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Lamarckian and Darwinian Conceptions of the Struggle for Existence

BY

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Presidential Address to the Zoological Section.

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It seems to us at this date both remarkable and surprising that so many naturalists in the early years following the appearance of the *Origin of Species* should have found great difficulty in grasping the meaning of Natural Selection as a motive cause of evolution. Thus, Darwin wrote to W. B. Carpenter on 18th November, 1859: ". . . I have found the most extraordinary difficulty in making even able men understand at what I was driving";[1] and in other letters he referred to the hopeless task of bringing new ideas into an already pre-occupied mind. The evolutionary thoughts of the days before the *Origin* were those of Erasmus Darwin, Lamarck and Buffon, and such thoughts, whether accepted or rejected, tended to prevent the acceptance of other interpretations. This is well exemplified by the position taken by Dr. Gray, Keeper of the Zoological Collections of the British Museum, as described in Darwin's letter of 14th December, 1859, to Sir Joseph Hooker: "Old J. E. Gray, at the British Museum, attacked me in fine style: 'You have just reproduced Lamarck's doctrine, and nothing else, and here Lyell and others have been attacking him for twenty years, and because *you* (with a sneer and laugh) say the very same thing, they are all coming round; it is the most ridiculous inconsistency, &c., &c.'"[2] Nearly a year later the same friend had another criticism to make, for we read in Darwin's letter of 28th September, 1860, to Lyell: "Dr. Gray of the British Museum remarked to me that, '*selection* was obviously impossible with plants! No one could tell him how it could be possible!' And he may now add that the author did not attempt it to him!"[3] We here again meet with the impact of Lamarckism—or, rather, of the belief that Natural Selection *is* a Lamarckian theory—upon Darwinism; for clearly it is far more difficult to imagine the evolution of plants by the older theory than the evolution of animals. How can we reasonably apply the con-

ception of the supposed transmission of "slow willing," of effort, memory, habit or instinct, all bound up with the nervous system, to the Vegetable Kingdom? Indeed, when we reflect on the subject, it seems surprising that the difference between animals and plants has not been more widely recognized as an insuperable obstacle to the general application of Lamarck's theory.

At this point I venture to remind you of certain humorous verses,[4] obviously intended—as shown by the dates of publication—to make fun of Darwinian evolution and yet, apparently unknown to their authors, referring exclusively to Lamarckian theories. First, however, it will be interesting to quote some pre-Darwinian lines from James Russell Lowell's *Biglow Papers* (1846-48)—lines evidently inspired by the Lamarckian idea of changes wrought by desire:—

"Some flossifers think thet a fakkilty's granted
The minnit it's proved to be thoroughly wanted,
Thet a change o' demand makes a change o' condition,
An' thet everythin's nothin' except by position;
Ez, fer instance, thet rubber-trees fust begun bearin'
Wen p'litikle conshunces come into wearin',—
Thet the fears of a monkey, whose holt chanced to fail,
Drawed the vertebry out to a prehensile tail."

Among the later amusing verses which appeared after the publication of the *Origin of Species* in 1859 we find, in 1861, the following by Lord Neaves:—

"A deer with a neck that was longer by half
Than the rest of its family's (try not to laugh),
By stretching and stretching, became a Giraffe,
Which nobody can deny."

Yet Wallace, in his section of the Joint Essay, read 1st July, 1858, before the Linnean Society, had written that the giraffe did not "acquire its long neck by desiring to reach the foliage of the more lofty shrubs, and constantly stretching its neck for the purpose, but because any varieties which occurred among its antitypes with a longer neck than usual at once secured a fresh range of pasture. . . ."

Then Courthope, in *The Paradise of Birds* (1870), tells of the Ornithorhynchus — most prudent and foreseeing of animals:—

"For he saw in the distance the strife for existence,
That must his grandchildren betide,
And resolved, as he could, for their ultimate good,
A remedy sure to provide.
With that, to prepare each descendant and heir
For a different diet and clime,
He laid, as a test, four eggs in his nest—
But he only laid two at a time.

On the first he sat still, and kept using his bill,
That the head in his chicks might prevail:
Ere he hatched the next young, head downwards he slung
From the branches, to lengthen his tail.
Conceive how he watched till his chickens were hatched,
With what joy he observed that each brood
Were unlike at the start, had their dwellings apart,
And distinct adaptations for food.

. . . . . .

From the bill, in brief words, were developed the Birds,
Unless our tame pigeons and ducks lie;
From the tail and hind legs, in the second-laid eggs,
The Apes and—Professor Huxley."

All this excellent fun refers, of course, to Lamarckian teachings and many years elapsed before May Kendall in her *Ballad of the Ichthyosaurus* (1887) wrote an amusing skit upon Darwinian Natural Selection:—

"E'er Man was developed, our brother,
We swam and we ducked and we dived,
And we dined, as a rule, on each other—
What matter, the toughest survived."

I must not, however, occupy too much of our time over these general considerations, interesting and amusing as they certainly are. I propose to bring before you strong evidence that Lamarckian theories cannot offer any help in understanding the evolution of insect adaptations—probably the most varied and remarkable of any to be found in the Animal Kingdom. The conditions of the struggle for existence between insects and enemies so much larger than themselves are such that we are driven to accept Natural Selection as the one essential guide. Thinking over this subject I re-read with very great pleasure the letter,[5] written on 20th November, 1862, by Darwin to H. W. Bates: "With respect to mimetic resemblance being so common with insects, do you not think it may be connected with their small size; they cannot defend themselves; they cannot escape by flight, at least from birds, therefore they escape by trickery and deception?" This thought leads us away from Lamarckian evolution by the transmission of experience, for failure means extermination and excludes the possibility of improvement. Therefore, in the vast majority of insects, adaptation is directed not to struggle with enemies but to escape detection by enemies—a result which may be achieved by a second attempt when the disturbed prey falls to the ground and is hidden among grass-stems or dead leaves.

Protective resemblances in desert areas afford striking illustrations of this principle and were recognized long before Natural Selection was introduced to the world in 1858 and 1859,

and even before Wells in 1818 and Patrick Matthew in 1831 had suggested it. Thus, the great African traveller, W. J. Burchell, on 14th September, 1811, at Zand Vlei (Sand Pool), near Prieska on the Orange River, noted a Mesembryanthemum (*M. truncatum*) and a Gryllus (*Acridian*) both closely resembling the pebbles abundant in the locality. This he explains by "the intention of Nature": "By their form and color, this insect may pass unobserved by those birds, which otherwise would soon extirpate a species so little able to elude its pursuers, and this juicy little Mesembryanthemum may generally escape the notice of cattle and wild animals."[6] But when the insect and the plant *are* observed by enemies there is no escape, no chance of learning by experience. A Lamarckian interpretation of the evolution of such adaptations is excluded: Natural Selection offers the only help. Referring to Burchell's words on "the intention of Nature," Thiselton-Dyer wrote[7] that he "was clearly on the track on which Darwin reached the goal. But the time had not come for emancipation from the old teleology. This, however, in no respect detracts from the merit or value of his work. For, as Huxley has pointed out (Huxley's *Life and Letters*, 1900, I, p. 457), the facts of the old teleology are immediately transferable to Darwinism, which simply supplies them with a natural instead of a supernatural explanation."

Before leaving these examples of similar protective adaptations in plants and animals, it is interesting to find that Burchell recorded, in an unpublished manuscript, his observation, on 5th July, 1812, of a little plant, a "Crassula (not in flower) so snow white, that I should never [have] distinguished it from the white limestones. . . . It was an inch high and a little branchy . . . and was at first mistaken for the dung of birds of the passerine order."[8] Resemblances of this kind, which are of course very common among insects, cannot, I believe, be explained as a product of Lamarckian evolution. Whenever, in their earlier stages of development, the sharp senses of enemies detected the imposture of plant or animal, this could only lead to destruction and the survival of others with a more convincing resemblance—in fact, to the normal operation of Natural Selection.

Excellent examples pointing to the same conclusion are to be found among the caterpillars of Geometrid moths, which closely resemble the twigs of the food-plant and maintain a rigid attitude by means of a silken thread fixed to the bark and of such a length that the larva is held at a natural angle with the supporting branch from which it appears to have

grown. If the thread were too long so that the larva made a right angle, or some other unnatural angle with the branch, and was detected by an enemy, by what possibility could the Lamarckian principle lead to improvement? Improvement of the species as a whole would certainly result by the elimination of the less fit. This reasoning applies with equal force to the other factors which combine to produce the wonderful perfection of the deceptive resemblance. It also applies to earlier stages when the larvae rest upon leaves and the attitude is entirely different, suggesting in some species the appearance of birds' or snails' excreta, a silk thread being spun when the weight and position are such as to require support. The caterpillar of the Large Emerald (*Hipparchus papilionaria* Linn.), with a short, catkin-like shape, can dispense with this assistance, as can the Great Oak Beauty (*Boarmia roboraria* Schiff) when it stands upright on the summit of a vertical twig and appears to be a prolongation of it. In this position the strain can be endured but not when the twig and larva are fixed horizontally. Another interesting departure from the common attitude is exhibited by geometrid larvae which feed on low-growing plants. Thus, in the Straw Belle moth (*Aspitates gilvaria* Schiff), the caterpillar, holding by the two posterior claspers to the edge of the leaf, is coiled into a flat spiral resembling a small bleached and empty snail-shell. I have mentioned a few of the different forms of protective resemblance adopted by these caterpillars and I believe that in attempting to explain their evolution we are in every instance obliged to appeal to Natural Selection.

A study of the protective patterns and attitudes of the perfect insect leads to the same conclusion—that detection by enemies means the extermination of imperfectly adapted varieties and cannot lead to their improvement. I will mention one or two examples from the Geometridae. The resting attitude of the Spring Usher (*Erannis leucophaearia* Schiff) was described by A. H. Hamm,[9] who observed that the insects nearly always settled with the body horizontal, thus making the strongly-marked lines of the wing-pattern parallel with the vertical cracks of the bark. In the more usual position adopted by moths, with the head uppermost and the body vertical, the wing-pattern of this species, with its strong lines cutting across the dark vertical shadows in the cracks, would lead to comparatively frequent detection and death. A similar example has been recently described[10] by J. J. S. Cornes from New Zealand, where the Geometrid moth, *Venusia verriculata*

Felder, rests so that the lines of the wing-pattern are parallel with those of the dead leaves of the larval food-plant, the Cabbage tree (*Corduline australis*).

It is necessary at this point to make brief mention of the very large amount of work which has been done in order to obtain evidence that insects, with the adaptations described and others of the same kind, *are* subject to attack by numerous enemies, especially birds. The experiments which Miss C. B. Sanders (Mrs. Hodson) and I conducted in 1898 and described at the British Association meeting in that year, showed that the pupae of the Small Tortoiseshell butterfly (*Aglais urticae* Linn.) were in much greater danger when suspended against backgrounds with which their appearance contrasted than against those with which it harmonized. Sir Guy Marshall, in his great memoir published in the *Transactions of the Ent. Soc. Lond.* in 1902, figured numbers of South African butterflies with injuries evidently inflicted by birds or in some instances by lizards. Evidence furnished by beak-marks on butterflies' wings, in some instances resulting from an attack actually witnessed, has been produced by Dr. W. A. Lamborn and, extensively for many years, by Professor Hale Carpenter. Striking proofs that conspicuous insects are rejected and protectively coloured accepted have been obtained by Dr. Morton Jones in North America, Dr. H. B. Cott, especially studying the preferences of Amphibia, and Dr. H. N. Kluijver, of starlings. Reference to the protective resemblances of Geometrid larvae leads me to write a few words upon R. Carrick's experiments[11] on those of the Early Thorn moth (*Selenia bilunaria* Esper), which, resting motionless on a small branch fixed over the nest of a wren, were unobserved by the parent bird, but seized when lying on a white surface beneath. A very important adaptation which cannot have arisen by Lamarckian evolution is the power of colour adjustment possessed by so many larvae developed from eggs which may be laid on two or more different plants with branches of different colours. Thus, the caterpillars of the Peppered Moth (*Biston betularia* Linn.) will become black, brown, green or white, resembling the colour of the branchlets or twigs on which they rest by day. This effect is not caused by food, for if a number hatched from the eggs of one parent are all fed on the same kind of leaf intermixed in different cages with differently coloured twigs or even white paper spills, the larvae will soon come to resemble those on which they rest.[12] This power has been shown to exist in a large number of species and it cannot be doubted that protection is conferred by it;

nor that less successful manifestations have no chance of improvement but, when detected, are devoured. An especially beautiful example is that of the Lappet Moth caterpillar (*Gastropacha quercifolia* Linn.) which, fed on hawthorn, becomes black, brown, or presents the most perfect likeness to bark with lichen, when pieces of stick with these appearances are intermixed with the food-plant.[13] Here, too, the development of susceptibility to the stimulus of reflected light requires the agency of Natural Selection. In reaching this conclusion, it must be remembered that the effective stimulus was always provided by coloured surfaces similar to those on which the wild larvae rested. Bright red or blue produced no corresponding effect, but only some one of the normal colours. The effect of white paper spills on *betularia* at first surprised me, but I afterwards found that white stems existed on some of the natural food-plants and produced their full effect on the caterpillars.

The most striking adaptations which provide the most convincing evidence of Darwinian, as opposed to Lamarckian, evolution are those which are prophetic—a preparation beforehand for future dangers. I will venture again to refer to Dr. W. A. Lamborn's[14] fascinating observations on the larvae of an African Tabanid fly, feeding in soft mud which will become hard and traversed by wide and deep cracks in the dry season, exposing embedded insects to attack. When the maggot is mature and about to become a pupa it crawls round and round, making a pillar in the still soft clay by enclosing it in a spiral tunnel which forms a line of least resistance when the dry season sets in and causes contraction and cracking. But by this time the pillar has separated from the rest of the mud and the cracks stop short when they reach it with the pupa lying deeply embedded and safe in the centre. Dr. Lamborn observed that the summits of these pillars, each about the size of a penny, were scattered over the surface of the dry clay, but that they were never traversed by the wide cracks; also that, when the fly had emerged, an empty pupal shell protruded from the centre of each. My dear friend, the late Professor J. Mark Baldwin, wrote to me when he heard of this discovery: "It seems *complete*—one of those rare cases of a single experience being sufficient to establish both a fact and a reason for the fact! It is beautiful." How is it possible on Lamarck's theory or on Hering's and Samuel Butler's unconscious memory, to explain a prophetic instinct like this—the preparation when the clay is soft for meeting dangers to

be encountered in the following season when it will become hard?

The cocoons of caterpillars also furnish admirable examples of prophetic adaptations for preserving life during the pupal stage. Some of the most remarkable of these were also discovered in Africa by Dr. Lamborn, one being the larva of the Hypsid moth, *Deilemera antinorii*,[15] which covers its cocoon with such good imitations of the small cocoons of Braconid parasites that they were kept under observation for some time in order to obtain the insects which it was supposed would emerge from them. As nothing happened, they were more carefully examined and found to be masses of hardened froth extruded from the anus of the caterpillar on the surface of its cocoon and then fixed in position by threads of silk. In another species, the Bombycid moth, *Norasuma kolga*,[16] the larva constructs a reddish cocoon on which it spins pretence parasite cocoons of yellow silk. It is improbable that this instinctive behaviour is adapted to prevent parasites from attacking the enclosed pupa, but that it is a safeguard against birds which have wasted efforts in opening cocoons containing the remains of parasitized larvae or pupae.

Of a different kind, but equally convincing as evidence of Darwinian evolution, are the preparations made by the larva for the ready emergence of the future moth from the cocoon. Especially remarkable is the behaviour of an Indian caterpillar, described by Lt.-Col. F. P. Connor, who has written:[17] "It was a striking fact to observe how the larva, after all but completing the cocoon, always 'remembered' to destroy part of its laboriously built home by biting out two deep clefts at one end, and how the valve-like door thus made was patiently tested several times to make certain of its being the right size, and then carefully closed on the inside with a little soft silk which would not interfere with the emergence of the imago." Here, again, there would be no opportunity for a moth to transmit the experience of an unsuccessful attempt to escape and no improvement by Lamarckian evolution.

If time permitted, it would be possible to bring forward an immense body of evidence from the study of mimicry in insects, and, before concluding, I wish to quote two passages from H. W. Bates's great memoir[18] on this subject: "The operation of selecting agents, gradually and steadily bringing about the deceptive resemblance of a species to some other definite object, produces the impression of there being some innate principle in species which causes an advance of organization in a special direction. It seems as though the

proper variation always arose in the species, and the mimicry were a predestined goal." Then, after mentioning other attempted explanations, he concludes that all are "untenable, and the appearances which suggest them illusory. Those who earnestly desire a rational explanation must, I think, arrive at the conclusion that these apparently miraculous, but always beautiful and wonderful, mimetic resemblances, and therefore probably every other kind of adaptation in beings, are brought about by agencies similar to those we have here discussed"—namely, those described only three years before in the *Origin of Species*.

We are led to wonder why a greater effect was not produced by this splendid memoir, published at so critical a time. The reason is, I think, given in Darwin's letter[19] to the author written on 20th November, 1862: "I have one serious criticism to make, and that is about the title[20] of the paper; I cannot but think that you ought to have called prominent attention in it to the mimetic resemblances. Your paper is too good to be largely appreciated by the mob of naturalists without souls; but, rely on it, that it will have *lasting* value, and I cordially congratulate you on your first great work."

1 *Life and Letters of Charles Darwin*, Vol. II, 1887, p. 222. Future references to this volume will be indicated by *L. and L.*

2 *L. and L.*, pp. 242-3.

3 *L. and L.*, p. 346.

4 Quoted in an Address to the "Boston Society of Natural History," 7th February, 1894, Proceedings, Vol. XXVI, p. 327. Reprinted in "Essays on Evolution," Oxford, 1908, pp. 102-104.

5 *L. and L.*, pp. 391-93. The quoted words, on p. 393, referred to Bates' great memoir on mimicry in the *Trans. Linn. Soc., Lond.* (1862), Vol. XXIII, p. 495.

6 *Travels in the Interior of Southern Africa*, I (1822), pp. 310, 311.

7 *Morphological Notes*, XI; *Protective Adaptations*, I; *Annals of Botany*, XX, p. 124.

8 *Darwin and the Origin*, Poulton, Lond. 1909, pp. 102, 103. Another plant (*Anacampseros papyracea*) exhibiting the resemblance described by Burchell is quoted from Thiselton-Dyer in a footnote on p. 102.

9 *Proc. Ent. Soc. Lond.*, 1902, p. xv; see also *Trans. Ent. Soc. Lond.*, 1906, pp. 483-5, pl. XXIX, fig. 1. The names of the moths, with the original spelling, were kindly confirmed by Mr. W. H. T. Tams.

10 *Nature*: 16 October, 1937: letter with Fig. 1. See also Prof. Hale Carpenter's letter on the same page.

11 *Trans. Roy. Ent. Soc. Lond.*, 1936, p. 131, pl. 2.

12 *Trans. Ent. Soc. Lond.*, 1892, p. 337, pl. XIV; also 1903, pp. 356-68.

13 *Trans. Ent. Soc. Lond.*, 1903, pp. 332-56, pls. XVII, XVIII.

14 *Proc. Roy. Soc.*, B, Vol. 106, 1930, p. 83, pl. V; see also *Proc. Ent. Soc. Lond.*, V, 1930, p. 14.

15 *Trans. Roy. Ent. Soc. Lond.*, 1931, p. 398; see also *Proc.*, 1911, pp. xcvi, xcvii.

16 *Trans. Roy. Ent. Soc. Lond.*, 1931, pp. 397-8, pl. XV; see also *Proc.*, 1911, xcv, vi.

17 *Journ. Bombay Nat. Hist. Soc.*, Vol. XXVI, 1919, p. 691.

18 *Trans. Linn. Soc. Lond.*, Vol. XXIII (1862), Pt. III (1862), Mem. XXXII, pp. 514-15.

19 *L. and L.*, II, p. 393.

20 *Contributions to an Insect Fauna of the Amazons Valley.*

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