and improvement of the thermometer. This first appeared in Italy about the same time as the barometer, and the conception of the steam engine may be traced directly to the introduction of those philosophical instruments and the enlargement of human knowledge they brought in their train. Fahrenheit, the German instrument maker of Amsterdam, was the first to make thermometers with adequate skill, and he also fixed, first the freezing point, then the blood heat, thirdly the extreme cold of a mixture of ice, water, and sal-ammoniac, and then the boiling point of water. Writing a hundred years later, Sir John Leslie, himself a great experimenter, said: "The Doctrine of Heat has in the course of the eighteenth century been advanced to the rank of a science. Its transfusion through the mechanical arts has communicated a grand movement to society and wonderfully augmented our natural wealth and resources." Leslie then went on to recall some of the most important discoveries: Fahrenheit's thermometric scale; Cullen's observation of the lowering of the boiling point under a decrease of pressure; Black's theory of latent heat and sensible heat; the introduction of the terms 'capacity for heat' and 'specific heat'; Lavoisier's and Laplace's experiments on calorimetry; Wedgwood's pyrometers; the registering thermometers of Six, and the production of artificial cold; but like Black he felt that the true theory of heat had yet to be discovered, remarking, "What seems wanted at present to complete our knowledge of heat, is not the vague repetition of experiments already carefully performed, but a nice investigation of several unexplored properties, directed with scrupulous accuracy on a large scale." Had Leslie but known it, even at the time he wrote, the famous essay of Carnot had already been published, while Joule, Rankine, Kelvin, Mayer, Clausius, Tyndall, and others were just beginning the careers during which they were to demonstrate by means of "nice investigations," "directed with scrupulous accuracy," that, as suggested by Black, the true theory of heat is not "chemical, but mechanical."

With Black's work on latent heat his course of discovery came to a close. In 1766 he removed to Edinburgh as professor of chemistry, and there for more than thirty years lectured on his favourite subjects. The friend of Watt, Adam Smith, Robison, Hume, Playfair, and Hutton, he passed his life in the quiet performance of his congenial duties, somewhat indifferent to honours, but cheerful and courteous to all alike. His death took place suddenly as he sat in his chair, on Dec. 6, 1799. Robison, who wrote a sketch of him and published his lectures, gave the date of his death as Nov. 10, and Ferguson gave it as Nov. 26, another mistake. It was Muirhead who first pointed out the discrepancy; the date Dec. 6 being confirmed from the newspapers of the time.

Life's Unsuspected Partnerships.[1]

By Prof. DORIS L. MACKINNON.

SYMBIOSIS is the word used by biologists to describe the state of affairs in which two or more different kinds of organisms are closely, and in some cases inseparably, associated for the greater part of their lives in a partnership from which both, in some degree, probably draw benefit. Within the last few years, many unsuspected interdependences have been revealed, and a vast field has been opened up for further research.

It has recently been claimed by Pierantoni and other workers that the luminescence of surface-living cuttle-fishes, pelagic tunicates, and certain reef-inhabiting fishes is produced by bacteria that are in constant symbiosis with them. Saprophytic light-giving bacteria are abundant in the sea, and are inevitably swallowed by feeding animals, in the dead bodies of which they multiply exceedingly, and, still glowing, produce the disconcerting phenomenon of phosphorescence which may be noticed, for example, in rotting fish.

Among the little sand-hoppers of the genus *Talitrus*, which are normally not luminescent, one is occasionally found glowing with a mysterious inward light. Such individuals are always diseased, and if their infected blood be injected into the bodies of other like crustaceans, these also begin to glow and soon die. It would look therefore as though, for some animals, the incursion of luminescent bacteria is directly harmful. But others have acquired immunity against the invaders, and have even turned the invasion to account. Such are the pelagic tunicates and the cuttle-fishes. The best-known example of tunicate phosphorescence is that of the creatures known as *Pyrosoma*, which form transparent, gelatinous, tube-shaped colonies floating on the surface of the warmer seas. The walls of the tube are composed of numerous individuals seated in a common gelatinous envelope and adding to their number by budding. The mouth of each person is directed outwards, and close behind it is a patch of tissue which is the light-organ. It has been discovered that the cells composing this organ contain luminescent bacteria, and it is the glowing of these that gives the animals their phosphorescence. It is not easy to imagine what advantage the *Pyrosoma* colony derives from this; the animals have no eyes, they are hermaphrodite, and they lie in close association; but some important advantage there must be, for the eggs that will give rise to new colonies are always furnished with a certain quantity of the bacteria, handed on from the parent.

When the *Pyrosoma* individual is sexually mature, some of the bacteria in its light-organ begin to form spores, which then leave the shelter of the cells in which they have developed and are carried by the blood-stream to the little sac in which the single egg is developing. Invading the cells of this sac, they seem to induce these to divide, and one of the

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[1] From a Friday evening discourse delivered at the Royal Institution on May 11.

daughter cells at each division moves into the space between the sac and the egg. This invasion continues and the infected cells continue to multiply and move in towards the egg until there are about four hundred of them. The egg itself has meanwhile begun to divide, and the infected follicle cells, glowing all the time, take up their position between the blastomeres. Each egg gives rise to four *Pyrosoma* individuals, which will be the founders of a new colony, and between these four the invading luminescent cells are scrupulously divided, taking up their definitive position, as time goes on, in the light-organs. In this way, from generation to generation, the sacred flame is handed on.

In the cuttle-fishes, the eyes are in their way as perfect optical apparatus as those of a vertebrate, the sexes are separate, and in the majority of species the luminescence is shown by the female only. The eggs of the cuttle-fish are enveloped in a shell which is secreted around them on their passage to the exterior by structures known as the nidamental glands. In front of the nidamental glands lies another, usually called the accessory nidamental gland; and it was always supposed that this furnished some contribution to the egg-shell. But now we know that it does no such thing; it is a phosphorescent organ, composed of tubes of three kinds and colours, white, yellow, and orange, each of which is crammed with bacteria of a different sort: it is those in the yellow tubes that are luminescent. The luminescent gland opens to the sea and the bacteria can pass out. The cuttle-fish, then, may glow with a more or less steady internal light, or it may eject streams of fire. In some cuttle-fish, the apparatus is further complicated by the development of a reflector behind the gland, backed by a pigment screen, and there is actually a lens in front, so that the animal has a veritable bull's-eye lantern. The opening of the light-organ is so arranged with relation to the genital duct that the eggs as they pass along get smeared by the expressed bacteria, and so the new generation is safely infected. We find the bacteria glowing inside the egg-shell, though how the embryo actually incorporates them we do not yet know.

The presence of three different kinds of bacteria is paralleled by the condition of things in certain insects. It is known that many bacteria are mutually interdependent, and will not flourish when isolated from their fellows; possibly we have here a second degree of symbiosis within the first. In these cases, then, the light would seem to be the product of captured and tamed bacteria; and we speak of a symbiosis, though we are very far from understanding yet the special advantages that accrue to the microbe partner.

Now, while the symbiosis productive of luminescence may give protective advantages or facilitate mating, the other and far commoner examples with which I propose to deal are concerned with nutrition. The primary concern of all living organisms is with food, the getting of it and the dealing with it when it has been secured; and we cannot even begin to understand the majority of symbiotic partnerships until we know something about the feeding habits of the organisms concerned. In the more intimate associations, as of green plant with fungus or bacteria, of animal and green plant, of animal and fungi and bacteria or protozoa, the microscopic partner has been called in to perform some function that the larger partner cannot perform for itself. Let us bear in mind that the green plant, the fungus, the bacterium, and the animal have each very different capacities of dealing with the material that composes what we call their food.

It must be admitted that, seen from our point of view, many of these associations appear very one-sided in their benefit and border closely on true parasitism, between which and symbiosis there is no hard-and-fast line to be drawn. Strictly speaking, we should use symbiosis to describe a condition where equilibrium is established between the partners, but we still use the term when one organism seems to derive more benefit than the other: true parasitism may be said to occur when the benefiting organism gets the upper hand so far that it lives actively upon its host's tissues or diverts so much of the available food that the host dies of starvation. Obviously, it is seldom to the advantage, even of a parasite, to kill the goose that lays such golden eggs; and where such a thing occurs, we may assume that perfect equilibrium has not yet been achieved. In the course of ages many harmful parasites, as we see them to-day, may become innocuous; and as their hosts develop an immunity, they may even become useful symbiotes.

It is well known that the leaf-cutting ants of the genus *Atta* do not feed directly on the leaves they cut up, but use these as manure for their fungus-gardens, and it is on the white mycelial nodules of the fungus that they depend chiefly for food. The greatest care is taken of the fungus-gardens, and we may say that the same sort of symbiotic relationship exists between the ants and their fungi as betweeen the ants and their green-fly 'cattle.' It has for a long time been a puzzle as to how the precious plant is transferred to the new nest when the young queen leaves the old colony; now it is known that the queen carries with her, in a little pocket under her chin, a sample of the necessary mycelium, and in the new nest she deposits this and cares for it as diligently as for the eggs she lays, until such time as the workers hatch out and are ready to take over these menial duties.

Strange to say, this same habit of fungus-culture is also found in one of the families of termites, and it occurs again among certain beetles, such as *Hylecoetus dermestoides*, the larvæ of which live in tunnels that they make in fresh wood. These larvæ, when they hatch out, feed upon the mycelial nodules, rich in protein, which line their tunnels. It has recently been shown by Buchner, that the adult female *Hylecoetus* has on her ventral side two elongated pockets filled with thick-walled fungal spores, and between these pockets lies a gutter also filled with spores. All these structures end just where the oviduct opens to the exterior, and the eggs as they are laid get smeared with the spores squeezed out on them by the muscles of the abdomen. The eggs are deposited on the bark of a tree, and the larva, in eating its way out of the egg-shell, devours with that the spores and so gets infected. The larva burrows into the wood, and the spores, passing through its body uninjured, are deposited in the excrement, germinate, and, even in the poor soil of the powdered wood in the tunnel, produce a flourishing supply of rich fungal food.

The wood-wasps of the genus *Sirex* do something of the same kind. Here the infecting apparatus consists of two syringes filled with the ooidia of a fungus, and between the syringes is a gland, the sticky secretion from which mingles with the fungal material as it is squeezed out when the eggs are laid. The mycelial growth that appears within the larval tunnels is never so rich as with *Hylecoetus*, and here it may be that the grub merely makes use of the fungus as an aid to the digestion of the gnawed wood, about 50 per cent of which is pure cellulose.

Cellulose does not occur in animal tissues, if we except the group of the tunicates, and there are very few animals that produce enzymes capable of splitting it up and putting it in a more assimilable condition. So far as we know, no vertebrate can digest cellulose unaided, and among the invertebrates the only established examples are those of certain snails, the shipworm, the crayfish, the earwig, and a butterfly. Innumerable insects live on vegetable matter containing a high percentage of this indigestible material; although they seem able to make use of it, they secrete no cellulose-splitting enzyme that we can discover. The suggestion is that they call in the aid of fungi and bacteria that have this peculiar power. We assume, then, that the fungus-gardens of the ants and termites and of other insects with wood-eating larvæ, furnish not only direct nutriment but also substances that will split up the cellulose for the animals that ingest these.

From the external fungus-garden in the nest or the burrow, it is only a step to an internal symbiosis. Why not carry one's garden around with one all the time ?

We find, in fact, that the majority of insects living on plant tissues or plant juices have outgrowths from the gut in which swarms of yeasts or of bacteria have their permanent abode. Sometimes, as in *Dacus oleæ*, the olive-fly, the symbiotes live free in the cavity of the reservoir. More often, perhaps, they are contained within the cells of which it is composed. How the micro-organisms are prevented from multiplying to excess we do not know; but that is what we should expect in a true symbiosis—that the host should have developed some power to keep its guests in useful check.

Here, as in *Hylecoetus* and *Sirex*, we find the most elaborate precautions for ensuring that the next generation shall be furnished with the necessary supply of the symbiote of the species. When the female insect is sexually mature, numbers of the bacteria or of the yeasts migrate to the hinder end of its body and take up their position in outgrowths from the gut opening just by the aperture from the oviducts. The yeasts are squeezed out on the shells of the passing eggs, and are presumably swallowed by the larvæ as they emerge; the still smaller bacteria frequently pass through the micropyle of the egg or through tiny pores alongside this, and the emerging larva is already safely infected.

It has also been observed that blood-sucking invertebrates habitually harbour micro-organisms, which may possibly help them to digest blood. Lice, bed-bugs, tsetse flies, culicine mosquitoes and leeches all have in their guts micro-organisms comparable with those we meet with in insects depending on a plant diet rich in cellulose. In some instances here also the transfer of the symbiote to the young of the host has been demonstrated.

It is not only in connexion with luminescence or with their immediate digestive activities that animals have called in the aid of symbiotes. Certain snails of the families Cyclostomatiidæ and Annulariidæ have long been known to have curious branched, concretion-containing 'glands' lying on the dorsal side of the intestine and in close proximity to the kidney. The concretions are spherical in form and are composed mainly of uric acid deposited in an organic matrix arranged in concentric lamellæ. They lie in special cells known as purinocytes, and alongside them within these cells there are almost always quantities of a bacillus. The purinocytes are undoubtedly excretory in function. The work of Meyer and others has shown that they remove from the snail's tissues and store the excess of nitrogenous waste in the form of the concretions. Then, according to Meyer, the bacilli invade the purinocytes and do their work, which seems to be the breaking up of the uric acid.

The tissues of the snail itself do not produce any uriolytic ferment, and the animal seems to depend on bacterial assistance at this point. A number of free-living bacteria are known to have this power of splitting up uric acid, and in the soil, among the decaying leaves on which the snail feeds, are found bacteria indistinguishable from those in its purinocytes. They also occur in the snail's gut, where they have come with the ingested food, and there seems every reason to suppose that they make their way thence to the excretory cells—though why they should show this special affinity for the purinocytes remains a mystery. (The same might be said of the yeasts in the 'mycetomes' of insects.) Presently certain cells in the neighbourhood of the purinocytes become actively amœboid and devour the purinocytes with their contents—the organic basis of the partially dissolved concretions, that is, *and* the bacterial symbiotes whose work is now over. Presumably the phagocytic cells then hand over to the snail's tissues the broken-down products, and presumably these are anabolised by the mollusc, especially during the periods of inertness which we call hibernation.

I say 'presumably.' It will be noticed that in nearly all these recently investigated examples of suspected symbiosis, we must still qualify our assertion. The inference is strong that the micro-organism is a true symbiote—its constant presence in the special situations, its unvarying character, its scrupulous distribution to the offspring, its powers of producing chemical changes of which the host is known to be incapable, but can, in its presence, effect. There is much circumstantial evidence. But we cannot say with certainty that the partnership exists, in however one-sided a degree, until we have proved by experiment that the containing animal suffers irreparably through removal of the guest, and is benefited by its return.

An experiment of this kind has been undertaken and carried through with success in the case of certain wood-eating termites. Some termites habitually cultivate fungus-gardens, and such species live on rotting wood and other vegetable matter plus the assisting fungus. The true wood-eating termites, and these form the majority of families, cut up and eat wood that is quite fresh ; and termites of these families do not cultivate fungus-gardens. The wood on which they depend for subsistence contains at least 50 per cent cellulose, and the experiments of Cleveland have proved that such termites, kept in the laboratory, can live for at least three years—perhaps indefinitely—on a diet of pure cellulose. In these experiments of Cleveland's, the cellulose was given in the form either of pure filter-paper or of specially prepared ligno-cellulose.

The cellulose-fed termites in the laboratory behaved in exactly the same way, and flourished just as well as the controls living on a more normal-seeming wood diet. That is to say, the workers always fed directly on the pabulum, and so did the nymphs of all the other castes. The royal forms likewise fed themselves until the so-called post-adult stages, when they, together with the second and third form adults and the adult soldiers, became dependent on the workers for food-supply, the muscles of their own jaws atrophying, or, in the case of the soldiers, the mandibles becoming so large and unwieldy as to be useless for wood-gnawing. The dependent castes fed either on the semi-digested food passed from the hind-gut of the workers, or on the secretions poured out from their salivary glands. It was the soldiers who seemed to live most constantly on the semi-digested gut-contents of the workers; the younger creatures—the nymphs and the royal and complementary forms in their later life depended on the salivary secretions.

Now cellulose is indigestible even by termites, which secrete no cellulose-splitting enzymes ; and these families have not even got fungus to aid them. But it has been known for a long time that the gut of the true wood-eating termite that does not cultivate fungus, harbours an extraordinary menagerie of protozoa not found anywhere else, if we except some small relatives from the hind-gut of the cockroach. Unless it has been seen, the writhing multitude of inter-sliding protozoan bodies that almost blocks the gut of a healthy termite worker and constitutes about half its total body-weight, is difficult to picture. In spite of their relatively large size and the vast numbers of motile threads covering their bodies, they are ranked by protozoologists among the flagellates, where they form a special and peculiar group, the Hypermastigina or trichonymphids. It seems that each genus of wood-eating termites has its own special association of trichonymphids. Now it is to be noted that the flagellates are found abundantly in all the castes at the stages when they do their own feeding. They disappear from the second and third forms in later life, and become less abundant in the soldiers after these have passed the nymph stage. Larvæ isolated from the time of hatching never have any ; but if they are placed with workers, they have protozoa in their guts within twenty-four hours. The soft protoplasmic bodies of the flagellates are generally crammed with tiny fragments of termite-masticated wood which they have picked up : they have no mouths, but probably take in the particles at the naked posterior end of the body.

It has long been suspected by protozoologists and by entomologists that these strange flagellates are not parasites of the termite, nor even mere commensals, but true symbiotes in the highest degree, conferring incalculable benefits on their hosts, and, richly compensated in return by food and shelter, become incapable of living a separate existence. It has been suspected that these protozoa, like certain fungi and bacteria, have the power of splitting up cellulose, living on the more assimilable products and handing over to their hosts a certain proportion thereof, adequate not only for the particular individuals they inhabit, but also for the dependent castes.

Cleveland's ingenious experiments have recently carried these suppositions into the realm of scientific fact. First he set about removing the protozoa from their termites without injury to the insects. This was difficult. He did it in three different ways—by starvation, by keeping the colonies at a temperature of 36° C., and thirdly, by subjecting them to oxygen under pressure. The first method, starvation, removes nearly all the protozoa in about fifteen days, but it is impossible to defaunate the insects completely before they themselves have begun to suffer in health. Incubation at 36° C. for twenty-four hours kills the protozoa without damaging more than a small percentage of their hosts. But an oxygen pressure of four atmospheres kills the flagellates in about half an hour without damaging their hosts at all, and this method has been found the most convenient for experiment. The various kinds of trichonymphids in one termite gut are variously susceptible to the effects of the poison. By varying the dose and the period over which it acts, Cleveland has found it possible to remove first one species and then another, thus altering the character of the particular intestinal fauna in which direction he will, for when one species dies out another there present multiplies rapidly and takes its place.

The termites defaunated by the oxygen poison are themselves perfectly healthy, but when they are supplied with wood to feed on, though they devour it greedily, they cannot digest it, and they die of starvation in three to four weeks. Supply them, however, with predigested humus or with fungus-digested cellulose, and they can get on all right. But the crucial test is yet to come. Put them back with other termites of their own kind containing protozoa, they rapidly become reinfected, are then once more able to cope even with pure cellulose, and can live on that indefinitely. There seems, then, no question whatever that the protozoa split up the cellulose for them, and that, in the course of ages, they have become absolutely dependent on these secret sharers for their essential food. The flagellates, for their part, cannot live for more than ten days apart from their termites, and then only in a special blood-serum medium to which finely powdered ligno-cellulose is added. They have never been known to form protective cysts, and, so far as is known, they do not occur anywhere else in Nature. The exact method by which they are transferred from termite to termite is not fully understood—though probably they pass in the semi-fluid substance from the anus of the workers.

The association between these partners is undoubtedly of very long standing—it must have taken many ages to evolve the exact adjustment between them and the extraordinary specialisation that we find. But complete and successful the partnership undoubtedly is. Many minor details have yet to be worked out. We do not yet know in what form the broken-up cellulose is handed on to the insect. A great deal of glycogen (animal starch) is always found in the bodies of the trichonymphids, though none occurs in the intestinal cells of the termite. Even when the diet has been pure cellulose for as much as three months, the protozoa still contain glycogen. The suggestion is that they split the cellulose into the sugar glucose, which they then build up into glycogen. How they hand over the excess to their partners we do not know, or whether, as seems possible, their own bodies are sacrificed in the process. Nor do we know yet how the termite gets the nitrogen necessary for the formation of protein when it is fed on pure cellulose. Possibly the bodies of the junior partners afford the immediate supply: but whence have *they* got their nitrogen? Have they the power of fixing free nitrogen, as certain bacteria have? Or do the termites themselves perform this un-animal-like feat? Do not let us forget, however, that along with the flagellates in the termite's gut there are also myriads of other micro-organisms—spirochætes, bacilli, and what not. It may be that these are, in their degree, essential partners in the process.

Obituary.

Sir John Isaac Thornycroft, F.R.S.

SIR JOHN ISAAC THORNYCROFT, whose death on June 28 we much regret to announce, was born on Feb. 1, 1843, at Rome. He was eldest son of Thomas Thornycroft, a sculptor, who had married Mary, the daughter of John Francis, who had taught him his art. Sir William Hamo Thornycroft, the sculptor, was another son of Thomas Thornycroft. Educated first at private schools, Sir John Thornycroft became a student of the University of Glasgow, and there came under the influence of Rankine and Kelvin. After gaining some experience in shops in the north of England, in 1866, the same year that Sir Alfred Yarrow started at Poplar, he began boat building at Chiswick, and soon became known for his success with steam-boat machinery. The little *Miranda*, built in 1871, was only 45½ feet long, but created considerable stir by steaming at 16¼ knots.

It was the adoption of the spar torpedo, and then the automobile torpedo for naval warfare, that opened a new field to Thornycroft, and in 1873 he constructed his first torpedo-boat for the Norwegian government. In 1877 he built H.M.S. *Lightning* for the Royal Navy. He was probably the first to use a locomotive boiler in a boat, and when this type of boiler proved troublesome, he invented a water-tube boiler. He early employed forced draught in his boats, and was a pioneer in the construction of fast-running, lightly constructed steam engines. His first vessel fitted with a water-tube boiler was the mission boat *Peace*, for use on the Congo. In the two torpedo-boats for the British Navy, Nos. 99 and 100, he introduced the flat stern and the double rudders which became a conspicuous feature of his designs. The history of the torpedo-boat destroyer begins with the *Havock* and *Hornet*, ordered by the Admiralty from Yarrow, and the *Daring* and the *Decoy*, ordered from Thornycroft. The *Hornet*, with Yarrow boilers, attained a speed of 27·3 knots, and was the fastest craft afloat. She was soon beaten, however, by Thornycroft's *Daring*, which attained a speed of 27·9 knots. Both these records were surpassed by the Russian *Sokol*, built by Yarrow in 1895, and by the *Forban*, built by Normand the same year, which did 31 knots. Reciprocating engines were used in this type of craft up to 1906, and Thornycroft built and engined many of the so-called thirty-knotters. On the adoption of the Parsons' steam turbine he was given the contract for some of the coastal destroyers, and in 1907 built and engined the ocean-going destroyer H.M.S. *Tartar*, which with oil fuel and triple screws driven by turbine attained a speed of 35·6 knots.

Thornycroft had been joined by the late John Donaldson in 1872, and later on by the late S. W. Barnaby, while for many years Mr. C. H. Wingfield was the chief mechanical engineer of the firm. Motor building had been added to the firm's activities in 1896, and after Donaldson's death in 1899 the concern was turned into a company. In 1906 the work having outgrown the capacity of the premises at Chiswick, a site was secured at Woolston, near Southampton, and it was there that all the later destroyers were built. During the War the firm built and engined twenty-nine torpedo-boat destroyers and flotilla leaders, with a total tennage of 37,210 tons and 957,000 horse-