PSYCHE.

ON THE PRESENT STATE OF OUR KNOWLEDGE CONCERNING CONTAGIOUS INSECT DISEASES.

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It seems to have been from the beginning characteristic of the Cambridge Entomological Club that, without undervaluing taxonomic work, our members have chosen for themselves the field of biological entomology. Not content with the mere orderly arrangement of the facts of insect structure in the form of a comparative anatomy or of a classification, we have been especially interested, as a rule, I think, in the attempt to philosophize such facts; to trace them to their causes and to follow them to their effects. Sympathizing heartily with this tradition of the society, I have selected as the principal topic of my address a subject requiring us to consider the insect as a living organism, in active vital relation to the living organic world,— a subject which frees us in great measure from the technical harness of a classification, and must even lead us quite beyond the borders of entomological science. It is one of those outlying subjects which come within the range of a *frontier patrol*, interested in the foreign relations of insect life, whether those of peaceful commerce or of depredation and defence. Topics of this sort are the food relations of insects and, allied to this, the captivating subject of their relations to flowers. Here also belongs the complex subject or group of subjects included under economic entomology; and here comes, of course, the special topic of this address, — that of contagious insect disease.

Contagious disease, wherever it has been traced to its origin, has proved to be a phenomenon of parasitism; and is included, consequently, under the general head of the interactions of organisms.

Rejecting the many cases of parasitism which have no very serious effect on the insect host, whether because the parasites are in their nature insignificant, or because — as in the case of the termites and many wood-eating species — the organism seems to have adjusted itself to continuous and extraordinary parasitism; and further excluding — since the outlines of our subject must at best be arbitrary — parasitism by other insects, I shall limit myself to cases of true disease of an epidemic and uncommonly destruc-

* For bibliography accompanying this address see the BIBLIOGRAPHICAL RECORD, p. 15.

tive character which have been traced to fungus or protozoan parasites as their causes.

Within these limits, I will undertake to summarize briefly existing knowledge concerning the leading forms of contagious insect disease, with such references to foreign literature as may be necessary, and with a fuller analysis of our scanty American contributions.

Of the protozoan diseases of insects, *pébrine* of the silkworm is the best known example, — an affection which has for the insect world a character so deadly as quite to overshadow any form of animal parasitism known among human kind. It is a plague rapidly and easily conveyed by contamination of the food, and exceedingly liable to hereditary transmission through infection of the forming egg in the ovary, — differing in this latter respect from any other insect affection known to me.

First clearly distinguished about thirty years ago, it has been thoroughly studied in most of its relations, and is now described, as it occurs in the silkworm, in every general work on silk culture, a very intelligent summary of its characters being given, for example, in Maillot's *Leçons sur le ver à soie du mûrier.* The best detailed description which I have seen of its symptoms and histology is that by Quatrefages in his *Études sur les maladies actuelles du ver à soie** (p. 229-306), to be read, however, in connection with Pasteur's critical remarks in his *Études sur les maladies des vers à soie* (v. 1, p. 99-106).

Its most evident symptoms are, externally, the peculiar black specking of the skin, from which it derives its name, and, internally, the appearance of similar black spots on the organs generally; and, in the blood, of the peculiar spores of parasites ("corpuscles" of Cornalia) to be mentioned later. Its characteristic pathological features are (1) the more or less extensive disorganization of the gastric epithelium, within whose cells the parasites begin their development; and (2) the general invasion of nearly all the internal tissues by these parasites and their spores, which also become abundant in the blood. At death the body has a certain elasticity quite in contrast with the flaccid condition of larvae dead with other forms of contagious disease. After death it mummifies without decay, and without that efflorescence of spores especially characteristic of muscardine and allied diseases.

The food of healthy insects may become infected by the discharges of diseased larvae, or even, at a considerable distance, by the dust of their excrement. The "germs" of the disease may also be introduced by means of accidental punctures of the skin, as larvae crawl over each other with claws soiled with their spore-laden excrement.

Concerning the characteristic para-

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sites of this disease, an unusual number of conflicting views have been held by successive writers. Leydig was the first to suggest their affinity with the psorosperms of fishes in 1857, but they were afterwards claimed by botanists and described, once as an alga (*Panhistophyton ovatum*), by Lebert, and again by Naegeli, as one of the Schizomycetes or bacteria (*Nosema bombycis*). Even in so recent and authoritative a work as that by Cornil and Babes, *Les bactéries, et leur rôle dans l'anatomie et l'histologie pathologiques des maladies infectieuses*, published in 1885, this view of Naegeli is taken, and the spores are classed as bacteria. But, since the thorough-going researches of Balbiani on their life-history, continued from 1867 to 1883, I think that there can be no longer a reasonable doubt of their animal nature, or of their agreement in general characters with those forms now commonly included under the head of *sporozoa*,— a parasitic subdivision of the protozoa, of which *Gregarina* is perhaps the best known type.

The fullest and most satisfactory account of their very simple life-history is that given by Balbiani three years ago, in his discussion of the *Microsporidia* in the *Journal de micrographie* (1883, v. 7, p. 313-323, and p. 404-411). It may be thus briefly summarized: —

The minute oval spores, colorless, highly refractile, homogeneous in appearance, 4 μ long by 2 μ wide, when swallowed with the food, penetrate in some way unexplained the cuticle of the alimentary canal, and, in the cells of its epithelium, open at one end and emit their contents, each in a form of an amoeboid speck of protoplasm. This grows to a spherical body and, by a process of internal segmentation common to the *sporozoa*, is soon converted into a mass of spores, each like the original. These spores everywhere undergo a like development, and load all the tissues with their products, slowly and gradually arresting all the functions of life. Their vitality is temporary—Pasteur's experiments showing that they will not germinate five weeks after drying out — and the disease is consequently maintained only by virtue of its hereditary character.

This microsporidion, or an extremely similiar one, produces an epizootic disease also in the oak silk-worm (*Attacus pernyi*), in France, in that species, however, being unable to penetrate beyond the epithelial layer of the intestine, and hence not appearing in the blood or in the tissues at large. Other forms of microsporidia have been found in *Coccus hesperidum;* in *Tipula pratensis;* in *Zygaena filipendula;* in two orthopterous insects (*Decticus griseus* and *Gryllus campestris*); in *Emus olens*, a coleopterous species; in the arachnid *Epeira diadema*; in the entomostraca, *Polyphemus pediculus*, *Simocephalus vetulus* and *Chydorus sphaericus*; in the genital tubes of a nematoid worm: and even, according to Vlacovich, in a colubrine snake (*Coluber carbonarius*).

That epizootic attacks are not more

frequently caused by them, is doubtless due to the sparse distribution and the isolated occurrence of many of these species.

Balbiani gives us in his latest work on this subject the interesting and important information that he has often succeeded in conveying *pébrine* to other insects by treating their food with the dejections of affected silkworms. *Bombyx neustria* he found more susceptible than the silkworm itself, but another bombycid, *Liparis chrysorrhoea*, proved wholly refractory, seemingly because the cuticular lining of the intestine is there unusually thick. Dipterous maggots, larvae of ants, and the meal worm (*Tenebrio molitor*) were also used by him in similar experiments, but quite without result.

I have myself, this year, attempted to convey *pébrine* of the silkworm to various other species, obtaining my material for infection from pupae a few days dead, reared by myself from worms conspicuously diseased. Larvae of *Telea polyphemus*, the fall web worm (*Hyphantria textor*), the common cabbage worm (*Pieris rapae*), the caterpillars of the thistle butterfly (*Pyrameis cardui*), various species of cutworms (*noctuidae*), and both adult and larval *Doryphora*, were infected, sometimes by way of the food, sometimes by puncturing the skin, but in every case without positive success. I obtained, it is true, one curious result; my specimens of *Melolontha*, *Pieris*, and *Telea* all developed unmistakably the characteristic specks and spots of *pébrine* subsequent to infection, but the most critical and protracted search of their fluids and tissues failed to discover the slightest evidence of parasitism,—a fact which I could only explain on the hypothesis that the marks on the skin were due to the direct action of the material ingested or injected from the silkworm, and not to any morbific substance elaborated within the bodies of the insects experimented upon.

You will perhaps allow me to add an item upon the possible economic applications of this disease. There is not the slightest probability that the *sporozoa* can be artificially cultivated outside the bodies of the animals which they may infest; neither have we yet any sufficient proof that forms normally occurring in one species will multiply or permanently maintain themselves in any other. We are consequently limited, practically, to artificial measures for developing and accelerating this disease wherever it may be found, and to more careful and extended experiments for its transfer from the silkworm to related noxious species.

The American literature of *pébrine* is an absolute blank, not a single item of new information concerning it having been published on this side of the water, nor a single observation of its occurrence in this country in any other form than in the common silkworm having been placed on record, as far as I can find.

The notable fungous diseases of in-

sects are readily divisible into two principal groups; schizomycoses, produced by bacteria, and hyphomycoses, due to fungi which form a more or less evident mycelium of cylindrical threads (*Hyphomycetes* and *Pyrenomycetes*). These are roughly distinguishable in two important particulars: (1) The bacteria invade the body from within, by way of the alimentary canal; and the thread fungi penetrate from without through the skin or spiracles; (2) Death from a schizomycosis is followed by rapid decay, which soon reduces the tissues to a putrid fluid; while after death from a hyphomycosis the often flaccid body hardens and mummifies without decay, usually swelling to more than its usual size, and frequently becoming covered with a flour-like efflorescence of spores or spore-like bodies. These last characters distinguish the hyphomycoses from the *pébrines*,—the body mummifying in the latter, but shriveling at the same time and never covering itself with spores, unless with those of a common mould of *post mortem* development. Further, the *pébrine* mummy contains only the minute oval spores of the parasite, while that of a hyphomycosis contains either a mass of mycelial threads or large thick-walled, spherical spores,—the lasting spores of an *Entomophthora* or, possibly, both spores and mycelium together.

Muscardine, longest-known of insect diseases — often a cause of astounding destruction both to domesticated and native species, and by far the most promising natural agent for the artificial restriction of noxious insects—is caused by a number of fungous forms—*Botrytis*, *Isaria*, *Cordyceps*,—several species of each—the classification and ontogenetic relations of which are not yet wholly settled. Some *Botrytis* forms have been unmistakably connected with some Isarias as an earlier developmental stage, and other *Botrytis* forms have been as clearly connected with *Cordyceps*, while all the entomochthonous Isarias are classed by Cooke as *Cordyceps* in a vegetative stage; but, on the other hand, the longest-known *Botrytis*—that of silkworm muscardine —has never been followed, that I can find, beyond an *Isaria* stage, and other species are in doubt. Hence, as one consciously beyond the limits of his proper territory, I will touch these dubious and contested matters in the lightest way, endeavoring only to get at and apply the very important entomological data which the cryptogamic botanists have incidentally worked up for us.

Generalizing the life histories of these fungi and their modes of attack on the living insect structure (which is for most of them the indispensable substratum of their later growth), we may say that they invade their hosts from without—or, sometimes, by the spiracles and tracheae — but never, so far as known, by way of the alimentary canal; that their minute spores germinate on the surface and send inward through the cuticle slender threads which grow through the body wall and then separate into small single cells—cylindrical conidia—that these pass everywhere, growing, dividing and again dividing as they go, deriving their nutri-

ment from the tissues and the blood, rendering the latter distinctly acid, as a rule ;—and that death slowly supervenes.

After this event, these conidia elongate, producing mycelial threads with which the body soon becomes stiffened and distended. Then they shoot upward through the skin a forest of little stems, fertile hyphae, which may branch much or little, according to the form, often covering the dead insect with a microscropic pile like that of velvet. From these hyphae other spore-like bodies—spherical conidia—are variously budded off, borne on the stems and branches singly, in heaps, in necklace strings, forming finally a dense powdery layer of cell-like particles, white or greenish, often excessively delicate and minute—in the silk-worm species not more than 2 μ or 3 μ in diameter. Here the development may stop—as it usually seems to do, indeed, in the best known form,—the *Botrytis bassiana* of the silkworm muscardine—the conidia detached germinating elsewhere, if they fall on favorable conditions, and directly reproducing this lowly vegetative stage. Under other conditions—sometimes on other insects—(the silkworm fungus on *Gastropacha rubi*, for example)—the fertile hyphae, instead of forming an infinitesimal surface pile, spring up in strong club-shaped tufts, bearing conidia on their threads—this being the so-called *Isaria* stage. Finally, the mycelium within the dead body of the insect may thicken, forming one or more compact masses, from which a strong stipe may spring up—like that from the mouth of the white grub (*Lachnosterna fusca*), of which all have seen examples, or at least illustrations—and at the end of this stipe, immersed in a head more or less distinct, another form of spores—ascospores or thecaspores — may be borne by a more complicated apparatus of reproduction. This is the final reproductive stage—the *Cordyceps*—best illustrated by our *Cordyceps melolonthae** of the common white grubs. These ascospores carry the fungus species over winter; but seem not always necessary to this end, as the spherical conidia of the *Botrytis* stage of the silkworm muscardine have been known to retain their vitality more than a year.

All these reproductive bodies—ascospores and conidia — of *Cordyceps*, *Botrytis*, and *Isaria*, have germinated freely again and again in sweetened water, in sterilized beer-mash, in solutions of gelatine and of gum, and may even grow to some extent in pure water. In these artificial cultures the *Botrytis* stage arises, and may form its spherical conidia in vast abundance ; and these have been used with perfect success for the infection of healthy insects in great variety.

Perhaps the most notable of these laboratory experiments have been made by Tulasne, De Bary, and Elias Metschnikoff—names of an authority so high as to leave not the slightest doubt of the correctness of their statements or the soundness of their results. Excluding the experiments of the older authors, made when the existing knowledge of these fungus species was probably insuf-

* SACCARDO, Sylloge fungorum, v. 2, p. 576.

ficient for accurate experiment, we find that these pyrenomycetous fungi have been found in one or more of their stages, spontaneous or as a consequence of experiment, on various hymenoptera, —*vespidae*, *sphegidae*, *formicidae*, *ichneumonidae*,—on larvae of *Papilio*, *Pieris*, *Anthocharis*, *Liparis*, *sphingidae*, *bombycidae* (especially the silkworm and *Gastropacha rubi*), *noctuidae*, and *tineidae* among the lepidoptera,—on dipterous pupae,—on adult or larval *carabidae* (*Calathus*), *staphylinidae*, *coccinellidae*, *melolonthidae* (*Anisoplia* and *Lachnosterna*), and other lamellicorns,—on larvae of *Tenebrio molitor*, *Saperda*, and *Buprestis*, —on *rhynchophora*, including especially *Cleonus* larvae and *Apion*. Various *orthoptera* have been found subject to them,—hemipterous insects,—a *Cicada*, and several *coccidae* (infested by *Sphaerostilbe coccogena*), — and, finally, *Mygale*, *Epeira*, and *Phalangium* among the *arachnida*.

The *Botrytis* and *Isaria* stages are remarkable for the number of insect species which each fungus species may infest,—differing sometimes as widely as larval *tenebrionidae* and *bombycidae*. The fact also that they are not strictly dependent upon living insects as the basis of their growth, but may, at least in the *Botrytis* stage, germinate and form their spherical conidia on moist surfaces elsewhere, makes them especially effective agents of contagion.

Among the most valuable papers on this topic are those by Turpin and by Audouin (Ann. sc. nat.; Zool., 1837, v. 8; and *Comptes rendus*, 1836, p. 170); those by Vittadini (Giorn. Institut. lombard., v. 3, p. 143); by DeBary (*Botanische Zeitschrift*, 1867 and 1869); and by Metschnikoff (*Zoologische anzeiger*, 1880, p. 44).

The American contributions are descriptions of species by Ravenel (Linnæan transactions, 1856, p. 159); descriptions and biological notes by Peck (N. Y state mus. repts. for 1875 and 1879); a description by Peck of a new genus and species of fungus allied to *Cordyceps* (*Appendicularia*) infesting *Drosophila* (Science, v. 4, p. 25); various notes on the prevalence of *Cordyceps melolonthae* Tul., on white grubs—including a mention and figure of this fungus as a new species (*Torrubia elongata* Riley)—in an agricultural weekly; a general article by Riley, on *Cordyceps* (Amer. entom., 1880, v. 3, p. 137); a note by Riley, (Rept. U. S. commiss. agr., 1883, p. 119) reporting the occurrence of spontaneous muscardine on *Plusia rimosella*—the same article containing the description of *Botrytis rileyi* by Dr Farlow; and, finally, an illustrated note on a coccid parasite belonging to *Cordyceps*, by Zabriskie, in the New York journal of microscopy (Vol. 1, 1886, p. 89). Additional minor memoranda will be found in the bibliographical list given with this paper.

The insect diseases which are probably most commonly noticed are those due to the *entomophthoreae*; nine tenths of the adult and larval insects found dead and stiff on fences, weeds, grass, etc., in ordinary collecting, being, according to my observation, victims of

these parasites. They are so well known as represented by the common house-fly fungus, *Empusa muscae*, that I may pass them rapidly by. The insect parasites of this group are variously classified: reduced by Winter to a single genus (1881); distributed by Brefeld (1884) among three genera; and divided by Eidam (1886) into four.

Concerning their methods and apparatus of attack on the insect body, I need only note their similarity to those of the *Botrytis* forms of the preceding group—internal and external conidia, the latter germinating externally or in the tracheae—the penetrating hyphae and subsequent mycelium;—the differences are insignificant to the entomologist. The conidia have, however, this important practical peculiarity; that they very soon lose their power of germination, the species being preserved from year to year by lasting-spores—(large, thick-walled, spherical cells forming within the insect body, dark in some cases, discoloring the blood); or else by the hibernation of diseased individuals, in whose bodies the fungus parasite is preserved until the following year. In grasshoppers, noctuid caterpillars, cicadas, and the like, these lasting spores almost completely fill the body after death, the mycelium which developed them shriveling away. Destructive epidemics due to these fungi have been noticed among grasshoppers—especially *Oedipoda* and *Pezotettix*; among various noctuid larvae—especially *Agrotis segetum* in Europe and some American cut-worms; among the two European cabbage worms (*Pieris rapae* and *P. brassicae*); among various diptera—the common house-fly, blow-flies, *syrphidae*, *Culex*, and even *Chironomus* larvae; and, finally, among *coccidae* and aphides—*Aphis corni* and *Aphis rumicis*—these last occurrences suggesting to the agricultural entomologists of France the use of *Entomophthora* for the destruction of the phylloxera.

These *Entomophthora* forms have proved, thus far, much more difficult of cultivation artificially than the other fungus parasites, the only successful attempt within my knowledge being that made by Brefeld in 1884. In his Entomophthorae (p. 72) he tells us that after many unsuccessful trials he succeeded at last in cultivating them in sterilized veal soup, the mode of growth and of conidia formation being identical with that in the body of the living fly.

In his *Botanische untersuchungen* for 1881 he describes (p. 98) an infection experiment with the conidia of *Entomophthora radicans* applied to one hundred and twenty cabbage caterpillars, with the consequence that eighty-one speedily died of the fungous disease resulting.

In this country, three species only have been described; one by Peck from the *Cicada* (Rept. Botanist, N. Y. state mus. nat. hist., 31, p. 19), first reported, however, by Leidy, in 1851 (Proc. Acad. nat. sci. Philad., v. 10, p. 235); one by Bessey in *Pezotettix* (Amer. nat., v. 17, p. 1280); and one by Arthur from *Phytonomus punctatus* (N. Y. Agr. exper. station rept. 1885, p. 258). The only experimental work attempted here grew out of the

interesting suggestion of the use of yeast as an insecticide, made by Dr. Hagen in 1879, — a suggestion based on the doctrine of Bail (1861) that *Empusa*, *Mucor*, and *Saccharomyces*, (the fly fungus, the common moulds, and the yeast plant), were merely different forms of the same species and mutually interchangeable. The practical test of this theory, as made by Riley, Prentiss, Smith, Cook, Willet, and others, failed to justify the method (although the results seem not to have been critically studied with the microscope), and its theoretical foundation has completely vanished, — so high an authority as De Bary referring to it in 1884 as an "item in the history of error" (Morph. und biol. der pilze, p. 172).

And finally we come to schizomycosis, the most interesting, probably the most important, far the most intricate and difficult, and consequently the least understood of the forms of insect disease,—perhaps, also, the one which, when fully investigated, will throw most light on problems of human pathology. It has only been possible within a very few years to study the bacterial diseases of insects satisfactorily, since the research has had to wait for the development of methods of bacterial research in general,— a development which did not really reach a stage of advancement sufficient to yield results that could stand the tests of time and repeated experiment until we had the homogeneous immersion objective and the methods of bacterial culture in solid media. A few conclusions have, however, now been made clear,— chiefly, so far as this particular division of our subject is concerned, by Pasteur and his followers in France.

It was in 1867 that *flacherie* or *morts flat* of the silkworm was first discriminated by Pasteur as a distinct contagious bacterial disease, capable of transmission to healthy larvae by infection of their food either with fresh excrement, or with the dust of infected silkworm nurseries of the year before. His personal researches were summed up in his classical work in two volumes (1870) *Études sur les maladies des vers à soie*, and these were followed by numerous other papers — those of Dr. de Ferry de la Bellone in *Actes et mémoires du Congrès séricicole international* for 1875 and *Comptesrendus sténographiques* of the same congress for 1878, being the ablest and most convincing that have come under my observation. No student of this affection, whose work I have seen, has made a critical botanical study of the species of bacteria involved, but these have been referred to only in general terms which serve to indicate that they include both bacilli and micrococci.

Another more recent and unusually successful research is reported by Cheshire and Cheyne in the *Journal of the Royal microscopical society of London* (v. 5, p. 585), on the disease of bee larvae known as foul brood,—demonstrated by them to be due to an intestinal *Bacillus*.

In America more has been done on these schizomycoses than on any other insect diseases,—chiefly, so far as systematic investigation goes, at the Illinois state laboratory of natural history. Here we have carefully studied jaundice of the silkworm and *flacherie* of

Pieris rapae and of *Datana ministra*, repeatedly isolating the bacterial species in pure cultures, fluid and solid, on gelatine films, and in tubes of agar-agar, drawing, photographing, and mounting many slides to illustrate every step of each experiment and finally testing our results, in every case, by applying the supposed disease germs to the food of healthy insects kept in strict comparison with check lots not so treated. By these methods we have clearly discriminated the species of micrococci characteristic of these diseases, as they have occurred with us, and have shown that the spontaneous *flacherie* of some of our common caterpillars may be unquestionably conveyed to other lepidopterous species and even to the white grubs.

All the bacterial diseases of insects thus far carefully studied, take first and principal effect on the epithelial layer of the alimentary canal,—no distinctively blood disease having yet been distinguished, if we except a supposed "*flacherie*" of *Cleonus* larvae reported by Metschnikoff in Russia, but apparently not critically investigated. These alimentary schizomycoses are extremely common affections, attacking native insects in the open air under all ordinary conditions, and are especially liable to appear among larvae in confinement. I have seen wide-spead epidemics of *flacherie* in the caterpillars of *Pieris rapae*, of *Pyrameis cardui*, and of *Nephelodes violans*, and have met it here and there in numbers of other larvae, both lepidopterous and hymenopterous.

For purposes of practical experiment these bacterial diseases have the great disadvantage that they require for the cultivation of their germs, a considerable degree of experimental skill and scientific training. They consequently promise less immediate and satisfactory results than the muscardines.

In conclusion, gentlemen, I think that you will see why, in trying to present this subject to you, I have not followed a common custom by limiting myself to a summary of the results of the most recent researches;—it was because so little is generally known to our entomologists on this topic, that almost nothing entomological has been done. You can hardly have failed to notice that most of what we know, has been acquired by the economists, like Pasteur, or the botanists, like De Bary and Tulasne—either by those generally indifferent to all but the practical end in view, or else by those using the insect organism only as a culture apparatus for the study of the life histories of fungi. But surely the entomological side of the relation is equally interesting and important—with its unsolved questions of physiology and pathology, its bearings on distribution as influenced by meteorological conditions, its promised contributions to a knowledge of the details of the struggle for existence, and of the general system of interactions obtaining among organic beings.

In the strict specialization of modern scientific work, are we not likely to drop many important subjects as between two stools? May we not safely recognize a group of specialties which shall comprise the study of the biological relations of living things, and give to results gathered from this field as cordial and intelligent a reception as to those of the embryologist or the comparative anatomist?