

## **On the transformation of Aegilops into wheat / by Professor Henfrey.**

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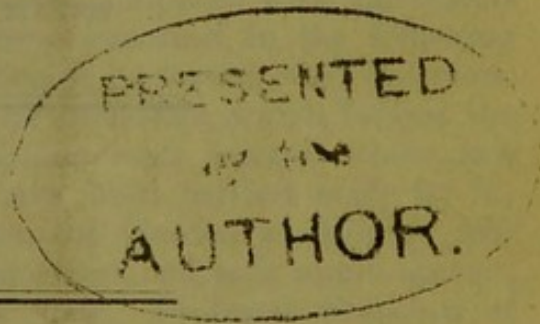
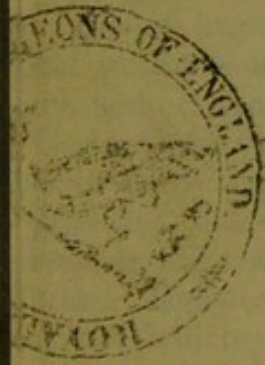
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ON THE

TRANSFORMATION OF ÆGILOPS  
INTO WHEAT.

By PROFESSOR HENFREY.



LONDON.

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## TRANSFORMATION OF ÆGILOPS INTO WHEAT.

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IN the 15th volume of the Journal of the Royal Agricultural Society of England (page 167) was published a translation of a paper written by M. Fabre, of Agde, in the South of France, the object of which was to show that cultivated wheat, the origin of which is altogether obscure, had been produced from the grass called *Ægilops ovata* through the influence of cultivation. The facts there brought forward naturally attracted much attention, but the opinions founded on them have been very different. In this country there is seemingly a tendency to admit M. Fabre's explanations as valid; but they appear by no means conclusive when compared with the results of the experiments of Dr. Godron, contained in the following pages, and which have been confirmed by several other botanists.

The suggestion that the *Ægilops triticoides*, which formed the first stage of transition from *Ægilops ovata* towards wheat, is a hybrid production, appears to have been earliest made by M. Regel, now Director of the Botanical Garden at Moscow, but M. Godron was the first to give practical, and, as it would appear, decisive proof in favour of this view. Professor Planchon of Montpellier has repeated the hybridizing experiments with success, as have also MM. Groenland and Vilmorin, near Paris. Professor Henslow has also found a *triticoid* form of *Ægilops squarrosa*, which proved barren; affording rather a presumption that it was a hybrid. Mr. Brown, of Colchester, has given an account of a similar form, which was fertile and was cultivated for four years, without however becoming *Wheat*. We subjoin reference to the notices on this subject, chiefly expressions of opinion, which have been published in this country since we printed M. Fabre's paper in 1854:—*Gardener's Chronicle*, 1855, p. 151; 1855, pp. 582, 587; 1857, pp. 617, 627, 796. (Notices by Messrs. Lindley, Bentham, J. D. Hooker, Henslow, Seeman, &c.)

The two papers here translated were published in the French '*Annales des Sciences Naturelles*,' in the 2nd and 5th volumes of the Fourth Series of that Journal, 1854 and 1856; M. Planchon's



observations appeared in the '*Annales de la Société Linnéenne de Lyon*,' nouvelle série, iv.; those of MM. Groenland and Vilmorin in the '*Bulletin de la Société Botanique de France*,' iv. p. 573 (1856), and in the Berlin '*Jahrbucher für wissenschaftliche Botanik*,' i. p. 514 (1858).

It is necessary to notice that the French botanists now distinguish the plant finally resulting from M. Fabre's experiments, under the name of *Ægilops speltaeformis*, from the form which occurs wild and is a simple hybrid, the *Ægilops triticoides*, of Requien.

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*On the Natural and Artificial Fertilization of Ægilops by Triticum.* By Dr. GODRON.

Notwithstanding that the attention of naturalists was awakened, more than a century ago, to the consideration of hybridity in the vegetable kingdom, the investigation of hybrid plants developed spontaneously was for a long time neglected. Yet this study is not only very interesting in itself, but, in addition, possesses undeniable scientific importance.

On the one hand *crossing* often renders certain species of plants very "critical," and the determination of these becomes almost impossible if we do not carefully distinguish the forms arising through hybridation from those which constitute genuine specific types. By this means Messrs. A. Braun, Koch, Wimmer, Fries, Nägeli, Lang, &c., have succeeded in elucidating certain genera of plants previously almost inextricable, and which were the despair of descriptive botanists. Of this we have examples in the genera *Cirsium* and *Carduus* (thistles), *Mentha* (mints), *Verbascum* (mulleins), *Polygonum* (docks), and *Salix* (willows).

On the other hand, hybrids, when fertile, tend to return after a certain number of generations to one of the two types which have given them birth; and as the crossings may take place in opposite directions, we sometimes meet with complete series of intermediate forms between two perfectly distinct species. Thus, M. Grenier has gathered, in a meadow in the environs of Pontarlier, such a series of forms between *Narcissus pseudonarcissus* and *N. poeticus*; and M. le Jolis has likewise observed a complete set of individuals presenting all the modifications which can exist between *Ulex nanus* and *U. europæus*, comprehending in the midst of them *U. Gallii*. Other exactly similar instances might be cited.

An observer, having before him one of these series which appear to unite and blend two species incontestably distinct,



would be naturally led, if he overlooked the hybrid origin of the intermediate forms, to regard, for example, *Narcissus pseudo-narcissus* as a simple metamorphosis of *Narcissus poeticus*, or, in other words, to admit the transformation of one species into another, whatsoever might be the morphological value of the characters which separated the two types.

The study of hybrids produced spontaneously is therefore useful to descriptive botany, but it has a far greater value in reference to the fixity of species. The observations and experiments which we are about to recount will place in a still stronger light the foregoing reflections.

The origin of cultivated wheat, which has not up to this time been found in a wild state in any part of the globe, already occupied attention among the naturalists of ancient times, and it was even attributed to *Ægilops* by the Greeks. This opinion has been revived in our own times by several botanists, and lately by M. Fabre, of Agde, and Professor Dunal. These skilful observers have done what their predecessors neglected to do: produced facts in support of their views, and it is necessary here to recall the results of their observations.\*

It is well known that the spike of *Ægilops ovata* breaks at its base when mature, that it does not become separated into pieces, and that it preserves its seeds tightly fixed to the floral envelopes. This spike is introduced into the soil all in one piece, and the four seeds it contains give birth in the following year to four plants of *Ægilops*, distinct from one another, but with their roots interlaced, and forming by their union a little tuft. Ordinarily all these seeds reproduce the parent plant; but sometimes one of the seeds gives birth to a plant very distinct from the first, and having an aspect which reminds us of cultivated wheat; this is *Ægilops triticoides*. This very interesting fact, ascertained by Mr. Fabre, I have often verified in the vicinity of Montpellier. M. Fabre took the resolution of sowing the seeds of *Ægilops triticoides*, and followed through twelve successive generations the products furnished by the seeds originally gathered from this wild grass. The plant assumed by slow degrees a taller growth, the spike became larger, it ceased to be brittle at the base, its glumes lost one of the two awns which distinguish *Ægilops triticoides*; in a word, this plant acquired, in part at least, the characters of wheat.

Must we conclude from these facts that cultivated wheat derives its origin from *Ægilops ovata*? This opinion has been expressed in the most formal manner by the learned Dean of the

\* See Journal of the Royal Agricultural Society, vol. xv. p. 167.



Faculty of Sciences of Montpellier. This conclusion seems to us serious, and we are led to ask if the opinion pronounced by M. Dunal really results from a rigorous induction from the facts observed by Mr. Fabre. To judge this question maturely, it appears above all necessary to take into account not only the principal fact, but also the circumstances in which it was produced; all having possible importance, none must be neglected, especially when we have to pronounce upon a subject of so high a scientific influence. An examination of these circumstances will conduct us to a solution which direct experiment will subsequently prove to confirm.

In the first place, where does *Ægilops triticoides* habitually grow? Our own observations, made in different localities of the South of France, have shown us that the *Ægilops triticoides* is always found on the borders of wheat-fields, or in their neighbourhood, and never in sterile places far removed from the cultivation of cereals. M. Fabre has, indeed, said that he gathered it in an uncultivated spot completely surrounded by vineyards. This is true; but it must be added that extensive wheat-fields exist at a short distance.

We may remark further, that *Ægilops triticoides* is never very abundant anywhere, but occurs scattered here and there as if really the product of accident.

On the other hand, this plant, gathered by M. Fabre at Agde, assumes, from the first year of cultivation, absolutely the habit of the *Touzelle* wheat, generally cultivated in the environs of that town, and this remarkable circumstance has been observed by M. Fabre himself. Hence, one is led to ask if the *Touzelle*, instead of originating from *Ægilops ovata*, transformed into *Ægilops triticoides*, may not, on the contrary, have something to do with the production of the latter plant. But this is not all: where beardless wheat is cultivated, *Ægilops triticoides* itself has the awns almost rudimentary; while, on the contrary, it is bearded where bearded wheat is grown. Thus, *Ægilops triticoides* varies; and since its variations are in relation with those presented by the wheats cultivated in each locality there is a probability that the wheat has some influence in the production of this form of *Ægilops*.

When M. Fabre sowed the seeds of the wild *Ægilops triticoides* the first time, he observed that few of the stems produced seeds, and those only furnished a small quantity. With the view of repeating the series of experiments made by this ingenious observer, we likewise sowed the seeds of the wild *Ægilops triticoides* in the autumn of 1852. The seeds germinated perfectly; but although the plants flowered they yielded no seeds,



yet several other species of *Ægilops* sown in the same place fructified very well.

Another circumstance, which must not be overlooked, is this: the same spike of *Ægilops* gives birth at the same time to plants of *Ægilops ovata* and of *Ægilops triticoides*; that is to say, to two plants, so distinct and so well characterised that, hitherto, no one has hesitated to consider them legitimate species. But this spike does not ever give birth to anything else: it has never produced forms intermediate between the two plants. Hence, we should have here a transformation always sudden, always equally striking. This pretended metamorphosis is never made by degrees, and does not require for its completion the long period of time which the declared partizans of the variability of species suppose to be an indispensable condition. Cultivation, so powerful a modifier, has never been seen to develop in plants changes so important, and, above all, so rapid. Therefore, we cannot admit that there is here a simple transformation of one species into another.

But science is now rich in facts similar to that discovered by M. Fabre: it furnishes us with a very simple explanation of the origin of *Ægilops triticoides*, and of the modifications through which it subsequently passes in approaching and becoming almost confounded with wheat. *Ægilops triticoides* presents all the characters of hybrid plants: sudden production of a plant which is linked by its character at the same time to two distinct species; influence of varieties and races upon the intermediate product; accidental origin here and there among the parents; fecundating action very little developed in the plant, and reversion of the fertile individuals towards the male type after a few generations. Not one of these characters is deficient; and it appears to us evident that *Ægilops triticoides* is nothing else than a hybrid, resulting from the accidental fertilisation of *Ægilops ovata* by *Triticum vulgare*.

Although the facts above indicated seem strictly to justify the conclusion I have deduced from them, I felt it requisite, in the face of a different opinion, pronounced by one who is an authority in science, to have recourse to direct experiment, and in this way to give to that conclusion the character of a complete demonstration. I have attempted, therefore, to reproduce *Ægilops triticoides* by the artificial fertilization of *Ægilops* by *Triticum*, and it merely remains to make known these experiments and the results they have produced.

I have adopted three modes of proceeding. In the first experiment I sought to effect the artificial fertilization without mutilation of the flowers of *Ægilops ovata*, submitting this plant



simultaneously to the action of its own pollen and that of the foreign pollen. In the second trial the mutilation was only partial; in the third it was complete. The experiments of fertilization were made at Montpellier in the month of May, 1853, and the products obtained were planted in pots at Besançon on the 27th of March, 1854, under protection from the action of late frosts.

*First Experiment.*—On the 20th of May, 1853, I scattered the pollen of *Triticum vulgare muticum* upon six spikes of *Ægilops ovata* which were about to flower, intending thus to place the *Ægilops* in the same conditions as are present when, growing on the border of a wheat-field, it is accidentally affected by the fecundating dust of that cereal. The foreign pollen penetrates the more readily into the flower from the circumstance that, at this epoch of the life of the plant, and until after the flowering, the glumellæ of *Ægilops ovata* naturally separate to the extent of about the twenty-fifth of an inch. These six spikes were gathered directly they were ripe, and planted in the spring of the next year. They furnished the following result: five of the spikes produced *Ægilops ovata* exclusively; the sixth likewise produced several stems of this grass, but one of the seeds gave birth to two stems much taller than those of the parent plant, and the spikes of these presented the most perfect resemblance to those of that variety of *Ægilops triticoides* in which the awns are half-abortive, and, as it were, rudimentary. This variety, which I have gathered in a wild state about Montpellier, is, therefore, the result of the fertilization of *Ægilops ovata* by the beardless wheat.

*Second Experiment.*—Not being able to foretell the success of the preceding experiment, and desiring to reproduce the very curious fact of two distinct plants arising from the same spike of *Ægilops ovata*, I had recourse to mutilation and artificial fertilization carried into effect upon two flowers only of each spike of the *Ægilops*.

The removal of the anthers before the natural fertilization can take place, and at a time when these organs are still enclosed in the flower, seems at first sight an operation very delicate to execute. But it is not at all so if the method of operating be followed that I adopted, and which requires no other instruments than the fingers and a small pair of forceps with very fine points. I am induced to describe this mode of operating because it is extremely simple; and a knowledge of it will enable all botanists to repeat and control my experiments. It consists in taking fast hold of the awns of the outer glumella, as near as possible to their origin, between the index finger placed beneath and the



thumb above; then, pressing with the cushion of the middle finger upon the base of the spike in such a way as to impress a slight see-sawing motion, which allows at the same time of fixing the spike firmly between this finger and the index finger. By this movement the external glumella is curved a good deal outwards, the flower is widely opened, and the reproductive organs can be easily distinguished. I must give warning that the outer glumella sometimes carries off the inner glumella in its movement: but as this latter is simply membranous, and projects above the external one, nothing is easier than to separate it. I then proceed to remove the stamens, extracting them one by one by seizing the filaments with a fine pair of forceps. For these organs is immediately substituted an anther of wheat, selected from those beginning to open, and this is placed transversely above the stigmas. The envelopes of the flower are then gently pressed together again. The wheat anther then discharges its pollen; moreover, its presence forms an obstruction to the access of the proper pollen of *Ægilops* to the stigmas of the flowers subjected to mutilation, which ensures the success of the operation.

I proceeded in this way with four spikes of *Ægilops ovata*, and I tried the fertilization upon two flowers of each of them with the pollen of *Triticum vulgare muticum*. I obtained from these four spikes, planted entire and at a distance from one another, a certain number of plants of *Ægilops ovata* and nine specimens of *Ægilops triticoides*, which only differed from those gathered at Agde by M. Fabre by their taller stature (the summer was wet) and their looser and completely green spike. But the variety of wheat which I used for the fertilization is distinguished from *Touzelle* wheat by precisely these last two characters. I operated on the same day, and in the same manner, upon two spikes of *Ægilops triaristata*; and upon two flowers of each of these spikes I replaced the proper anthers by anthers of *Triticum durum barbatum*. One of the spikes reproduced *Ægilops triaristata* exclusively; the other afforded me three specimens of a hybrid remarkable for its long beards, and which, so far as I know, has never been observed before.

*Third Experiment.*—On the 25th of May, 1853, I completely removed the anthers from four spikes of *Ægilops ovata*, removing the upper spikelet, which contains only male flowers. I placed in each previously perfect flower an anther of *Triticum spelta barbatum* beginning to open. I obtained two stems of a new hybrid, and not a single representative of the parent plant.

From all these facts we may draw the following conclusions:—

1. Hybridity may occur spontaneously among the grasses, and



*Ægilops triticoides* is the first known example of a hybrid observed in this family.

2. The species of *Ægilops* must be united generically with *Triticum*; which is, besides, confirmed by the shape of their fruit, an organ which, in the family of the grasses, furnishes far more important characters than the conformation of the floral envelopes.

3. The observations of M. Fabre upon *Ægilops triticoides* do not in any way prove that cultivated wheat originates from *Ægilops ovata*, or that one species can be transformed into another.

*On Ægilops triticoides and its different Forms.*—Second Memoir  
by Dr. GODRON.

When MM. Fabre and Dunal announced that *Ægilops triticoides* originated from a spike of *Ægilops ovata*, while some seeds of the same spike simultaneously reproduced exactly the latter plant, a fact so unexpected riveted attention, and most of the botanical journals published in Europe, and even in America, discussed the important questions raised by this discovery. The well-known talent for observation of M. Fabre, and the scientific authority of Professor Dunal, made it difficult to suppose that there had been any error of observation, in reference to a fact so easy to verify.

Two eminent botanists, however, neither of whom have ascertained for themselves, in the plains of Languedoc and Provence, the assertions which had been promulgated, received the memoir of MM. Dunal and Fabre in very different ways.

Dr. Lindley, in England, raising no doubt as to the reality of the facts, likewise admits the conclusions which those two observers had drawn from them, sacrificed his old idols and accepted the doctrine of the variability of species.\* The publication of my memoir on the Fertilization of *Ægilops* by *Triticum* (see above) did not at all modify his new convictions, and he will persist, he says, until I have made known the origin of wheat. But as Dr. Asa Gray,† has very properly remarked, my object was not to discover the origin of wheat, but that of *Ægilops triticoides*.

M. Jordan, in France, in a memoir published in 1853,‡ simply denied the principal fact observed by MM. Dunal and

\* This is not a clear statement of Dr. Lindley's view, as we understand it. He does admit *variation* of species, but not *mutation*. He regards *Ægilops ovata* and *Triticum vulgare* as forms of one species.—A. H.

† Silliman's Journal, 2nd ser., vol. xx. p. 134.

‡ Jordan, 'Sur l'Origine des divers Variétés et Espèces d'Arbres Fruitiers, &c.'



Fabre. I was the more surprised at this from the fact that, having been previously consulted, I had assured him that, after a rather large number of observations made in the environs of Agde and Montpellier, I had remained perfectly convinced that *Ægilops triticoides* originated from *Ægilops ovata*. Was this on my part the result of preconceived ideas, which had blinded me to such an extent that I saw what did not exist? This fact shocked my convictions as to the fixity of wild species as strongly as it had done those of M. Jordan. But I was compelled to acknowledge it as incontestable, and my first care was to study the circumstances under which it is produced. The facts I observed, and which I have indicated with the details in two successive memoirs,\* put me on the road to the discovery of the hybrid origin of *Ægilops triticoides*. Therefore my point of departure was not a simple hypothesis; and, even if it had been so, this should not have been turned into a weapon against me, now that this hypothesis is confirmed by direct experiment. Besides, has not hypothesis been the origin of a number of important scientific discoveries? In this question now under discussion only two suppositions are possible; either we must admit, with MM. Dunal and Lindley, the variability of wild species, or acknowledge that the very striking differences which distinguish *Ægilops triticoides* from *Ægilops ovata* are due to hybridity; there is no other possible alternative, and M. Jordan himself, as we hope to demonstrate, must choose between them.

But I return to the fact of the two forms of *Ægilops* springing from the same spike of *Ægilops ovata*, because it is of the first importance for the solution of this question. Not content with having assured myself of it in the plains of the South, I have reproduced it by the artificial fertilization of *Ægilops ovata* by *Triticum vulgare*. My spikes of *Ægilops* partially fertilized by wheat, were planted entire and separately in pots, at Besançon. I did not sow *Ægilops triticoides* at the same time, I had none of it at my disposal; therefore there could not have been any error, any mixture of seeds. I will add that perhaps no case of hybridation has ever been accompanied by so many circumstances calculated to assure its authenticity. The Society of Emulation of Doubs took a warm interest in these experiments, and named a committee composed of naturalists, who traced the vegetation of these *Ægilops*, and made to that learned Society a written report which affirmed in a positive manner the facts contained in my memoir on the fertilization of *Ægilops* by *Triticum*. Specimens of the different products obtained were sent to M.

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\* 'Quelques notes sur la flore de Montpellier,' p. 11, and the first memoir translated in this article.



Adolphe Brongniart, who had seen them in a young state at Besançon; and this distinguished naturalist, who has investigated so successfully the fertilization of plants, was good enough to make a verbal report, on the occasion of presenting them to the Institute, in which he stated that he considered the hybrid nature of *Ægilops triticoides* proved.

Now, from the examination of these products it follows, with the greatest evidence: 1, that from the same spike of *Ægilops ovata* have originated plants of this plant and plants of *Ægilops triticoides*; 2, that the spikes of *Ægilops ovata* fertilized by *Triticum vulgare barbatum* have given birth to *Ægilops triticoides* furnished with long beards, such as Requier observed; and 3, that from *Ægilops ovata* fertilized by beardless wheat, originated an *Ægilops triticoides* possessing very short awns. This last form, perfectly distinct from the preceding, of which M. Jordan does not speak, is wild, and even tolerably common at Montpellier; it is conformable to the specimens which I obtained by artificial fertilization.

These facts—to my eyes so precise and conclusive that if they be not admitted we must also deny the experiments of Koelreuter, of Gaertner, &c—excite doubt and even incredulity in the mind of M. Jordan.\* It would have been easy, however, for this industrious naturalist to verify them, by repeating my trials of artificial fertilization; he would then have pronounced judgment with full knowledge of the case.

According to him, *Ægilops triticoides*, whether regarded as a hybrid—and he still doubts if it be really one—or of some different origin, is but a simple malformation of *Ægilops ovata*.

Let us examine first the second supposition; we will return to the other afterwards.

If *Ægilops triticoides* is a malformation of *Ægilops ovata*, without intervention of foreign pollen, this is a serious fact for the doctrines of M. Jordan and for those of all the botanists who, like him, suppose the immutability of species, not only wild but even of cultivated species. Look at the differences which separate *Ægilops triticoides* from *Ægilops ovata*. Without dwelling on the characters derived from the organs of vegetation, the spike has a very different general form in the two plants; so different that this character alone suffices to distinguish them at the first glance, and that probably no person has ever confounded them. The plant of Requier, moreover, possesses much more numerous spikelets. The valves of the glume of *Ægilops ovata* are regularly rounded on the back, and the principal nerves, which

\* 'Mémoire sur l'*Ægilops triticoides*.' Ann. des Sc. Nat., 4 ser. Botanique, t. iv. p. 298.



terminate at the middle of the base of each of the awns, are almost equal to each other; so that each valve may be divided longitudinally into two halves nearly symmetrical. In *Ægilops triticoides*, on the contrary, not only are the valves of the glume larger, but one of the lateral nerves—the last but one—acquires greater development than the others, and forms then a keel, strongly marked above, dividing the valve into two unsymmetrical parts. This keel is certainly less projecting than in the true species of *Triticum*, but it is very clearly visible; and it is not observed in *Ægilops ovata*. The awns of the glume are three or four in number on each valve of *Ægilops ovata*, and moreover they spread outwards; habitually only two exist in *Ægilops triticoides*, and these are constantly erect. It is true that between the two awns of this latter plant we ordinarily see a tooth which represents an abortive awn, but this is not constant; and sometimes this tooth is wanting altogether in the lower spikelets of *Ægilops triticoides*, which separates it still farther from *Ægilops ovata*: we shall recur to this fact. Now these distinctive characters are much more decided than those which separate *Ægilops triticoides* from *Ægilops speltæformis*. This is so evident that M. Jordan himself, in his memoir on the Origin of Varieties and Species of Fruit-trees, considers *Ægilops triticoides* as a species quite distinct from *Ægilops ovata*; and he confounds *Ægilops triticoides* with *Ægilops speltæformis*, as is proved by the following passage, which I quote from that work:—"Thus, therefore, the plant of which M. Fabre sowed the seeds is exactly *Ægilops triticoides* of Requien: he is right in this point; but that which he obtained from their seeds, and cultivated for twelve years, is still exactly the same *Ægilops*, and he is deceived when he believes that he sees something different, or even a notable change of characters. We have attentively compared cultivated and wild specimens of his plant, . . . and it has presented only unimportant differences, insufficient even to constitute a variety, and analogous to those presented by every plant, when we compared specimens grown in a good soil with those which have been taken from a sterile field. M. Fabre is equally deceived when he believes that his wild *Ægilops triticoides* has been derived from *Ægilops ovata*; there is no reason why we should suppose that *Ægilops ovata* has produced *Ægilops triticoides* rather than the latter has produced *ovata*. Both hypotheses are absurd, doubtless, but one is not less defensible than the other." M. Jordan expressed himself thus in 1853. The plant cultivated by M. Fabre, which three years ago M. Jordan did not regard even as a simple variety, is now a legitimate species; it is *Ægilops speltæformis*. This form had been well distinguished by M. Fabre at the time when M. Jordan completely ignored it; but if



this plant is now in the eyes of the latter a real species, how can he regard *Ægilops triticoides*, much better characterised, as a simple malformation of *Ægilops ovata*—an opinion which M. Jordan himself, in 1853, held to be “an enormous absurdity”? We have to do here with plants of the same genus, in which the characters drawn from the glume and its awns ought to have equal value as specific characters; but if M. Jordan refused to admit that differences so decided and so easy to appreciate, which separate the two species of *Ægilops*, are insufficient to distinguish them, what is to be said of some of the other species which M. Jordan has established in characters appreciable by him, but which escape all other observers? \* Now since M. Jordan at present considers as scarcely a variety the *Ægilops triticoides*, which was recognized before M. Fabre’s discovery as a well-characterized specific type, by botanists most scrupulous in respect to the vegetable species, it follows necessarily that the indefatigable botanist of Lyons (M. Jordan), not only completely invalidates a great number of species which he has published, but, beyond this, he recognizes implicitly the variability of species, even wild ones.

But admitting for a moment that *Ægilops triticoides* is merely an accidental malformation of *Ægilops ovata*, how will M. Jordan explain the fact, which he affirms in a positive manner, that *Ægilops triticoides* sometimes grows in places where *Ægilops ovata* is not met with? This last plant would, in such case, be deformed even in localities where it does not exist. It is his business to reconcile with his new opinions this fact, which he was the first to make known, and which, so far as we know, has not been re-observed by anyone else.

Is this supposed transformation of *Ægilops ovata* into *Ægilops triticoides* the result of the sterility of the latter plant?

In the first place, is *Ægilops triticoides* always sterile? In supposing this absolute sterility, M. Jordan takes his stand upon negative facts sufficiently vague. But it would be important to know if the attempts made in the gardens of Avignon and Montpellier to reproduce the seeds have been frequently renewed, and at what epoch of the year the sowings took place; for, as is well known, the *Ægilops* of the South of France begins to germinate in autumn. M. Jordan relies upon the testimony of M. Touchy, which I do not question: indeed I rely upon it also myself. In 1852, I received from M. Touchy two specimens of *Ægilops triticoides*, and I find on the label the following indication:—“Appeared in a field of millet, in 1848, and has been propa-

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\* In thus expressing ourselves we have no intention of proscribing in mass all the new species published by M. Jordan. We admit that he has created some very safe ones; but of others we are not convinced of their legitimacy.



gated in the same field up to the present time,"—that is to say, for four years. Now these two specimens each have the valves of the glume furnished with two short awns and an intermediate tooth; this is the form *submutica* of *Ægilops triticoides*, of which we have spoken above.

In the autumn of 1852, I myself sowed in my garden, separated from cultivated corn by the whole length of a suburb of Montpellier, seeds of the same form of *Ægilops triticoides*, gathered by me in the environs of that town. They germinated perfectly; the plants flowered, but yielded no seed. Yet this plant had evidently been reproduced at least in one generation.

It is shown, besides, in M. Fabre's experiments, that during the earlier years of the sowings he obtained but a small number of seeds, and that a certain number of plants, although belonging to the second and the third generation, yielded none. This refers to *Ægilops triticoides*, not yet to *Ægilops speltæformis*, for M. Fabre carefully noted that the majority of the plants of the first two years of cultivation presented two awns on each valve of the glume; among them some were fertile, and the sowings were thus capable of being continued for a long series of years.

If it is accurate to say that the wild plants of *Ægilops triticoides* rarely produce seeds, which is easily to be ascertained in herbaria, the preceding facts, nevertheless, prove that this plant does sometimes possess them, and that it is able to propagate for a considerable number of generations. There is nothing in this contrary to the doctrines usually held respecting hybridity; on the contrary, these facts confirm them, and this was even one of the circumstances which made me suspect the hybrid nature of *Ægilops triticoides*.

But admitting, even hypothetically, that absolute sterility, would it thence follow that *Ægilops ovata* became transformed into *Ægilops triticoides*? This is pure supposition, in favour of which there does not exist any known fact or even any analogy. Does the sugar-cane, which, after reproduction by buds for a long series of years, has lost the faculty of producing seeds, present flowers and a panicle different from those of the wild sugar-cane? The *Phragmites* and many other grasses which propagate vigorously by stolons, are very often sterile, but do not, on that account, exhibit appreciable transformations in their floral organs. Why should it be otherwise in *Ægilops ovata*?

But this is not all: how shall we explain, if we adopt M. Jordan's supposition, that *Ægilops ovata*, when its flowers have been smeared with a foreign pollen, or its own stamens have been removed and replaced by those of wheat, produces, in the following generation, not only plants of *Ægilops triticoides*, but two modifications of that plant, according as the foreign pollen applied



in the preceding year belonged to a bearded or a beardless wheat? This result has been demonstrated by my experiments.

It still remains to notice, that M. Jordan, who has so strongly opposed the opinion promulgated by MM. Dunal and Fabre—that wheat is only a transformation of *Ægilops ovata*,—if he admits, definitively, the supposition which we combat, would accept by this very admission the idea that this transformation of *Ægilops ovata* into wheat went through, really, one-half of the course which has been assigned to it by those skilful observers.

The constant sterility of *Ægilops triticoides*, if really demonstrated, would not explain the origin of the differences which separate this plant from *Ægilops ovata*.

Let us now examine the second supposition of M. Jordan. If it be admitted that the transformation of *Ægilops ovata* into *Ægilops triticoides* is the result of hybridation, which we believe we have demonstrated, is it true that this latter plant is yet merely, as he thinks, a modification of *Ægilops ovata*, presenting nothing of the paternal type? The stature of the hybrid *Ægilops*, which rises far above that attained by *Ægilops ovata*; its erect direction; its far more robust aspect, even in the wild state; the breadth of its leaves; the general form of its spike, which reminds us of that of wheat, and which has earned for this plant the name of *triticoides*, which M. Jordan justly regards as “very happily chosen;” the direction of the awns; and, above all, that keel which descends from the principal awn at some distance from the internal border of the glume,—are not these characters which belong to wheat, and by no means to *Ægilops ovata*? It follows from this, that if *Ægilops triticoides* preserve some of the characters of the maternal type, which I am far from denying, but affirm, yet it also presents very prominent marks of its paternal origin.

But the argument upon which M. Jordan especially insists, is, that in spite of the modifications undergone by *Ægilops ovata* by hybridation, the hybrid product which results from its fertilization by wheat would not cease to belong to the genus *Ægilops*.

The genus *Ægilops* is a purely artificial genus, preserved by tradition, out of respect to our predecessors, but which does not rest upon a single character really generic, and which, in my opinion at least, may not be separated from the three species of *Triticum*. M. Jordan distinguishes the two groups by the following characters: 1. in *Ægilops*, the spike at maturity becomes detached from the stalk or breaks up into pieces; the spikelets are not contracted at the base, which at least equals the breadth of the rachis; the valves of the glume are rounded on the back and possess numerous nerves; they bear several awns or teeth



which represent abortive awns. 2. In *Triticum* the spike is not brittle, and is not detached when ripe; the spikelets are contracted at their base, which is not so broad as the rachis; the valves of the glumes are keeled, the nerves are few, and the awn single.

To this definition of the genera I will oppose the following facts: *Ægilops speltæformis*, that at least which M. Fabre obtained after twelve years' cultivation, has a spike not brittle at the base,\* and I am certain of this fact, as I shall explain further on. The spikelets are not contracted inferiorly in *Triticum villosum*, P. Beauv., *T. hordeaceum*, Coss., and *T. bicornis*, Forsk., and this base equals or exceeds the rachis in breadth. *Ægilops triticoides* and *speltæformis* have a keel upon the valves of the glume, less prominent than in *Triticum*, but occupying the same position. The nerves are numerous upon the glume of *Triticum spelta*, L. There exists only a single tooth representing the awn to the valves of the glume of *Ægilops speltoides*, Tausch. (which must not be confounded with *Ægilops speltæformis*, Jordan); and except for this tooth the summit of these valves is truncate and rounded at the sides. *Triticum monococcum*, L., has the same organs, terminated by two very strongly-marked teeth, in which the nerves terminate, as is the case in *Ægilops caudata*, L., *cylindrica*, Host., and *ventricosa*, Tausch. Finally, the presence of a tooth representing a second awn is not rare in *Triticum spelta*, L., and is also sometimes seen in *Triticum vulgare*, Vill., *durum*, Desf., and *amyleum*, Seringe.

So that these distinctive characters have nothing precise about them, and with regard to some species, it has been thought necessary to transport them successively from the genus *Triticum* into the genus *Ægilops*, or *vice versâ*, the generic question not having been hitherto definitively settled in reference to these species; I may cite as examples *Triticum bicornis*, Forsk., *Ægilops macrura* and *Ægilops loliacea*, Jaub. and Spach, &c. It is questionable, moreover, whether characters drawn from an organ so unimportant as the glume of the Gramineæ, which represent simple bracts, are of a nature to form the sole basis of natural genera. The fruits, on the contrary, which, since the time of Tournefort, have been considered as furnishing generic characters of high value, have been generally too much neglected in the establishment of genera in this very natural family. Now *Ægilops* and *Triticum* have similar fruits, and these important organs distinguish them very well from *Agropyrum*, *Lolium*, &c., I will add, that the fact of hybridation between *Ægilops* and *Triticum* goes to confirm the union of these two genera into one.

\* See M. Fabre's paper in the Journal of the Royal Agricultural Society, vol. xv. p. 175.



If *Ægilops triticoides* has preserved some of the characters of *Ægilops ovata*, which should be the case, it is not therefore a necessary conclusion that these have the importance of characters truly generic, and that our hybrid has preserved none of the characters of *Triticum*; it is, in our eyes, perfectly intermediate between the two species which have given birth to it.

Hence I think myself authorized in maintaining the three conclusions which I have deduced in my memoir on the fertilization of *Ægilops* by *Triticum*; they express clearly what I desired to demonstrate in this essay.

I now arrive at *Ægilops speltæformis*, which in my opinion is only an accessory, an accident, in the question forming the object of my anterior investigations of *Ægilops triticoides*. Whatever opinion may be accepted as to the new species created by M. Jordan, this opinion cannot in any way weaken the proofs of the hybrid origin of *Ægilops triticoides*, a question which seems to me now settled.

According to M. Jordan, I have confounded *Ægilops speltæformis* with *Ægilops triticoides*, and also with *Triticum vulgare*, whence, in virtue of the axiom that things which are equal to the same thing are equal to one another, he concludes that I have also confounded *Ægilops triticoides* with wheat. This is trying to prove too much. I regret to say it, but both these assertions are quite inexact.

In the first place: is the question about *Ægilops speltæformis*, cultivated for twelve years by M. Fabre, specimens of which I have communicated to M. Jordan? What I have said in my last memoir on this subject is, "The plant has gradually acquired a more elevated stature; its glumes have lost one of the two awns which distinguish *Ægilops triticoides*; in a word, this plant has acquired, in part at least, the characters of wheat." This passage has doubtless escaped M. Jordan; at this time I having nothing to add, and nothing to subtract from it.

Is the question relative to the wild *Ægilops speltæformis*? Here confusion was impossible either with wheat or with *Ægilops triticoides*. I have never seen *Ægilops speltæformis* in a wild state, although I have investigated most carefully the species of *Ægilops* which grow in the environs of Agde and Montpellier.

On his side, M. Jordan nowhere says that he himself has seen wild specimens of this plant; he only remarks that M. Fabre speaks of having found it wild in the neighbourhood of Agde, confounding it in this state with *Ægilops triticoides*. I will take the liberty to observe that M. Fabre merely affirms that he has gathered *Ægilops triticoides*, that it has been reproduced with two awns to each valve of the glume, in most of the specimens during the first two years of cultivation, and that in the succeed-



ing generations it preserved only one of these awns. In the absence of well-established facts showing that M. Fabre has made a mistake, and that he has confounded two forms (which nevertheless he has taken so much pains to distinguish), facts which M. Jordan does not bring forward, there is not at present any motive for rejecting as erroneous the observations made by so exact and intelligent a person. In addition to this, the locality of Agde, this locality surrounded by a belt of vineyards, where this skilful observer first gathered his seeds—would be the only one, according to M. Jordan, where *Ægilops speltæformis* has been met with. Now in this very locality, which I have visited under the guidance of M. Fabre, I have seen and collected only the typical form of the *Ægilops triticoides* of Requien; I have still before me the specimens which I brought from there, and which M. Jordan has himself seen in my herbarium. Therefore there is no proof that *Ægilops speltæformis* has been found wild in the South of France, and still less in the East. Yet it would have been rational to have previously established this important fact before throwing doubt upon the modifications which M. Fabre assured us he had obtained by the cultivation of *Ægilops triticoides*. But M. Jordan starts from metaphysical principles which he has created as to species, and which he has expounded at length in the first twelve pages of his work upon the Origin of Fruit-trees. Now if he meets with facts opposing these same principles he systematically denies them, as he has himself taken care to warn us, with much frankness, in the following passage, which is too interesting not to be quoted: "It must be observed," says M. Jordan, "that as the laws of being cannot be contrary to the laws of thought, and as experience can never give results having *absolute* validity, since it is limited in its field of study—if it happen that certain facts appear contrary to the necessary and evident conceptions of the reason, *they must always be rejected*."\* It seems to us it would be equally justifiable, when the facts disagree with M. Jordan's principles, to conclude that his metaphysics do not rest on a very solid foundation. They do not guide even him safely, since at this time he entertains, as we have shown above, and as indeed he avows, an opinion concerning *Ægilops triticoides*, which three years ago he contested and then pronounced judgment on with the greatest severity. We shall not follow him on to this ground; material facts alone are in question here. I will first observe that the three hybrid forms of *Ægilops* which originate spontaneously in the South of France, whether from *Ægilops ovata* or *Ægilops triaristata*, and two

\* Jordan, 'De l'Origine des divers Variétés ou Espèces des Arbres Fruitiers,' p. 12.



other forms obtained in my experiments of artificial fertilization—that is to say, five hybrid forms—present, in spite of the differences which separate them, such analogy, that they constitute a little group extremely natural, or if it be preferred, a section of the genus, intermediate between *Ægilops* and *Triticum*. Now by its aspect, the form of its spike, the keel of the valves of the glume, and by its nerves, *Ægilops speltæformis* is referable exactly to this section, and I know of no *Ægilops* recognised as a legitimate species which can be arranged there in this way. Does this leave any probability that this plant originated differently from the other five?

What I have said of the successive modifications undergone by *Ægilops triticoides*, in the hands of M. Fabre, through long cultivation, I borrowed from his memoir. The facts are, in addition, supported by the authority of Professor Dunal, who possesses numerous specimens derived from the different years of M. Fabre's cultivation. I will add that the specimens of the later years, although ripe and tied in little bundles, do not break below the spike; I have been able to verify this fact myself. Now it is quite different with the *Ægilops speltæformis* which I cultivated last year, which I have in cultivation again this year, and the seeds of which I owe to the kindness of M. Decaisne. Here the spikes separate readily from the stalks when mature; therefore this is the form described by M. Jordan. From this it follows that we must suppose that the plant of the earlier cultivation of M. Fabre has become modified, or that there exist two forms of *Ægilops speltæformis*; for this character, derived from the fragility of the spikes, acknowledged as excellent for distinguishing *Agropyrum junceum* from its congeners, and which M. Jordan regards even as a generic character in *Ægilops*, should have in his eyes sufficient value for the establishment of a new species. I will observe in addition, that the nerves of the valves of the glume are diminished in number, and that several of them have been singularly weakened in the plant cultivated for twelve years by M. Fabre, while these nerves have remained numerous and pretty conspicuous in the specimens with a brittle spike, which are probably nearer to the wild state. Nevertheless these are very real modifications, although M. Jordan does not admit them as possible.

I will further remark, in support of the modifications undergone by *Ægilops triticoides* through cultivation, that this plant is not absolutely constant in the wild state, and this new fact goes to confirm, what all experimenters have observed, that hybrids are far from having the same fixity in their characters as legitimate species. In several specimens of wild *Ægilops triticoides* in my herbarium, I see, sometimes in the lower spikelet only,



sometimes in several, that the valves of the glume have two awns, between which the intermediate tooth is altogether wanting; it re-appears in the intermediate spikelets of the same spikes, and in the upper ones it is developed into a third awn, sometimes of great length. I also find, in some of my specimens of the same *Ægilops* obtained by artificial fertilization, the same absence of the intermediate tooth in the lower spikelet, and in one of these specimens all the spikelets but one present this peculiarity, and, moreover, one of the two awns is reduced almost to nothing. Now this exceptional lower spikelet scarcely differs from those of *Ægilops speltæformis*, in which the second awn sometimes re-appears, as even M. Jordan acknowledges. What is there surprising then in the fact of this peculiarity becoming permanent, or almost so, in *Ægilops speltæformis*, when we know that, in this species of *Ægilops*, it is especially the lower spikelets which are fertile? What becomes then of this specific character, resting on a tooth or an awn more or less, to distinguish specifically (and not as forming a passage) *Ægilops speltæformis* from *Ægilops triticoides*, especially since it has been demonstrated that the latter plant is sometimes fertile.

To sum up, it appears to me that the hybrid origin of *Ægilops triticoides* is incontestable; that *Ægilops speltæformis* is proved by the observations made by M. Fabre, and the new facts indicated in this essay, to be only a form, distinct doubtless, but originating from *Ægilops triticoides* modified by cultivation. The question, therefore, rests where I left it in my former memoir, and that is easily explained. Does M. Jordan, on taking up the question of *Ægilops triticoides* a second time and after three years' silence, add any new element calculated to modify it? Has he followed the only truly scientific method, that of observation and experiment, to destroy or weaken the value of the facts produced in the discussion? By no means. His memoir on *Ægilops triticoides* and that on the Origin of Fruit-trees, are reducible, in reference to the present question, to metaphysical considerations, to pure and simple negation of facts observed by other botanists, and to doubts thrown upon their experiments.

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One of the editors of the *Annales des Sciences Naturelles*, apparently M. Decaisne, adds the following note:—"I quite agree with M. Godron in reference to the fragility of the spike in the supposed *Ægilops speltæformis*, seeds of which I received from M. Fabre himself, in 1852, under the name of *Ægilops triticoides*. The spike is so caducous when ripe, that the slightest touch makes it fall; it finally falls spontaneously, simply through



becoming dried. I may add that plants of this form which I have caused to be cultivated here (Jardin des Plantes, Paris), since 1852, among other cereals, have always been respected by the birds, which devoured the latter.

"The fact of the successive modification of *Ægilops triticoides*, which after a certain number of years' cultivation tends more and more to approach wheat, far from being improbable, seems to me on the contrary, to agree with the opinion of various experimenters, who think that the descendants of fertile hybrids incline gradually towards the type of one of the two parents, through the gradual elimination of the characters of the other. M. Naudin has recently made known a remarkable example of it in the posterity of a hybrid *Primula*, which, in the second generation separated into two series, one returning to the paternal, the other to the maternal type." \*

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\* Comptes Rendus de l'Académie des Sciences, April, 1856, p. 625.



Observations made at Montpellier on the awned and awnless forms of *Ægilops triticoides*, which are met with there in a wild state, led the author to regard this plant as a hybrid of *Ægilops ovata* fertilized by the pollen of wheat ("Quelques Notes sur la Flore de Montpellier," Besançon). Desirous of confirming or negating this supposition by direct experiment, Dr. Godron tried, in 1853, to reproduce this vegetable form by artificial fecundation, and in 1854 he obtained plants of *Ægilops triticoides* ("De la Fécondation des *Ægilops* par des *Triticum*," Ann. des Sc. nat. sér. 4. Botanique, ii. p. 218). These facts were confirmed, in 1856 and 1857, by the experiments of MM. Regel in Germany, Vilmorin and Grœnland at Paris, and Planchon at Montpellier. *Ægilops triticoides* is therefore a hybrid plant. The author considers that no doubt can remain on this question. (See Journal of the R. Agric. Soc. of England, xix. part 1. p. 103, 1858.)

*Ægilops triticoides* is most frequently sterile; but sometimes, though rarely, it affords fertile seeds; and it is these seeds which, in the hands of M. Fabre of Agde, have produced *Ægilops speltaformis*. As Dr. Godron could not doubt the exactitude of the facts reported by this skilful and conscientious observer, and was on that account quite convinced that *Ægilops speltaformis* arose from *Ægilops triticoides*, he at first sought to explain this transformation on the foundation of a law accepted by almost all the authors who have studied the physiological phenomenon of hybridity, namely that fertile hybrids return to one of their original types after a certain number of generations. *Ægilops triticoides* seemed to present a new confirmation of this law; *Ægilops speltaformis* is, in fact, more nearly approximate to wheat than *Ægilops triticoides*; and supposing the law in question to be true, the natural conclusion was, that *Ægilops speltaformis* reverted insensibly to *Triticum vulgare*. The author now doubts much whether that law is solidly established. On the one hand, this return of *Ægilops triticoides* to its male type, through *Ægilops speltaformis*, is so long in coming to pass, that it may be despaired of. On the other hand, the experiments he has made upon hybrids in general, and especially hybrids of *Verbascum* and *Digitalis*, have led him to think that fertile hybrids are ordinarily only produced when they are fecundated anew by one of the two specific types which have given birth to them. All the hybrid plants he has hitherto obtained by artificial fecundation have been sterile, with the exception of flowers which he has fecundated with the pollen either of the male or female parent; he has then mostly obtained fertile seeds, and the product of this new fecundation then approached nearer to the male type.

Might it not be the same with *Ægilops triticoides* when it is fertile? Dr. Godron was desirous of making certain of this by the experimental method, and for this purpose it was necessary to produce this *Ægilops* anew at Nancy, as he had previously done at Montpellier. He obtained several plants of it, some of which were fecundated with wheat in the summer of 1857. This new fecundation by the male type afforded nine seeds, which germinated perfectly. They were sown in autumn, and protected from excessive cold in a frame. These plants flowered, and produced *Ægilops speltaformis* resembling that which Dr. Godron had cultivated for four years, and which was derived from seed from the Paris Garden. Dr. Godron compared the two plants in a fresh state; they were sown at the same time, but separately; they flowered in the same week, and he could not detect any difference between them. Finally, he adds, that the ovaries of this *Ægilops speltaformis* obtained artificially have already (June 29th) acquired their normal size, and appear well developed: he has reason to think that they will furnish fertile seeds, like the *Ægilops speltaformis* cultivated by M. Fabre.

*Ægilops speltaformis* is, then, a new hybrid plant resulting from the fecundation of *Ægilops triticoides* by *Triticum vulgare*; it is a true *quadroon*, if we may use here a term by which is designated one of the degrees of crossing between the Negro and the Caucasian race.

The author anxiously invites botanists interested in this question to repeat his new experiments, and they will be convinced. This same year, however, experiments similar to the above, the results of which are as yet unknown to him, will serve to control the author's. They have been made by MM. Vilmorin and Grœnland. Lastly, M. J. Gay brought from Beziers last year a seed of the wild *Ægilops triticoides*, which has germinated. This learned botanist will doubtless make known the result which it will produce.—*Comptes Rendus*, July 19, 1858.



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