & Tanaka 1958). It seems reasonable to presume that *A. squarrosa* must have been a weed in wheat crops before 6000 B.C. when the crops concerned would have consisted of some form of *T. turgidum*. If so, hybridization could well have taken place in conditions of cultivation – that is, bread wheat might have been derived from a hybrid between the crop and its weed. This also implies that the hexaploid wheat could not have emerged until cultivation had spread to the areas in which *A. squarrosa* was endemic.

However, to describe the equivocal nature of the evidence on the form of *T. turgidum* that gave rise to hexaploid wheat, it is necessary to discuss the genetic basis of the differences between the subspecies of *T. aestivum*. Three genetic loci are involved in determining the syndrome of characters that distinguish ssp. *vulgare* from ssp. *spelta*, *compactum* and *sphaerococcum*. Ssp. *spelta* is homozygous recessive *q q* while *vulgare* is *Q Q*. Ssp. *compactum* is homozygous dominant *C C* while ssp. *vulgare* is *c c*. Ssp. *sphaerococcum* is homozygous recessive *s*1 *s*1 while ssp. *vulgare* is *S*1 *S*1. The *Q* locus is on chromosome 5A, the *C* locus on 2D and the *S*1 locus on 3D. Putting together the conditions at all three loci the subspecies are genetically:

	chromosome/locus		
	5A	2D	3D
vulgare	*Q Q*	*c c*	*S*1 *S*1
spelta	*q q*	*c c*	*S*1 *S*1
compactum	*Q Q*	*C C*	*S*1 *S*1
sphaerococcum	*Q Q*	*c c*	*s*1 *s*1

It is the *Q* locus which creates the problem in explaining the origin of *T. aestivum* since *T. turgidum* ssp. *carthlicum* is the only tetraploid homozygous for the dominant *Q* allelle which is present in *T. aestivum* spp. *vulgare*. If, as suggested by the archaeological evidence, ssp. *vulgare* were the original hexaploid from which all other subspecies arose by mutation, then it must be presumed that it was derived from a tetraploid carrying the *Q* allelle, that is like ssp. *carthlicum*. But there is no evidence of a *Q*-bearing form of *T. turgidum* existing before the origin of ssp. *vulgare*. Indeed it has even been suggested that the *Q* allelle of ssp. *carthlicum* might have been introgressed into *T. turgidum* from *T. aestivum* (Morris & Sears 1967).

This issue is further complicated by the suggestion of Muramatsu (1963), following dosage studies, that the *Q* allelle could have been derived from *q* by a numerical repetition of the *q* segment within the locus. If this interpretation of the status of the *Q* allele is correct it means that, while it could be derived from *q*, the reciprocal change could not occur unless preceded by the origin of *Q* by a repeat mechanism.

There are few ways by which the archaeological and cytogenetic evidence can be reconciled – the former implying that ssp. *vulgare* was the first hexaploid and the latter that it must have been ssp. *spelta*. Two possibilities exist, however. The tetraploid parent of the first hexaploid may have been a rare mutant in the *T. turgidum* population that happened to carry the *Q* allele and ssp. *spelta* may have arisen independently from a subsequent hybridization between a *q*-carrying form of *T. turgidum* and *A. squarrosa*. Alternatively some of the early archaeological finds attributed to *T. aestivum* ssp. *vulgare* might have been from a tetraploid form corresponding to ssp. *carthlicum*, which gave rise to *T. aestivum* ssp. *vulgare* but which has left no extant derivatives at the tetraploid level. It must be confessed that neither of these suggestions is very plausible but the reconciliation of the evidence forces strained explanations.

In addition it must be admitted that the origin of *T. aestivum* ssp. *vulgare* and ssp. *spelta* by separate hybridization events appears unlikely because, although interchanges of segments between genetically unrelated chromosomes have occurred quite often in wheat, some forms of ssp. *vulgare* and ssp. *spelta* have chromosome complements with identical structures (Riley, Coucoli & Chapman 1967). This is not entirely incompatible with the idea of their polyphyletic origin but makes it slightly less probable. Finally in support of the notion that ssp. *spelta* was derived from ssp. *vulgare* are the observations that so-called 'speltoid' forms arise in ssp. *vulgare* by mutation (and without the loss of chromosome 5A which can give a similar phenotype). By contrast I know of no example of a form resembling ssp. *vulgare* arising from ssp. *spelta* by mutation.

Turning to some of the other issues that have been raised during our discussions, J. R. Harlan, Barbara Pickersgill and T.-T. Chang referred to the interrelations of crops and weeds and the significance that this has had for the evolution of crop plants. Other lessons can also be learnt from weeds, as W. van Zeist showed the occurrence of *Plantago* weed pollen in the pollen sequence can be used to infer that forest clearance had occurred in the area. In addition I am sure that those concerned with the excavation of seed material now pay attention to weed as well as to crop seeds, since the kinds of weeds present may give useful guidance to the kind of farming system employed.

Furthermore, we must not forget that plant species that we now call 'weeds' often formed part of the heterogeneous product of agriculture in the past.

Heather Jarman talked of the insurance that domestic animals might have provided for the cultivators of crops. Also T.-T. Chang pointed out that mixed cropping is often practised in peasant agriculture. This should remind us all, in addition, that it is only recently that, in some crops, our cultivars have become relatively homogeneous for genotype. Genetic diversity even within a single crop species, as pointed out by J. B. Hutchinson, may provide valuable protection against irregular environmental adversities.

Another area of discussion has been crop dispersal. T.-T. Chang and J. B. Hutchinson both drew attention to the rapidity of transport and to the long distance of migration of crops and of agricultural systems in ancient times. I suppose that this should not surprise us because we have recorded, from the recent past, the speed with which crops like the potato became established in the Old World – even though communication systems were relatively poorly developed. Only archaeology can tell us the rates of spread of the use of new or introduced crop species, and it is encouraging that this problem is now discussed more frequently.

E. M. Jope was clearly correct to draw our attention to the improved possibility of recognizing the relationships of domesticants and of their wild ancestors following comparisons of products, such as polypeptides, that are built directly from a template consisting of nucleic acid. In comparisons of this kind, however, it would be unwise to ignore the opportunities now offered by the direct comparison of the DNA of related organisms by molecular hybridization and by study of the response to temperature of melting in the resulting heteroduplexes. By these and other related procedures, for example, my colleagues Dr M. D. Bennett and Dr R. B. Flavell have shown that nuclei of diploid rye have about 30 % more DNA than those of diploid wheat. Further the extra DNA appears to consist entirely of a particular kind of reiterated fraction. Thus an important determinant to the separation of these closely related cereal species is revealed. Moreover, knowledge of this distinction between the genomes of wheat and rye may help us to understand the basis of the rarity of meiotic chromosome pairing between wheat and rye chromosomes which causes a barrier to gene flow between the two species.

Among the most fascinating observations referred to during our discussion were those of L. T. Evans in describing what he called the photosynthesis paradox. This is expressed in the condition that the rate of photosynthesis per unit area of leaf is lower in the more advanced and highly productive cultivar than it is in the more primitive less productive forms from which they were derived. Thus the agricultural selection which has resulted in greatly increased productivity per unit area of land has not been achieved by superiority in the capacity to fix carbon. So far we are all at a loss to explain the *Evans paradox* but it presents a problem to research which will surely attract much attention in the future.

As one of the organisers of this meeting, as I listened to L. T. Evans, I asked myself why his was the only paper dealing with the physiology of domestication. Similar questions that we put to Evans could have been asked of animal physiologists and nutritionalists. Since much animal improvement has been in food conversion rates apparently there is little analogy between the nature of the improved metabolic efficiency following domestication in plants and animals. I suspect, however, that in a few years time we shall be able to contemplate the value of holding a symposium on the physiology of domestication of plants and animals. L. T. Evans referred to the harvest of components, seeds or roots for example – which are matched by eggs or milk or the harvest of entire organisms as in herbage crops – which are matched by meat animals. The analogies and the contrasts in the physiology of domestication in a range of organisms could be examined with profit.

The practice of agriculture – especially arable agriculture – requires foresight and planning and timeliness. It demands the capacity to measure in space and time, to survey land and to use the calendar. Particularly from arable agriculture, therefore, we may presume that 'measuring' societies grew. Evolution from these to our present science-based societies may now seem to have been inevitable. It is, therefore, highly appropriate that we should have discussed the early history of agriculture in the rooms of the Royal Society, one of the first established societies devoted to natural science.

Finally, it is my great pleasure to thank all of those who have contributed formally to the Discussion Meeting and those who have been with us and participated in informal ways. This is not the first time that the British Academy and the Royal Society have jointly organized Discussion Meetings and in this case, as is displayed by the spread of contributions, the chosen field was truly interdisciplinary. The meeting has done much to bring together workers from the extremes of our widespread field.

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