In the Wash, about fifty years ago, were enormous oyster beds; one extending nearly the whole length of the Wash and continuing outside about 50 miles. One bed in particular, which was discovered about forty years ago, being (as the fishermen state) a fathom and a half deep, with nothing but oysters. Now everything is changed; the oysters on these beds are nearly exhausted, there not having been a fall of spat for a great number of years, owing, I believe, to the low temperature of the summers, the temperature of the last twelve years not having exceeded 62° Fahr., generally under 59°, of the waters of the Wash.

The Wash is, or should be, the natural nursery for shrimps, soles, flounders, and other flat fish, but owing to the incessant practice of catching shrimps all the year round with small-meshed trawls, the mesh being barely capable (when strained) of letting a wire through, this fishery is at a very low ebb.

KING'S LYNN, ENGLAND,
April 21, 1882.

DISEASE AMONG THE SALMON OF MANY RIVERS IN ENGLAND AND WALES.*

By S. WALPOLE AND PROF. T. H. HUXLEY.

We desire to draw attention to the remarkable outbreak of a disease among the salmon of many rivers. The disease was noticed originally in the autumn and spring of 1877 in two rivers, the Esk and the Nith, which flow into the Solway Firth. It soon spread to the Eden and other adjoining rivers. In the spring of 1879 it was observed in the Tweed, when it rapidly became very serious, and in 1880, when a commission was appointed to investigate it, it had extended to the Nith, the Annan the Esk, the Eden, the Cree, and the Dee, all flowing into the Solway Firth; to the Doon and the Ayr in Ayrshire; to the Derwent in Cumberland, the Lune in Lancashire, and to the Tweed. Since then the disease has broken out in the Seiont, the Ogwen, and the Conway in North Wales, and in the Tay and North Esk in Scotland.

We have very little doubt that the disease, which first excited attention in 1877, had existed, at any rate in a sporadic form, for many years. It was stated in evidence before the late commission that Dr. Crosbie, formerly surgeon to the Challenger expedition, carefully investigated a case of the disease so long ago as in 1852. His observations will be found in the Commissioners' Report, p. 44. Other witnesses similarly

* Reprinted from a pamphlet entitled: Twenty-first Annual Report | of the | Inspectors of Fisheries (England | and Wales.) | (For the year 1881.) | Presented to both Houses of Parliament by command of Her Majesty. | London: | Printed by George E. Eyre and William Spottiswoode, | Printers to the Queen's Most Excellent Majesty. | For Her Majesty's Stationery Office. | 1882. |

stated to the commissioners that they had observed sporadic cases of the disease for years. We may add that we have recently understood from a lessee of fisheries on the North Esk that he had seen disease, fish, without recognizing them as diseased, for very many years; and we have very little doubt that sporadic cases of the disease occur in almost every river.

The first symptom of this disease is the appearance of small grayish or ashy discolorations of the skin, usually upon those parts of the body which are devoid of scales, such as the top and sides of the head, the delicate valvular membrane on the inside of the jaws, the adipose fin, and the soft skin at the bases of the other fins. Where such discoloured patches occur on the scaly parts of the body the scales are hidden by a film, and it might readily be supposed that they had been detached. But if the discoloured film is gently washed or wiped off, the scales will be found beneath perfectly undisturbed. On the scaleless part of the body, also, the discoloured places often look as if they were the effect of bruises or abrasions, but careful examination of the skin fails to reveal any evidence of external injury.

The exact character of this affection of the skin may best be observed in the recently formed isolated patches, not bigger than a sixpence, in which the disease appears on the soft integument of the head. Such a patch is usually nearly circular, and has a well-defined margin separating it from the healthy skin. The central region of the patch is somewhat raised and more discolored than the rest, and faint ridges may commonly be seen radiating from it, through the marginal zone, to the edge of the patch. A single patch of this character may be observed on a fresh-run fish, which, from its activity, the excellent condition of its flesh, and the perfectly normal aspect of its internal organs, shows itself otherwise to be in full health.

When a patch of diseased skin has once appeared, it rapidly increases in size and runs into any other patches which may have appeared in its neighborhood. The marginal zone, constantly extending into the healthy surrounding skin, retains its previous characters, while the ashy central part changes. It assumes the consistency of wet paper, and can be detached in flakes, like a slough, from the skin which it covers. If the subjacent surface is now examined it will be found that the *epidermis*, or scarf-skin, has disappeared, and that the surface of the vascular and sensitive *derma*, or true skin, beneath, is exposed. As the diseased area extends, the papyraceous coat more and more completely takes the place of the epidermis, until, in extremely bad cases, it may invest the back and sides of a large salmon from snout to tail.

The affection, however, is not confined to the epidermis. As the patch acquires larger and larger dimensions, the derma, or true skin, in its centre becomes subject to a process of ulceration; and thus a deep, bleeding sore is formed, which eats down to the bones of the head and sends off burrowing passages, or sinuses, from its margins.

In severe cases, the skin of the top of the head, of the snout, of the gill covers, and of the lower jaw may be almost completely destroyed, and the affection may extend far into the interior of the mouth. Cases of the blinding of fish by extension of the disease over the eyes are reported. It is also said that the gills are attacked; but, although careful attention has been paid to this point, the gills have been unaffected in every fish that has come under our notice, however severe and extensive the disease might be. In far-advanced cases the edges of the fins become ragged; and, sometimes, the skin which invests the fin rays is so completely destroyed that they stand out separately.

All observers agree that the flesh of a diseased salmon, however extensive the morbid affection may be, presents no difference in texture, or in color, from that of a healthy fish; and those who have made the experiment declare that the flavour of a diseased fish is as good as that of a healthy one. No morbid appearances are discoverable either in the viscera or in the blood. Moreover, when fresh-run fish are diseased, they may exhibit just as large an accumulation of peritoneal fat as healthy fish. Nevertheless, it is certain that the cutaneous affection causes much irritation. The fish exhibit signs of great uneasiness, often dashing about and rubbing themselves against stones and other hard bodies in the water. Eventually they get weaker, become sluggish, and often seek the shallows before they die.

The disease spreads with great rapidity after it has commenced, three or four days being said to be sufficient to enable it to extend over the whole body of a large salmon.

In the early stages of the malady, the peculiar appearance of the parts of the skin affected might readily be, and certainly often has been, ascribed to mechanical injury. It has already been remarked that the scales often appear to have been detached when in reality they are only hidden by the pellicle which covers them; nor, so far as inspection with the naked eye goes, is there anything to suggest that the disease, in its most advanced form, is anything but a sloughing ulceration of the skin. But, when the papyraceous substance which constitutes the apparent slough is subjected to microscopic examination, it proves to be something totally different from mere dead tissue of the fish, such as a true slough would be. In fact, the comparison with wet paper turns out to be more exactly correct than might have been anticipated; for, like wet paper, it is chiefly composed of a felted mass of vegetable filaments, intermixed with which are *débris* of the tissues of the skin of the salmon and all sorts of accidental impurities; especially shells of Diatoms and multitudes of very minute sand grains, derived from the water in which the salmon swim. The filaments vary in thickness from $\frac{1}{600}$ of an inch to $\frac{1}{3000}$ of an inch, the majority lying between $\frac{1}{3000}$ and $\frac{1}{2000}$ of an inch. Each filament is tubular, composed of a thin wall, which contains cellulose, or the essential proximate principle of wood, lined by a thicker or thinner layer of finely granular protoplasm, within which, again, is a watery fluid. The whole filament is colorless and usually transparent,

but sometimes the granules are sufficiently numerous to render it opaque; and then it looks white by reflected light. Sometimes the filaments are simple as far as they can be traced; sometimes, on the other hand, they are much branched; but they never exhibit any transverse partitions, the cavity of each filament being continuous throughout. Wherever the free end of a filament is to be seen it is rounded, closed, and often no larger than the rest; or the filament may taper to its extremity. But the free ends of a greater or less number of the filaments are slightly enlarged, so as to be club-shaped, or they may be pyriform, or even almost spheroidal, and the layer of protoplasm which they contain is very thick. The cavities of some of these enlarged ends are shut off by a transverse partition from the rest of the filament, thus giving rise to a closed case. In others the protoplasm is broken up into a number, greater or less, according to the size of the enlargement, of equal-sized spherical masses, each rather less than $\frac{1}{2000}$ of an inch in diameter, which lie separate, but closely packed in the interior of the case, like shot in a cartridge. (Fig. I, p. 433.) In others the case is seen to be open at the end, and a portion or the whole of the "shot" have passed out. In yet others, again, a full unopened case is seen to lie inside an empty one.

The papyraceous mass is, in fact, what is known as the *mycelium* of a fungus. It answers exactly to the similar, wet-paper like, crust which is formed by the common fungus, *Penicilium glaucum* (usually known as "blue mould"), on the surface of a pot of jam. The filaments are the stems of the fungus, and are technically known as *hyphæ*. The enlarged ends of the hyphæ, which are converted into the "cases," are the *sporangia*, or fruits of the fungus, and they are termed *zoosporangia*, inasmuch as the spheroidal bodies or *spores*, under certain circumstances, are actively locomotive, after the fashion of many animalcules, and are therefore termed *zoospores*. It is a peculiarity of this particular fungus that, when a zoosporangium has emptied itself, the hypha on which it is supported begins to grow afresh, sends a prolongation through the centre of the empty sporangium, and dilates into a new one within or beyond it. Hence the appearance of a full sporangium, surrounded by one, or it may be two or three empty ones, one inside the other. (Fig. II, p. 433.)

This structural feature is peculiar to the genus *Saprolegnia* among fungi, and it enables mycologists to identify the fungus, of which the papyraceous incrustation characteristic of the salmon disease is a product, as a species of that genus.

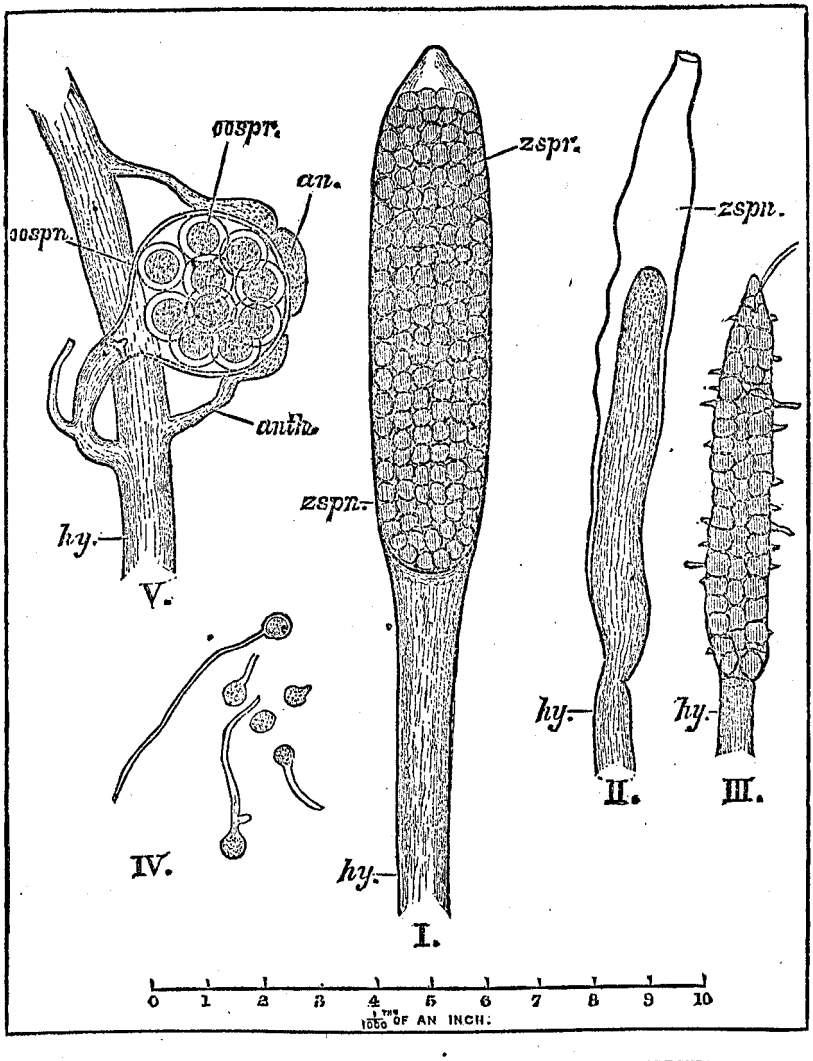
Thanks especially to the labors of Pringsheim,* Cornu,† DeBarry,‡

* "Die Entwickelungs-geschichte der Achlya prolifera." Nova Acta, 1851, and several later papers in the Jahrbücher für Wissenschaftliche Botanik for 1857, 1860, and 1874.

† "Monographie" Annales des Sciences Naturelles, Botanique, 1872.

‡ De Barry and Woronin. "Untersuchungen über die Peronosporeen und Saprolegnien," 1881.

and Brefeld,* a great amount of accurate information respecting the *Saprolegniæ* has been accumulated of late years.



CHARACTERISTIC FORMS OF THE SPORANGIA AND SPORES OF SAPROLEGNIA.

I.—A zoosprangium full of nearly ripe zoospores from the skin of a living diseased salmon.

II.—An empty zoosporangium, through the center of which the hypha is growing in order to produce a new zoosporangium. From the fresh growth of *Saprolegnia* on the diseased jaw membrane of a salmon, cut off and placed in water.

III.—A dictiosporangium from salmon *Saprolegnia* cultivated on a dead fly. The spores have remained in the interior of the zoosporangium, and, after encasing themselves, have there germinated.

IV.—Zoospores of salmon *Saprolegnia*, germinating in water.

V.—An oosporangium of *Saprolegnia* from the pike, cultivated on a dead fly. The oosporangia of the salmon fungus in all respects resemble this.

Signification of the letters: *hy*, hypha; *zspn*, zoosporangium; *zspr*, zoospore; *oospn*, oosporangium; *oospr*, oospore; *anth*, antheridial filament; *an*, antheridium.

* Botanische Untersuchungen. Heft IV, 1881, pp. 109, 110.

They may be defined as a kind of water-moulds, which usually live at the expense of dead and submerged animal and vegetable substances, and are especially common upon dead insects and other invertebrate animals. Their delicate hyphæ form a white cottony fringe to such matters.*

A dead fly which has fallen into water is a favorite nidus for *Saprolegnia*, the hyphæ of which radiate from it in all directions, so that the fly appears to be inclosed in a pale white fluffy ball. Careful examination shows that such a fly represents the soil in which an immense number of the minute *Saprolegniæ* are implanted. One-half of each fungus consists of branching hyphæ, which answer, in a fashion, to the stem and branches of an ordinary plant, and are visible externally; the other half of the fungus corresponds, in the same general way, to the root and rootlets, the hyphæ ramifying in the interior of the fly, and the two parts being connected by a portion which traverses the dense cuticle with which a fly's body is coated.

The stem-hyphæ answer exactly in size and structure to the hyphæ of the salmon fungus. Moreover, a large number of them terminate in zoosporangia of the same character, which evacuate their zoospores, and are reproduced in the same way.

Flies, or parts of flies, such as the legs, on which *Saprolegniæ* are healthily growing, can be isolated and watched for any needful time under the microscope, so that the whole process of the formation of the zoosporangia and zoospores can be followed step by step. It may then be observed that the simple sub-cylindrical free end of a hypha enlarges, that protoplasm accumulates in it, and that its cavity finally becomes shut off by a transverse partition from the rest of the hypha, as a zoosporangium, the summit of which is usually slightly conical. The protoplasm is then seen to break up, simultaneously, into from eight or ten to a hundred and fifty zoospores, according to the size of the zoosporangium. The apex of the latter then opens and the zoosporangia are emitted. Each zoospore, as it leaves the zoosporangium, is usually in active motion, being propelled by the rapid lashing of two vibratile cilia which are attached to one point of its surface. After a few minutes it becomes quiescent and surrounds itself with an extremely delicate transparent coat. But this repose is of a very short duration, as it soon emerges from its envelope, and moves about even more actively than before. It has now an elongated oval shape, and has two cilia which proceed from one side of the oval. This second active state may last for a day, or perhaps two; and it is obvious that, from the activity of the motion of the zoospores, to say nothing of accidental currents, they may thus be carried a long way from the parent stock. Sooner or later, however, they again come to a state of rest, which is final, and they then usually germinate. That is to say, one, or perhaps two, delicate

* Whence the name σαπρός, *sapros*, rotten, and λέγνον, *legnon*, the edging of a garment.

filaments grow out and represent the primitive hyphæ of a new *Saprolegnia*. (Fig. IV, p. 433.)

If the spore has attached itself to some body which is incapable of affording it nourishment, it may not germinate at all, or if it germinates it speedily dies. But if it falls upon an appropriate soil, such, for example, as the body of another dead fly, the spore sends a prolongation inwards which perforates the tough chitinous cuticle of the fly, and gives rise to a system of root-hyphæ in its interior; while, simultaneously, it grows outwards into a similarly ramifying stem-hypha, the branches of which soon enlarge into zoosporangia and give rise to zoospores, as before.

The growth and development of the *Saprolegnia* take place with extraordinary rapidity. In 36 hours from the first infection of the body of a dead fly with the *Saprolegnia* spores, it may be covered with a thick coat of stem-hyphæ a fifth of an inch long; and in the course of the second or third day a thousand of these may have developed and emptied their sporangia, thus setting free some 20,000 zoospores, every one of which is competent to set up the same process in a new fly-corpse. As all this production takes place at the expense of the tissues of the fly, the supply of nutritive material gradually diminishes. At about the fourth day, or perhaps not till later, new forms of sporangia, termed "dictyosporangia," (Fig. III, p. 433,) in which the spores encase themselves and often germinate while still within the sporangium, make their appearance, and the ordinary zoosporangia diminish in number. Not unfrequently, about this time or subsequently, the hyphæ tend to break up into short joints which are themselves capable of germination. Finally, after the fifth or sixth day, a new kind of sporangium usually makes its appearance, which is termed an *Oosporangium*, inasmuch as the spores to which it gives rise are more like eggs or seeds than the products of the zoosporangia or those of the dictyosporangia.

The summit of a hypha, or a short branch of a hypha, dilates into a spheroidal sac, the cellulose wall of which becomes thickened, but presents here and there thin places, looking like clear circular dots or apertures under the microscope. Protoplasm accumulates in the spheroidal case thus formed, and either remains a single rounded mass, or divides into a smaller or greater number of spheroids, each of which, much larger than a single zoospore, is an *Oospore*. The oospore or oospores thus formed eventually become invested by a thick cellulose coat. Before this happens, in some forms of *Saprolegnia*, slender twig-like branches are given off either from the stalk of the oosporangium or from an adjacent hypha, and the terminal portion of one or more of these twigs applies itself to the oosporangium. This terminal portion becomes shut off from the rest of the twig by a transverse septum, and is an *Antheridium*. The antheridium pierces the wall of the oosporangium, divides into as many branchlets as there are oospores, and one branchlet applies itself to each oospore. In all probability something

passes from the antheridium into the oospore, and effects fecundation. (Fig. V, p. 433.)

Thus the oosporangium represents a female reproductive organ, and the oospore takes the place of an egg or an embryo cell. The antheridium represents a male organ, and its contents represent the essential substance of spermatozoids or the fertilizing matter of a pollen tube; and, after fecundation, the oospores answer to impregnated ova or fertilized seeds.

The oosporangium may burst and give exit to the oospores, or it may fall with them to the bottom. And, as a general rule, the oospores remain for a long time, sometimes several months, unchanged. Sooner or later, however, they germinate, and this process may take place in various ways:

1. The contents of the oospore may divide directly into locomotive zoospores, which are set free.

2. The oospore may send out a hypha, the apical part of which becomes converted into a zoosporangium.

3. The oospore may send out a hypha, and this coming into contact with the body of a fly, or some such matter, may develope into a mycelium in the ordinary way.

The whole series of phenomena now described represents the fullest set of changes known to occur in any one form of *Saprolegnia*. But, even in the same form, the series may present notable variations. Thus, the zoospores may germinate without passing into an active condition; or they may germinate immediately after they assume the first quiescent state. Again, in one and the same form, antheridia are sometimes developed and sometimes absent. In some forms, indeed, anteridia never make their appearance, and consequently fertilization does not occur. Nevertheless, the unfertilized oospores germinate and produce new *Saprolegniæ*, apparently just as well as if they were fertilized.

The commonest species of *Saprolegnia* has received the name of *S. ferax*, and both Pringsheim and De Bary agree that several so-called species, namely, *S. monoica*, *S. thureti*, and *S. torulosa* are merely more or less permanent varieties of *S. ferax;* that they are all, in fact, members of the *S. ferax* group.

It has been seen that the fungus which grows on diseased salmon is unquestionably a species of the genus *Saprolegnia;* and it is commonly identified with *S. ferax*. But this identification has rested upon very slender grounds. It is practically almost impossible to determine the species of a *Saprolegnia* until the characters of its oosporangia and of its antheridia (if it have any) have been accurately made out. At present, not only are we without any sufficient account of these organs in the salmon *Saprolegnia*, but it is certain that they are, at most seasons, extremely rare. Mr. Stirling* speaks of having observed only four in

*Mr. Stirling's valuable contributions to our knowledge of the salmon disease are contained in the "Proceedings of the Royal Society of Edinburgh" for 1878 and 1879.

the course of all his investigations; and not a single specimen has presented itself in the considerable number of diseased salmon from the Conway, the Tweed, and the North Esk, which have come under our observation during the last four months.

When our inquiries commenced, there was, strictly speaking, no proof that the salmon *Saprolegnia* could live on anything but a salmon. It was, therefore, quite possible that, since there are many species of *Saprolegnia*, that of the salmon might be peculiar to it, just as, in the analogous case of the potato disease, *Peronospora infestans* is different from all the species of *Peronospora*, which abound upon European wild plants, and will not live on them any more than these other species will live on the potato.

However this may be, it is easily proved that the *Saprolegnia* is not dependent on living salmon. In fact, if a patch of diseased skin is cut off and placed in a vessel of water it will be found in twenty-four hours to be covered with a new growth of young hyphæ, close set, and of nearly equal lengths, so that the surface resembles a miniature cornfield. A piece of the diseased membranous valve of the mouth of a salmon was placed in water on the 4th of March, 1882; on the 6th it was covered with young hyphæ one-fifth of an inch long; and on the 7th these had elongated and developed inultitudes of zoosporangia.

Moreover, there is not the least difficulty in proving that the salmon *Saprolegnia* is not dependent upon salmon at all, but that it is capable of living on dead insects and pieces of wet bladder. If a recently killed fly is gently rubbed two or three times either over a fresh patch of diseased salmon skin, or over one which has developed the fresh growth just mentioned, and then placed in a vessel of water by itself, it will be found in the course of eight-and-forty hours to be more or less extensively beset with short delicate cottony-looking filaments, which rapidly increase in length and in number until, at last, the fly's body is inclosed within a spheroidal coat half an inch in diameter. These filaments are hyphæ having exactly the same size, form, and structure as those of the salmon *Saprolegnia;* their ends give rise to zoosporangia of the same character; and these produce zoospores of the same size, which germinate in the same way.

Between December, 1881, and April of the present year, repeated experiments of this kind have been made with diseased salmon from the Conway, the Tweed, and the North Esk, upon dead flies, and small pieces of wet bladder, always with the same result. There appears, therefore, to be no doubt that the *Saprolegnia* of the salmon, like other

Mr. W. G. Smith, in a paper on the salmon disease in the "Gardener's Chronicle," May 4, 1878, not only affirms that "the resting spores are common enough," but figures them. However, Mr. Smith's figures of the zoosporangia are so unlike anything ordinarily observed in the salmon *Saprolegnia*, and his statement that "the fungus has invariably vanished with the death of the fish," is so strangely contrary to common experience, that it is difficult to know how much weight ought to be attached to his observations.

Saprolegniæ, is capable of living and flourishing on a variety of dead animal matters.

When the *Saprolegnia* is established on one such substance it is easy to transmit it to another. The *Saprolegnia* obtained from diseased salmon was thus cultivated for many weeks (from the end of December, 1881, to the first week in April, 1882) in the hope of obtaining the oosporangia and thus identifying it with one or other of the described forms of the *S. ferax* group. Up to the last-mentioned date, however, no oosporangia appeared on any of these cultures. The course of events was this: for two or three days zoosporangia were very abundant, and thousands of zoospores were set free. But in no case which came under observation for several months were these zoospores provided with cilia, or actively locomotive. They were discharged from the zoosporangia as simple spherical corpuscles, which flowed passively away, and were very often seen germinating by sending out a single delicate hypha. Immense numbers of these spores accumulated among the hyphæ.*

After this condition had lasted for a day or two, the ordinary zoosporangia diminished in number, and "dictyosporangia" made their appearance in place of them. In other words, the spores, instead of being discharged, were retained within the zoosporangium, and began to germinate in that position.

At the same time, the protoplasm accumulated in certain regions of the hyphæ, which often became swollen, and these accumulations were shut off from the rest by transverse partitions. The hyphæ thus assumed a jointed or beaded appearance, as in the *S. torulosa* of De Bary, and the joints might eventually separate from the intervening empty parts of the hyphæ, as a sort of buds or *gemmæ*, which, after detachment, might begin to germinate by throwing out delicate hyphæ at one or many points. Sometimes these buds were terminal and spheroidal and closely simulated oosporangia, but they did not give rise to oospores. No trace of antheridial branchlets was ever visible.

In the third week of April, however, oosporangia and antheridia, in all respects similar to those of the "*monoica*" form of *Saprolegnia ferax*, made their appearance in a copious growth of the fungus on a fly, which was infected on the 24th of March from a culture on bladder, which was

* Among previous observers, Mr. Stirling and Mr. W. G. Smith describe and figure locomotive zoospores as if they were of ordinary occurrence. Mr. Brook, on the other hand ("Notes on the Salmon Disease in the Esk and Eden." Transactions of the Botanical Society of Edinburgh, 1879), appears never to have seen locomotive zoospores; and Mr. George Murray, of the Botanical Department of the British Museum, who has been kind enough to make a series of observations and experiments, continued over six or seven weeks, on crops of *Saprolegnia*, raised upon dead flies infected from Conway salmon, has met with the same negative results. Quite recently, however (March 16), locomotive zoospores have been emitted from one of our specimens of salmon fungus cultivated on bladder. But, as in our specimens, so in those cultivated by Mr. Murray, *no trace of oosporangia had appeared up to that time.*

again derived from a fly, infected directly from a North Esk salmon on the 14th of March.

It may be safely concluded, therefore, that the salmon fungus is not a parasite peculiar to that fish, but that it is a form of the *Saprolegnia ferax*, which, so far as our observations go—and it must be remembered that these extend over only the quarter of the year between Christmas and the spring equinox—remains devoid of oosporangia so long as it infests the fish, and tends to persist in this condition for a long time, even when it is cultivated on those matters upon which the *Saprolegnia* more usually subsists. Further observation must determine whether oosporangia are developed on the *Saprolegnia*, while still growing on salmon, later in the year. The evidence of the fact at present extant is extremely unsatisfactory; and it is a remarkable circumstance that the figures which have been published show no trace of antheridial filaments.

That living fish may be attacked and destroyed by epidemic diseases, of which a *Saprolegnia* is either the cause or the constant accompaniment, has been known for a very long time.

Forty years ago the eminent German botanist, Unger,* described a disease which broke out among some carp in a pond in the Botanic Gardens at Gratz, and was obviously caused by a fungus, at that time known as *Achlya prolifera*, but which the description and figures given by Unger clearly prove to belong to the genus which is now distinguished as *Saprolegnia*, and indeed to be very similar to, if not identical with, *S. ferax*. More or less distinctly circumscribed pale spots appeared upon the skin of the back and of the fins. The fish became sluggish, and sought the surface of the water. A velvety investment, formed of very delicate colourless close-set threads, showed itself on the spots affected, which rapidly became confluent, and extended from mouth to anus, and even on to the gills. The scales of the affected parts became detached, red, and swollen, and sometimes ulceration occurred. The animals could no longer move without appearing to suffer great pain; they remained at the surface of the water, lying either on their backs or on their sides; and death took place in eight-and-forty hours. Unger found that the disease could be transferred to perch by inoculation.

Again, there seems no reason to doubt that the fungus which accompanied the epidemic disease affecting roach, dace, gudgeon, small pike, and perch, at Ightham in Kent, of which a very full and interesting account is given by Mr. Stirling,† is to be referred to *Saprolegnia ferax*. Here, however, ulcerative destruction of the skin does not appear to have occurred, and the mortality is said to have arisen from suffocation, the fungus obstructing the respiratory passages.

Pike kept in aquaria not unfrequently become covered with a fungus.

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*"Sur l'Achlya prolifera." Annales des Sciences Naturelles. Botanique. Serie III. 1844.

†"Additional Observations on Fungus Disease of Salmon and other Fish." Proceedings of the Royal Society of Edinburgh. X., 1879.

The fish do not appear to be inconvenienced, and the fungus is very easily washed off. In a case of this kind which we recently examined, the fungus was a *Saprolegnia*, the mycelium and the zoosporangia of which were altogether indistinguishable from those of the salmon fungus. Moreover, the hyphæ burrowed in the epidermis and distorted the cells with which they came in contact in just the fashion described below (p. 442). As it was not desirable to kill the fish, it was impossible to determine whether the derma was penetrated or not; but the absence of sores, and the ease with which large flakes of epidermis, in which the *Saprolegnia* was rooted, could be detached, lead to the conclusion that the *Saprolegnia* had not penetrated beyond the epidermis. The zoosporangia of the *Saprolegnia* taken from the fish emitted actively locomotive zoospores, but no oosporangia could be detected.

Dead flies, infected with this *Saprolegnia* on the 18th of March, 1882, yielded an abundant growth, quite similar to that obtained in the same way from the salmon *Saprolegnia;* and on the 24th, that is in six days, the characteristic oosporangia and antheridia of *Saprolegnia ferax* (*monoica*) made their appearance.

It appears, therefore, that *Saprolegnia ferax* is capable of attacking a great variety of fishes during life, but that the concomitant pathological phenomena differ in different fishes.

Mr. Stirling's experiments on the transmissibility of the salmon fungus to other fish yielded only negative results. Diseased salmon skin was put into a vessel containing minnows, which nibbled the skin, and were none the worse. Experiments of this rough and ready sort, however, really prove nothing; and a great deal of light will assuredly be thrown upon the whole question of the salmon disease by carefully conducted experimental investigations.

At the present moment, we possess evidence that at least three distinct affections of the skin of fresh-water fishes have been confounded together under the name of "Aquarium fungus." One of these is associated with a *Saprolegnia* identical with that which attacks salmon; another is attended by the very closely allied fungus, *Achlya;* while the third is not accompanied by the growth of any fungus, but is a very curious morbid affection of the skin itself, apparently allied to epithelioma. We have hitherto observed it only in carp, the head, body, and fins of which sometimes appear covered with white patches, which present a most deceptive resemblance to those caused by *Saprolegnia*, the more especially as the edges of the fins may be eroded, and ragged fragments hang from the white patches. These patches, however, contain no fungus, but result from the abnormal growth of the epidermis, sometimes to eight or ten times its ordinary thickness, not unfrequently accompanied by a corresponding elongation of the papillæ of the derma.

Having thus dealt with the question of the nature and affinities of the fungus which is the constant concomitant of the "salmon disease," the

next point of consideration is the relation of the fungus to the affection of the skin. Is the growth of the fungus the cause of that affection, or does the fungus merely find a favorable nidus in the products of the affection?

The *Saprolegniæ*, as we have seen, habitually grow on dead animal and vegetable substances; and it is therefore a fair supposition that some morbid affection may cause the local death of the skin of the fish; and that the fungus simply implants itself in the dead tissue, as if it were the dead body of a fly.

On the other hand, our knowledge of the destructive epidemics caused by *Empusa* in flies, *Botrytis* in silkworms, and *Entomophthora* in other caterpillars, and of the multifarious fungi which produce bunt, smut, and mildew in plants, affords at least equal ground for the supposition that the ulceration and destruction of the skin are caused by the invasion of healthy fish by the *Saprolegnia*. The decision of this question is obviously of the greatest importance.

Direct experimentation by infection of healthy salmon, in the manner in which dead flies were infected from the diseased salmon, being out of the question, at present, on account of its practical difficulties, the only profitable way of investigation lay in the study of the minute structure of the healthy and of the diseased skin, so as to ascertain the exact relation of the fungus to the morbid appearances.

The skin of the salmon, like that of vertebrated animals in general, consists of a superficial, cellular, non-vascular, scarf skin, or *epidermis*, covering a deep fibrous and vascular true skin, or *derma*. The former is divisible into a superficial, a middle, and a deep layer of cells, the last being in immediate contact with the derma. The deep cells are vertically elongated, the middle ones more or less broadly spindle-shaped or rounded, while the thin superficial layer consists of flattened cells. The deep cells are constantly multiplying by fission, and their progeny become middle cells, the outermost of which, for the most part, becoming flattened, give rise to the superficial layer, which is continually shed and replaced. Some of the cells of the middle layer, however, enlarge, take on a more or less spheroidal form, and become filled with a mucous fluid. As they rise to the surface, they open and pour out this fluid, which lubricates the surface of the fish. In any vertical section of a properly prepared portion of salmon skin more or fewer of the openings of these cells are to be seen. The derma is composed of matted bundles of connective-tissue, traversed by blood-vessels and nerves, and containing numerous lymphatic spaces. The superficial layer of the derma contains a number of dark pigment cells, of which there is a close-set zone immediately beneath the epidermis.

In a thin vertical section of the skin of the head of a salmon, which has passed from the sound skin through the centre of a diseased patch, the various structural elements which have been described, disposed with great regularity, are alone visible in the healthy part of the sec-

tion. But, on advancing within the margin of the diseased area, hyphæ of the *Saprolegnia* are seen to penetrate horizontally between the cells of the middle layer, thrusting them asunder with so much force that the cells become bent and distorted, and adhere to a hypha as if they were spitted on it. And, in fact, it is because bundles of such hyphæ are thrusting themselves in this manner, as the roots of an ordinary plant thrust themselves into the soil, between the epidermic cells, that the radiating ridges which appear on the marginal area of the diseased patch are formed. Close up to the free ends of these hyphæ, however, the epidermis is perfectly healthy; and this fact suffices to prove that the growth of the fungus is the cause of the morbid affection of the epidermis, and not its consequence.

Proceeding further towards the centre of the diseased patch, the hyphæ become more numerous and take a vertical as well as a horizontal direction. Of the vertical ones, some traverse the epidermis outwards, thrusting aside and disturbing its cells, and terminating in short free ends on the surface. Others of the vertical hyphæ, on the contrary, are directed inwards; and, as root-hyphæ, not only traverse the deep layer of the epidermis, but pierce the superficial layer of the derma, and penetrate into its substance for a short distance. Yet nearer the centre, the epidermis is completely broken up into fragments and detached cells, which lie in the meshes of the thick mycelium formed by the horizontal and vertical stem-hyphæ of the fungus. The vertical stem-hyphæ attain their full length, often branching, and begin to develope zoosporangia. Towards the derma, the root-hyphæ are so numerous and close-set that they are often separated by interspaces which hardly exceed their own diameter, where they penetrate the superficial layer of the derma. Moreover, they branch out in the latter to a depth of a tenth of an inch, often penetrating the bundles of connective-tissue. Their ultimate ramifications usually end in curiously swollen extremities. Still more towards the centre of an ulcerated patch, the place of the epidermis is taken by the felted mycelium of the *Saprolegnia*, the superficial layer of the derma has disappeared, small vessels have often been laid open, and blood has been effused.

All these appearances become perfectly intelligible, if we suppose that, when *Saprolegnia* spores reach the surface of the body of a live salmon, they behave in the same manner as we know they do when they reach the surface of the body of a dead fly. If it should light upon one of the apertures of the mucous cells, an easy road into the soft interior of the epidermis is open to the hypha of the germinating spore. But, apart from this, the flat superficial cells are certainly as easy to pierce as is the tough cuticle of a fly. No doubt, as in the fly, the hypha grows directly inwards, and piercing the superficial layer of the derma, comes into direct relation with the abundant nutriment it finds there. The fungus then ramifies, on the one side, in the derma, on the other in the epidermis, sending off, in the latter, vertical branches which soon

develope sporangia, and horizontal branches, which are driven, like subsoil ploughs, into the middle layer of cells. The zoosporangia emit multitudes of zoospores, many of which are deposited on the epidermis in the neighborhood of the first; and, penetrating it in the same way, add to the *Saprolegnia* plantation. Thus the disease constantly spreads centrifugally; and, as the oldest and most luxuriant growth of *Saprolegnia* is in the centre, so is the mechanical destruction of the epidermis first effected there. But it is in this region, also, that the greatest number of root-hyphæ penetrate the derma. They cannot fail to interfere with the nutrition of the tissues which they traverse; in fact, their ramifications are often so close-set that the proper tissues of the superficial layer of the derma almost disappear. Sooner or later, therefore, necrosis sets in, and then ulcerative sloughing takes place, resulting in an open sore. No doubt the morbid process thus described is accelerated and intensified by the irritation caused by the innumerable small grains of sand and other foreign bodies entangled by the mycelium. But that the primary cause of all the mischief is the parasitic fungus does not appear to be open to doubt. If it were otherwise, the structural alteration of the skin should precede the fungus and not follow it, as it actually does.

In fact, the *Saprolegnia* is the cause of the salmon disease exactly as the closely allied fungus *Peronospora* is the cause of the potato disease. In symptoms, progress, and results, there is the closest analogy between the two maladies. *Peronospora*, like *Saprolegnia*, gives rise to spores which may be ciliated and actively locomotive, or may germinate without passing through an active stage. When these spores germinate on the surface of a healthy potato plant, their hyphæ perforate the walls of the cells with which they are in contact, and then ramify, as a mycelium, in the inner substance of the plant, carrying destruction wherever they go. The mycelium gives off hyphæ which pass through the stomates to the surface; and there they throw off abundant spores, which repeat the process until the whole plant is destroyed. Even the tubers are invaded; but, in them, the mycelium becomes quiescent on the approach of the winter season, to break out again, in full vigour, if the tubers are planted in the following spring. Moreover, there is as much uncertainty about the occurrence of antheridia and oosporangia, and of any sexual method of reproduction, in the *Peronospora* of the potato, as in the *Saprolegnia* while it infests the salmon.

There is a great deal of reason to believe that the *Saprolegnia* growing on salmon is killed by salt water; and that the injured skin may heal and become covered with a new epidermis when a diseased salmon enters the sea. But the discovery that the root-hyphæ of the *Saprolegnia* ramify in the derma, where the sea water cannot reach them, raises a curious and important question. It becomes possible that a diseased salmon returning to the sea may regain a healthy epidermis and appear perfectly sound; but that, like a potato-tuber invaded by

Peronospora just before the approach of winter, the fungus in the derma may simply lie dormant, and be ready to spring into activity as soon as the fish returns to fresh water. Cases of the appearance of the disease in quite fresh-run fish are occasionally reported, which would be readily explicable should this supposition turn out to be well founded.

Another possibility was suggested by the same fact. We know that the spores of the *Empusa*, a fungus which attacks living flies, germinate and bore through the cuticle in much the same fashion as the *Saprolegnia* enters dead flies. But the hypha of the *Empusa*, which has thus entered the fly, immediately breaks up into short joints, which diffuse themselves through the body of the fly and everywhere multiply by division, until they have appropriated all the nutritious matters which are available to them. It was therefore justifiable, on analogical grounds, to suppose that the hyphæ of *Saprolegnia*, which had entered the derma of a salmon, might break up in a similar way; and that the segments might be conveyed through the lymphatic and blood vessels into all parts of the body, and either produce blood poisoning by a septic fermentative action, or develope centres of obstruction by lodgment in the narrower channels of the vascular system. However, there is no evidence to justify this suspicion. The hyphæ in the derma show no signs of division, nor have any toruloid bodies, or other structures that can be regarded as derivatives of *Saprolegnia*, been observed, either in the blood or in any of the viscera.

The salmon disease, in fact, appears to be a purely cutaneous affection; and the fish seem to die partly from irritation and consequent exhaustion, and partly, perhaps, from the drain on their resources, caused by the production of so large a mass of vegetable matter at their expense.

The opportunities for the investigations, the chief results of which have now been detailed, have arisen only during the last three or four months; and a great deal more time and attention must be devoted to the subject before it can be expected that many of the obscurities and difficulties which still hang about it can be cleared up.

It is neeedful to discover the conditions under which the fungus exists in those rivers which are infested by the disease when the full-grown salmon have deserted them; whether it lingers in isolated cases among the parr, trout, or the non-salmonoid fish; or whether it contents itself with the bodies of dead insects, and other dead animal, and perhaps vegetable substances; or whether, in the late summer, oosporangia may not be formed and give rise to oospores, which, as De Bary's experiments show, may have a dormant period of three or four months; that is to say, sufficient to preserve them till the next return of the salmon.

On all these points, persons conversant with the use of the microscope, who are resident in the neighborhood of salmon streams, might obtain information of great value, hardly to be procured in any other way.

Although all the evidence leads to the conclusion that the *Saprolegnia* is the immediate and primary cause of the salmon disease, and that, in the absence of the fungus, the disease never makes its appearance, however polluted the water may be, or however closely the fish may be crowded, yet in this as in other epidemics caused by parasitic organisms, the prevalence and the mortality of the malady, at any given time and in any given place, must be determined by a multitude of secondary conditions independent of the immediate cause of the disease.

In the case of the potato disease, it is well known that dry weather is extremely unfavourable to the growth and diffusion of the *Peronospora*. In such a season a plant may be affected here or there, but cases of disease are so rare that they escape notice. But if even a few days of rain with a thoroughly damp atmosphere supervene, the fungus spreads from plant to plant with extraordinary rapidity, and field after field is devastated as if struck by a sudden blight. So with the epidemic disorders of mankind. In a large town, isolated cases of smallpox, measles, diphtheria and the like constantly occur, and every case is the source of a vast quantity of infectious material. Nevertheless, it is only under certain conditions that this infectious material takes effect and gives rise to an epidemic.

At a moderate estimate, the *Saprolegniæ* on a single dead fly may carry a thousand zoosporangia. If each sporangium contains twenty zoospores, and runs through the whole course of its development in twelve hours, the result will be the production of 40,000 zoospores in the course of a day, which is a number more than sufficient to furnish one zoospore to the cubic inch of twenty cubic feet of water. Even if we have this rate of production, it is easy to see that the *Saprolegniæ* on a single fly may yield a sufficient abundance of zoospores to render any small and shallow stream, such as salmon often ascend for spawning purposes, dangerous for several days. For a single one of these spores, if it adheres to the surface of the skin of a salmon and germinates, is sufficient to establish the disease. Other things being alike, of course the greater the quantity of *Saprolegnia* in a stream the greater the chances of infection for the fish which enter it.

In looking for the causes of an epidemic of salmon disease we have therefore to inquire, in the first place, into the conditions which favour the growth of the *Saprolegnia*. It is known that the *Saprolegniæ* subsist not only on dead insects and on dead crustacea and mollusks, but on some other dead animal matters and on decaying plants. The particular form which infests the salmon, as we have seen, flourishes as well upon dead flies; it can also be grown upon pieces of bladder, but whether it can be transferred to decaying vegetable substances has yet to be determined.

Hence it follows that, within certain limits (active putrefaction appearing to be unfavourable to *Saprolegnia*), an increase of the quantity

of dead insects and other such organic matters in a river must tend to favour the growth and multiplication of any *Saprolegniæ* which it contains, and hence to increase the liability to infection of the salmon which ascend it.

And that this is no mere hypothetical deduction is very well shown by a remarkable case which was carefully investigated by Goeppert* nearly 30 years ago.

A peculiar water-mould, commonly known as *Leptomitus lacteus*, but which is so closely allied to *Saprolegnia* that Pringsheim places it in that genus, is widely spread in running waters, where it grows on all sorts of dead organic substances.

A factory for making a spirit from turnips was established near Schweidnitz in Silesia, and the refuse was poured into an affluent of the river Westritz, which runs by Schweidnitz. The result was such a prodigious growth of *Leptomitus* that the fungus covered some 10,000 square feet at the bottom of the stream with a thick white layer, compared to sheep's fleeces, choked up the pipes, and rendered the water of the town undrinkable. Scattered hyphæ of this *Leptomitus* may sometimes be found among those of *Saprolegnia*, growing on fresh-water fishes; and the two forms are altogether so similar, that conditions analogous to those which stimulate the growth of the one may safely be assumed to favor that of the other.

Brefeld has pointed out that there is no better medium for the culture of fungi of all sorts than an infusion of dung ("mistdecoct"). Land under high cultivation undoubtedly supplies the waters in its neighborhood with something that nearly answers to an infusion of dung; and this must be taken into account in discussing the possible factors of salmon disease.

Again, it is known with respect to many of the common moulds, such as *Penicillium* and *Mucor*, which are habitally *saprophytes* (that is to say, live on decaying organic matter, as *Saprolegnia* does), that they flourish in certain artificial solutions containing salts of ammonia. It is quite possible, though whether the fact is so will have to be experimentally determined, that *Saprolegnia* is capable of living under the same conditions. Fungi are also extremely sensitive to slight differences in the acidity or alkalinity of water, so that even apparently insignificant changes in this respect may come into play as secondary conditions of salmon disease. Hence, although there is not the slightest ground for regarding "pollutions," whether they arise from agricultural or from manufacturing industries, as primary causes of salmon disease, they may have a most important secondary influence; they may in fact determine whether, in any river, the disease shall be sporadic or epidemic.

But of all the conditions which determine the increase of *Saprolegnia*, and, therefore, multiply the chances of infection of healthy fish, the

* "Botanische Zeitung," XI, p. 163. 1853.

presence of already diseased fish is obviously one of the most important. A large fully diseased salmon may have as much as two square feet of its skin thickly covered with *Saprolegnia*, and its crop of spores may be taken as equivalent to that of several hundred flies. It may be safely assumed that 40 such salmon might furnish one spore to the gallon for all the water of the Thames which flows over Teddington Weir (380,000,000 gallons) in the course of a day.

In 1878, 350 dead salmon were taken out of a very small river, the Esk,* in three days. If the zoospores which these gave off had been evenly diffused through the water of the Esk, the difficulty is to understand how any fish entering it could escape infection.

In fact the objection easily arises that these arguments prove too much; and that, if the *Saprolegnia* is the cause of the disease, and its spores are thus widely diffused in an infected river, not a fish which ascends that river should escape the disease.

But such an objection loses its force if it is remembered that, though the *Saprolegnia* is the cause of the disease, and though a single spore is undoubtedly sufficient to kill a salmon; yet, in order to produce that effect, the spore must, in the first place, reach and adhere to the epidermis of the salmon; in the second place, it must germinate; and, in the third place, the delicate hypha which it sends out must bore its way through the epidermis into the derma.

Each of these conditions of successful infection may be modified in endless ways of which we know nothing—by the state of the epidermis of the fish; by the motility and the general vital energy of the spore; by the composition of the water, and especially by that of its gaseous and acid or alkaline contents.

To take only one of these conditions. If the spores germinate within the zoosporangia, or are not locomotive after they leave it, their chances of diffusion, and hence of reaching a healthy fish, will be vastly less than if they are locomotive, for even a short time. And again, their chances will be far less if they germinate after the first locomotive state, which lasts only a few minutes, than if they enter into the second locomotive state, which may endure for four and twenty hours or more. So, if the salmon *Saprolegnia* produces oosporangia in the late summer, and these lie dormant at the bottom until the following spring, the chances of infection of fresh-run fish will be greater than they will be if the continuance of the existence of the *Saprolegnia*, through the winter, depends upon the accident of a sufficient supply of dead organic substances.

Moreover, any one who has practised the cultivation of *Saprolegnia* is familiar with the difficulties which arise from the swarms of *Infusoria* and *Bacteria* which devour, or otherwise destroy, the fungus, notwithstanding all his efforts to preserve it.

The struggle for existence rages among fungi as elsewhere; and the

* Stirling, "Proceedings Royal Society of Edinburgh," vol. ix, p. 726.

question whether a salmon which enters water in which *Saprolegnia* is present shall be infected or not depends upon the mutual adjustment of a vast variety of conflicting agencies. Until we have learned something more than we at present know of these agencies, and of the history of the salmon *Saprolegnia* itself, there can be no thoroughly safe foundation for any view which may be put forward as to the best mode of dealing with the disease.

Nevertheless, since it is evident that every diseased salmon which remains in a river must immensely increase the chances of infection of the healthy fish in that river, the policy of extirpating every diseased fish appears, theoretically, to be fully justified. But whether, in endeavor to carry such a policy into effect in any given river, the cost would not exceed the loss from the disease, is a point which must be left for the consideration of boards of conservators.

We have the honor to be, sir, your obedient servants,

S. WALPOLE,
T. H. HUXLEY,
Inspectors of Fisheries.

The Right Hon. the SECRETARY OF STATE
FOR THE HOME DEPARTMENT.