this, but excused himself on the ground that, while he had originally worked honestly, Stewart had never checked his results, so that the blame must be his.

Some reference should be made to a little volume, "The Unseen Universe," published in 1875, and intended to reconcile science with revealed religion. It appeared anonymously at first and, though probably forgotten now, it created a sensation at the time, running rapidly through many editions, in the later ones of which the authors' names—Balfour Stewart and P. G. Tait—were given. Referring to Tait's contribution, Stewart told me that when he first approached him, suggesting a joint publication, his consent was subject to the condition that Stewart should write the book while he would make himself responsible for the preface. When this was agreed to and the manuscript of the preface arrived, Stewart was amused to find that it was almost entirely taken up with an attack on John Tyndall, who was Tait's *bête noire*. It had to be re-written, and to judge from internal evidence I should surmise that not much more than the first paragraph was Tait's work. I am under the impression, nevertheless, that Tait's share in the book was not negligible, and that though he acted mainly in an advisory capacity at first, he made substantial additions in the later editions.

Towards the close of his life Stewart became much interested in so-called spiritualistic phenomena, but he always insisted—sometimes with great vigour—on his disbelief in messages from the dead, which were contrary to his religious convictions. With regard to unexplained phenomena, in which fraud may possibly have a share, it must be said that Stewart's confiding nature rendered him quite unfit to act as a judge. He was like a child in these matters. A certain personage near Buxton—so far as my recollection goes, a clergyman—wrote to Stewart about his powers of second sight, which enabled him to find a hidden object or name a card drawn at random out of a pack. Stewart went to see him several times and was impressed. "What is most remarkable," he told me after the second or third visit, "is that the power can be transferred to others. There is a servant girl in the house who, after a stay of a few weeks, has acquired it and can now name an unseen card just as well as her master." Not a shadow of suspicion had crossed his mind.

Stewart's conversation was always suggestive and sometimes witty. The Principal of Owens College had a habit of writing letters to the professors when he had any fault to find. These always began with some complimentary remarks, the sting being reserved for the concluding sentence, or frequently a postscript. "Every billet has its bullet" was Stewart's comment after receiving one of these communications.

The Theory of Evolution since Darwin.[1]

By Prof. E. W. MacBride, F.R.S.

THE most recent development of the doctrine of evolution is the revival of Lamarckism—that is, the belief in the inheritable nature of the effects of use and disuse. Just as Bateson in 1894 enunciated the doctrine of the origin of species by sports long before this view was consecrated by the experimental labours of De Vries and given the name of the "mutation theory," so Eimer (1887) and Cope (1888) rebelled against the Weismannian conception of an unalterable germ plasm totally independent of the effects of the experiences of the body. Eimer put forward the doctrine of orthogenesis. This theory states that variations are the results of the effects of the environment on the complex constitution of the living organism, but that this constitution determines the character of these variations; they are not indefinite, but take place in a few definite directions. Eimer, who chose for his special subject of observation the wall-lizard *Lacerta muralis*, and later the swallow-tailed butterflies, pointed out that new variations make their first appearance in the later stages of growth and become inherited earlier in life as the generations succeed one another. A beautiful example, he explains, is afforded by the Ammonites, in which new features are first distinguishable in the outer coil of the shell, which is, of course, the youngest and latest to appear, whereas in succeeding strata the new feature is found affecting the more central coils. Thus it will be observed that Eimer draws the most decisive support for his theory from palæontology. Eimer seems to suppose that he is an opponent of Lamarck, but the only difference between them that I can discover is that Eimer seems to regard external conditions as altering the hereditary tendencies by direct action as sulphuric acid acts on metal, whereas Lamarck considers that external conditions stimulate an organism to make a response, and that it is this tendency to response that is inherited.

Cope, in his book "The Origin of the Fittest," likewise advocates the inheritance of the effects of use and disuse, and relies on palæontological evidence to support his view. He points out that if the development of the Ungulates during the Tertiary period followed, we find evidence that the shocks and strains to which the leg bones were subjected, and which in moderation create enlargement and strengthening of those bones during the lifetime of the individual, gave rise, as generation succeeded to generation, to permanent thickenings, fusions, and elongations of these bones; and that the modifications in teeth can likewise be explained as reactions to the changing character of the food by which the Ungulata were supported. Cope's views have become increasingly prevalent amongst North American palæontologists, and are almost universally accepted by them to-day.

The first great blow to Weismannism was delivered by the cytologists and experimental embryologists. The foundation stone of the "germ-plasm" theory was the fundamental distinction between body cells and germ cells, and the theory that, as development proceeded, the body cells were specialised so that each could only give rise to its special part of the body. But Driesch showed (1900) that if certain segmenting eggs were fragmented, a piece so small as one-eighth of the whole could give rise to a complete embryo, and Hertwig and Driesch further proved that the arrangement of these cells could

1 Continued from p. 55.

be entirely altered by pressure, so that cells which normally gave rise to the front or back were displaced to the sides, and yet that perfectly typical embryos were formed. More exact methods of investigation showed that the structure of all the nuclei in the body was alike, so that each cell might be regarded as a potential germ cell, and that the differentiation of the organs of the body was not accompanied by a differentiation of the nuclei but was due to local changes in the protoplasm. Therefore the same kind of nucleus—if the nucleus was to be regarded as the fount and director of life in the cell—must respond differently to different stimuli in different parts of the body.

Previous supporters of Lamarckism had assumed the necessity of the inheritability of the effects of use and disuse in order to account for changes which could be shown to have occurred, but it was not until 1908 that definite experimental evidence was adduced to show that changes artificially induced had, as a matter of fact, been transmitted to posterity. If this evidence were accepted, it was clear that the whole status of the questions must undergo a profound change, for a *vera causa* for the production of functional variations—in a word, of adaptations—would have been discovered. We have seen that strong evidence has been brought forward to show that minute differences distinguishing brothers and sisters of the same family were not inheritable, while "mutations" or "sports" were strongly inherited. These sports are, however, invariably pathological or monstrous in character, and if they occurred in Nature would have no chance of surviving or propagating their like.

The evidence in favour of Lamarckism was based on experiments with salamanders and toads which were carried out in Vienna. There exist two kinds of salamander in Europe, and one of them gives rise to only two young which at birth resemble their mother. The gilled fish-like larval stage with which the typical amphibian begins its free existence is in this salamander passed over within the womb of the mother. The colour of the skin is black and the animal lives on the cool Alpine uplands—it is named *Salamandra atra*. The other species of salamander is marked with bright yellow spots on a black background; it is an inhabitant of the lowlands and it gives birth to a considerable number (about thirty) of gilled young, which live for six months in the water before the gills drop off and the animals come on land. This species is named *Salamandra maculosa*. Now Dr. Kammerer, the investigator who performed these experiments, showed that if *Salamandra atra* was gradually accustomed to living in warmer and moister conditions, as reproductive period succeeded to reproductive period, it produced more young at an increasingly earlier period of development, and that when these young were reared to maturity and allowed to pair, the second generation gave rise to about half-a-dozen gilled young which took to the water and acted like the larvæ of *Salamandra maculosa*. Conversely, if *Salamandra maculosa* were made to live in comparatively cool and dry conditions, it began to carry its young for longer periods in the womb; fewer were produced at a birth, but these were born at a more advanced state of development. Finally, when these were reared to maturity and allowed to pair, the second generation gave rise to only two or three at a birth, and these were provided only with vestigial stumps of gills, so that they at once took up a terrestrial life.

If, again, the young of *Salamandra maculosa* just after metamorphosis were reared in cages the walls of which were painted yellow and black respectively, in those confined in yellow cages the yellow spots extended in area as the animal grew to maturity, so that after four years they were arranged in two conspicuous rows along the back. If two such animals were allowed to mate and produce offspring, when the resulting generation grew to maturity under the same conditions as did their parents, the yellow extended to such an extent as almost to suppress the black pigment. Those salamanders, on the contrary, which were reared in the black cages contracted the area of their yellow spots as they grew up; and when the second generation were reared under similar conditions, the animals became almost, if not quite, as black as *Salamandra atra*. The full effect, therefore, required two generations exposed to the same conditions to show itself, and the second generation started, so to speak, where the parents left off. If the offspring of salamanders which had been reared on a yellow background were reared on a black background, the yellow spots increased in area during the first six months of the animal's life; only after this period did the black begin to gain the predominance; in a word, the animal during the first period of its life *recapitulated* the history of the previous generation. This experiment constitutes, so far as I can determine, the first experimental proof of the biogenetic law which has ever been made. When the offspring of salamanders which had been reared on a black background grew up on a yellow background a unique effect was produced: the animals developed a single median stripe of yellow on the back. This is a form which is practically never found in Nature and can only be produced by experiment.

If we now turn to the experiments on toads, we may observe that nearly all toads, like the frogs, pair in water in the spring-time. The male embraces the female with his forearms and keeps her firmly in his grasp for a considerable period—often for weeks—until she emits her spawn, which he then fertilises. In order to enable him to retain a firm hold of his partner's slippery body, he has developed under the index finger a horny pad covered with minute asperities, the so-called nuptial pad. Now Alytes differs from all other toads in that pairing takes place on land, and as the female's body is comparatively dry and thorny the male does not require a nuptial pad in order to enable him to retain a hold on her. The eggs are fewer and larger in size than are the eggs of other toads; but as in other species, they are emitted in a string connected together by a cord of jelly. The male winds these cords round his legs and remains encumbered with them until the young tadpoles hatch out, a curious habit which has earned for him the name of "midwife toad." The tadpoles of ordinary toads emerge from the egg provided with three feathery gills on each side; as they grow these gills become covered over with a fold of skin proceeding from the head, and the larvæ assume the familiar form of a rounded body and flattened tail characteristic of the tadpole. The tadpoles of Alytes, however, pass through the stage with external gills whilst still within the egg-shell and emerge only when the body has become, as in the later toad-tadpole, rounded and plump. Whilst in the egg-shell they have only *one* external gill on each side.

Now Kammerer showed that although Alytes normally lived in cool spots, it could be induced to live at a warm temperature if it were provided with a basin of water in which to lave itself. In these circumstances, however, the male and female paired in water, and the eggs slipped off the legs of the male and lay in the water. By taking special precautions to keep the water aseptic, some of these were hatched and the resulting tadpoles reared to maturity. The next generation reared under similar conditions produced more numerous eggs which were smaller than those of the normal Alytes. Out of these eggs the tadpoles hatched in the external gill stage with one external gill on each side. In the next generation reared under similar conditions the tadpoles were provided with three external gills on each side as in ordinary toads, and in this generation the males developed horny pads.

These experiments aroused a quite different kind of criticism from that which had been evoked by any previous work, and one which strongly recalled the "odium theologicum" with which the first presentation of Darwin's theory of evolution was received in 1859. The experiments were admitted to be conclusive if true, but some critics declined to accept them. Kammerer visited England less than two years ago, bringing with him critical specimens, amongst them salamanders with a median stripe of yellow and a male Alytes showing the horny pad. Even then the critics were not convinced. It was asserted that the pad in the normal frog or toad was on the upper side of the hand and not on the lower side, and that therefore the specimen produced had not a true horny pad. In answer to this Kammerer asserted that in his Alytes—as his critics would have seen if they had examined it carefully—the nuptial pad was developed on the dorsal surface of the fingers but extended also round to their palmar surfaces; and to this answer I can add that the first four male frogs which I examined after this discussion all showed the pad on the lower surface of the hand as well as on the upper. But Kammerer showed other specimens on the same occasion which reduced all the discussion on the subject of the pad of Alytes to the level of "straining at a gnat and swallowing a camel." For all critics and supporters of Lamarckism alike admit that Alytes is descended from ancestors which, like more normal toads, possessed pads, and that the appearance of a pad in Alytes is therefore an atavism.

The most wonderful experiment, however, which Kammerer has ever published was that in which, *in one generation*, he had induced the blind cave-newt Proteus to develop a fully-formed eye. These creatures he brought with him to England, and there was no possibility of mistake about the matter. Proteus cannot be confounded with anything else; its pale flesh colour and reduced limbs are characteristic, and newts of this kind with large well-formed eyes were shown at the discussion. One is inclined to ask whether it is easier to produce a fully-formed eye than a mere cornification of the skin.

Kammerer's results have in the meantime been confirmed by the independent work of Durkhen on the colour of the pupæ of white butterflies. This work was carried out in the University of Breslau, and was published in 1923. The pupæ of this species normally have an opaque skin of a greyish-white colour, but in a small percentage (about 4 per cent.) this colour is absent and the skin is transparent, and so the pupa appears green, owing to the green blood shining through. If, however, the caterpillars are exposed to orange light, the formation of the white pigment of the pupa is largely inhibited, and the proportion of green pupæ rises to 65 per cent. If these pupæ are allowed to develop into adults and produce offspring and the caterpillars of the second generation are exposed to the same conditions, then the proportion of green pupæ rises to 95 per cent.; if the caterpillars of this generation are, however, left in ordinary daylight, the proportion of green pupæ diminishes, but is still 34 per cent. as compared with 4 per cent. in the controls. Here, as in Kammerer's experiments, we see that the reaction to the environment on the part of the first generation affects the second generation, and that a trace of it persists even when the second generation is replaced in the original conditions.

In England, Dr. Heslop Harrison, of the University of Durham, has observed that a certain melanic variety of moth is found where the food plants are infected with manganese salts derived from the smoke of adjacent factories. He fed the pale variety of this moth on food impregnated with the salts of manganese, and after several generations succeeded in obtaining melanic specimens, and from these he obtained a melanic progeny which bred true.

We are, therefore, in a position to state that after the lapse of the first quarter of the twentieth century, the doctrine of Lamarck has been submitted to the crucial test of experiment and proved to be true. Now evidence of the actual course of evolution is derived from three classes of facts, namely, those of systematic zoology (*i.e.* the mutual relations of varieties and species), those derived from a study of embryology, and, finally, those deduced from palæontology or the study of fossils; and systematists, palæontologists, and embryologists alike have been forced to the conclusion that the effects of habits must be inherited in order to account for the facts which they find in Nature. We are therefore justified in saying that habit, which is the reaction of the animal to its environment, has been the great factor in evolution, and that the splitting of the original stock into divergent species has been due to different members of the same stock under the stress of different environments adopting different habits. Prof. McDougall in "Psychology" has shown that this readiness to adopt new habits is a universal characteristic of living beings. "An animal when its activity is roused by a stimulus," writes McDougall, "pursues an end, and its activity continues till that end is attained or until it is exhausted. If it fails to attain that end in one way, *it will endeavour to gain it in another* until it achieves success." In this sentence, we venture to think, is contained the key to the riddle of evolution.

We might leave the subject here, but considering the vogue that the mutation theory of evolution has had, it is proper to consider whether any definite cause for these mutations can be found, and if so, what relation this cause bears to the reactions which set up habits.

Nothing has been more remarkable than the consensus of opinion of the upholders of the mutation theory that mutations are due to "chance," and yet, as Huxley remarked, one had hoped that a belief in chance had been finally exploded. Quite recently, however, a physiological cause for mutations has been suggested by Tornier, and much evidence in favour of it has been collected by him. The special subject of his investigations was the goldfish. The most bizarre races of this creature have appeared, and these races when crossed produce offspring which obey the Mendelian rules. Now Tornier showed that the races of goldfish had been derived from a small species of carp which inhabits the rivers of China. He found that the Chinese breeders kept their stock in small dark jars under insanitary conditions in which they were scantily supplied with oxygen. Much of the spawn died, and among the survivors all sorts of abnormalities turned up; from these the most striking specimens were selected and used to found the new breeds. These facts suggested to Tornier the view that the cause of the mutations was the weakening of the developmental energy of the germ by the abstraction of oxygen during an early and critical period of development.

Tornier showed that this weakening had two consequences: (1) it made the embryo sluggish in its movements; and (2) it diminished its power of regulation of the various processes on the harmonious co-operation of which the upbuilding of the body depends. Thus enormous fins were produced by the swelling of the yolk in consequence of undue absorption of water underneath the skin-area from which the fin developed, telescopic protruding eyes by the engorgement of the growing eyeball with water, and so on. By treating the eggs of newts and toads in such a way as partly to suffocate them for a short period after fertilisation, similar embryos were produced. Independently of Tornier, Jansen had arrived at a similar explanation of the cause of human deformities, the part played by the pressure of the swollen yolk in the goldfish's egg being assumed in the human embryo by the pressure of a too closely adherent amnion. What is inherited is, according to Tornier, not a factor or gene for an enlarged fin or protruding eye, etc., *but a certain grade of germ-weakness which in each succeeding generation produces the same morphological effects.*

If this view is correct—and all the evidence available conspires to show that it is—then mutations can have played no part whatever in evolution. Since they are the outward and visible signs of a weakened constitution, they are in a state of Nature ruthlessly weeded out by natural selection. Nevertheless they, like functional adaptations, are the result of the action of the environment—only in their case the animal has *failed to respond* to the changed conditions, whereas evolution depends on cases where the animal *has successfully responded.* In the last resort, therefore, like Darwin we come back to natural selection, only what is "selected" is not a chance variation or peculiarity but the constitutionally vigorous individual with ability of self-adaptation; what is rejected is the individual of weakened constitution.

Obituary.

Sir William E. Garstin, G.C.M.G., G.B.E.

SIR WILLIAM GARSTIN, whose death at the age of seventy-five occurred on January 8, commenced his career in India in 1872 as an officer of the Public Works Department, after studying engineering at King's College, London. Thirteen years later he was invited by Sir Colin Scott Moncrieff, who had just taken charge of the Public Works Ministry in Egypt, to make one of the small group of Indian engineers who were undertaking the reorganisation of the irrigation system of Egypt, which was at that time in complete disorder.

In charge of the Circle of Irrigation which included the eastern half of the Nile Delta, Garstin spent seven arduous years in effecting his share of the restoration of the irrigation system, and then, on the retirement of Col. Justin Ross in 1892, he was appointed Inspector-General of Irrigation for the whole country. A few months later, on the retirement of Sir Colin Scott Moncrieff, he became Under-Secretary of State in the Ministry of Public Works.

At that time the irrigation system was being rapidly improved; the basin irrigation of Upper Egypt had been largely remodelled by Col. Ross, improvements in the Delta had led to large increases of crops, and larger supplies of water in the early summer were urgently required. Plans for a reservoir in or near the Nile Valley were being studied, and it fell to Sir William Garstin to advise on the scheme to be adopted. As a result, the Aswan Dam with subsidiary barrages at Assiut and Zifta were built, and by these means, and later developments of them, Egypt's low-stage water supply was assured.

As soon as Omdurman had fallen and the Sudan had been retaken, Garstin took prompt measures for the clearing of the Bahr el Jebel and the Bahr el Ghazel from the "sudd"—those blocks of drift and growing vegetation which had closed many of the channels. Sir William visited the Sudan on numerous occasions, and especially in 1901, and again in 1903, when he traversed Uganda also to see the headwaters of the Nile system. The investigations and surveys which were then initiated have since furnished a mass of hydrographical information of the highest value both to Egypt and to the Sudan.

Although his work in relation to irrigation is the most known in Great Britain, Garstin's position as the senior officer of the Ministry of Public Works in Egypt brought him in contact with many other forms of the public service. On his recommendation a geological reconnaissance of Egyptian territory was started in 1896, which soon developed into the present Geological Survey. The Survey of Egypt commenced in the Ministry of Public Works while he was in charge, and