

2. Further remarks on the flagellate parasites of *Culex*. Is there a generic type, *Crithidia*?

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(With 1 figure.)

eingeg. 3. Januar 1914.

In a preceding Note in this Journal (Zool. Anz. Vol. 53, No. 8, p. 370). I have described the various forms of a parasite found in hibernating *Culex pipiens*, which I have regarded as "*Crithidia*" *fasciculata* Léger (1). These forms agree on the whole closely with those described by Novy, McNeal and Torrey (2) from the same Insect, which they also refer to Léger's parasite. I pointed out, however, that I was quite unable to see anything that could be safely interpreted as an undulating membrane, either from the movements of the parasites, both short and elongated forms, or from their appearance in fixed and stained preparations. In regard to this point, the account of the American authors is somewhat confusing. In one place they say that in this form the existence of such an organella could not be satisfactorily established. A little further on, however, they state that, in certain of the longer individuals, a distinct wave-motion at the anterior end could be seen in life, giving evidence of the presence of a membrane; and they conclude finally that this parasite ("*C.*" *fasciculata*) has an imperfect (i. e. rudimentary) membrane. Having regard to these last definite statements of Novy, McNeal and Torrey, I considered that probably the reason why none of my forms shewed any membrane was because they occurred in fasting females and were only rejuvenated, as it were, into activity by the addition of the fluid in which they were examined; whereas those investigated by the American authors were always examined at a period when some hours had elapsed after a meal of blood, when the parasites were swarming in the stomach. For there can be no doubt, I think, that both they and I have been dealing with the same form.

On the other hand, Léger, in his original account of *C. fasciculata*, figured a phase with a quite unmistakeable membrane, extending along part of the body and for some distance along the flagellum, as belonging to this parasite. The American workers suggested, as an explanation to account for this discrepancy, that Léger was really dealing with a mixed infection and had included phases belonging to two distinct parasites in his description; this view was also taken by Patton (3). As supporting their suggestion, Novy, McNeal and Torrey shewed clearly (so far as can be judged) that a mixed infection does occur in the "wild" *Culex*, and separated a parasite which they

term *Trypanosoma* (*Herpetomonas*) *culicis* from *Crithidia fasciculata*, both on morphological grounds and by means of cultivation. Adopting this view, it would result that Léger's *fasciculata*, the type-species¹, was a small form, with only a rudimentary membrane, and lacked the elongated phase with wavy membrane shewn by many other crithidial parasites.

On further consideration of the whole subject, however, and especially since, for the purpose of this note, I have been comparing the various phases of the different "Crithidia" which have been described, I prefer another explanation, which is, I think, much more probable. In the first place, I can see no reason for concluding that Léger has indeed described more than one form in his account of "*Crithidia*" *fasciculata*. This parasite is by no means the only form with an undulating membrane, i. e. a *Crithidia*, which possesses a short, oval or pear-shaped, so-called "gregariniiform" phase, serving for attachment (I propose to call this the haptomonad phase). Thus both the "*Crithidia*" *minuta* and "*C.*" *subulata* (which latter is not a *Herpetomonas*) subsequently described by Léger shew very similar stages in their life-history, certain individuals having just the same truncated appearance shewn by many of the small forms of *fasciculata*; and so has equally the "*C.*" sp. described by Patton (4) from *Tabanus* sp. In view of this I fail to understand why Patton should have thought it necessary to suppose that Léger's small forms of "*C.*" *fasciculata* should belong to a *Herpetomonad* (rather a *Leptomonad*, see below) and not to the *Crithidia*; particularly when, as he has himself specially pointed out, it cannot be determined from the short, haptomonad phase alone whether a parasite is a *Crithidia* or a *Leptomonad*, since in both this phase is essentially of the same type, with the two nuclei usually close together and the rhizoplastic part of the flagellum drawn back. Contrary to the opinion both of the American authors and of Patton, I think it most likely that all the forms described by Léger under the name *fasciculata* do belong to that parasite, because they form a regular and connected series. This being so, it appears also most probable, in the second place, that the parasite from *Culex pipiens* which the American workers and myself have had under observation is not Léger's actual form, "*C.*" *fasciculata*, but is on the contrary preferably regarded, so far as can be judged from the phases at present known, as a *Leptomonad* rather than a *Crithidia*.

Before going further, however, a brief explanation is desirable as to why I use the term *Leptomonad*, and not *Herpetomonad*, in this connection. Hitherto, both

¹ The specific name *fasciculata* would have to be applied, of course, to the parasite first described, i. e. the small "crithidial" form.

these terms have been used, often more or less indiscriminately, to denote a type which, in the elongated, monadine form, has typically the kinetonucleus near the anterior end of the body and well separated from the trophonucleus, and concurrently, the flagellum springing directly from the anterior end of the body, becoming at once free; it follows from this that there is no trace of a membrane, the flagellum being connected with the body only by a short rhizoplastic portion. *Herpetomonas muscae-domesticae*, the type-species of this genus, was considered by Pro wazek and others to possess a double flagellum (i. e. to be biflagellate); the species of *Leptomonas*, on the other hand, have only a single flagellum. Occurring associated with *H. m.-d.*

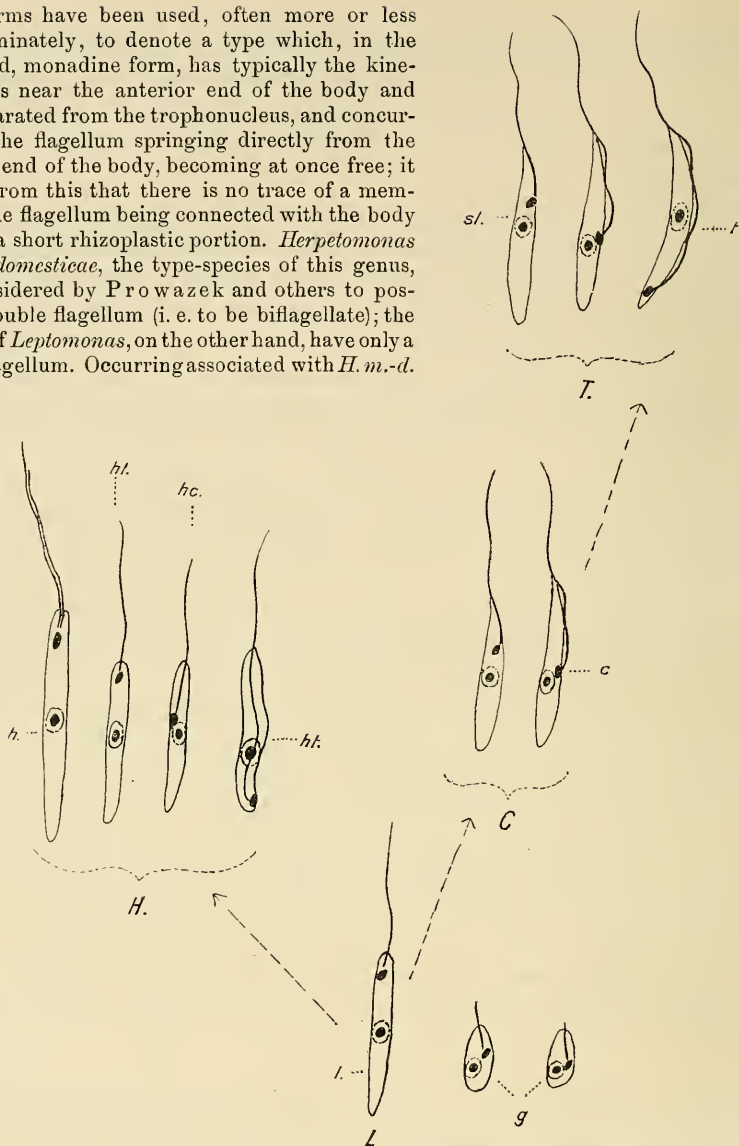


Fig. 1. Scheme illustrating the relationships of the different types discussed in the text. (For the sake of completeness it may be added that the figures of *Leptomonas* would serve also for *Leishmania*.)

L = *Leptomonas*; *H* = *Herpetomonas*; *C* = *Crithidia*; *T* = *Trypanosoma*. *l*, leptomonad form; *g*, haptomonad (so-called gregariniform) phase for attachment, possessed by all four types; *h*, herpetomonad form; and *ht*, leptomonad form of the *Herpetomonas*. (The distinction between these two phases is chiefly one of size and precocious division of the flagellum and is probably not so manifest in many cases.) *he*, crithidial (or "crithidiform") phase of *H*.; *ht*, herpetotrypaniform phase ("trypanoid"); *e*, crithidial form (or "trypanomonad" in the case of *Trypanosoma*); *sl*, semi-leptomonad phase of *Crithidia* or *Trypanosoma*; *t*, trypaniform phase of *T*.

in house-flies, such a *Leptomonas* (a smaller form) has been described by various workers (e. g. Roubaud, Flu, Rosenbusch), which possesses in addition crithidial and trypanosome-like phases. This latter parasite is quite comparable in short to the various Leptomonads with leptotrypaniform phases (trypanoids), which have been described especially by Roubaud, Chatton and their co-workers from African flies (e. g. *Drosophila* sp.). Most of these authors have regarded the two forms as distinct parasites and have retained the generic name *Herpetomonas* for the large form and adopted that of *Leptomonas* for the other type. Dunkerly (5) has recently given a very good account of both forms from British house-flies, and while not able to connect them definitely, has suggested the possibility of their being both different forms of one parasite. Lastly, Wenyon (6) has just published a paper on this subject in which he shews clearly that all the different forms actually belong to the life-cycle of one parasite. He proposes to retain the generic name *Herpetomonas* for this parasite of house-flies, and to use that of *Leptomonas* for those Leptomonads (with a single flagellum, of course) which have not, so far as is known, any crithidial or trypanosome-like phase in their life-cycle. With this view I agree entirely. For, as he points out, although we do not yet know whether the type-species of this latter genus (*L. bütschlii*) possesses these additional phases, it is quite as likely that it lacks them, for several parasites are now known which certainly seem not to have them (e. g. the parasites described as *Herpetomonas jaculum*, *lygaei*, *aspongopi*, to name only a few). All these are best placed provisionally in the genus *Leptomonas*, as *L. jaculum*, and so on. On the other hand, all the forms of Roubaud, Chatton and others, which possess crithidiform phases and trypanoids (or "herpetotrypaniform" phases), come in the genus *Herpetomonas*. Because, in addition to connecting the large *Herpetomonas* of the house-fly with the smaller (*Leptomonas*) form, Wenyon (l. c.) has come to the conclusion that the first-named is not to be regarded as really biflagellate, but as possessing a single flagellum which is frequently found precociously divided. Chatton himself, in one of his more recent papers (7) also expressed the same opinion and considered that *H. muscae-domesticae* and his *L. drosophilae* and other sp. were not so separate as had been formerly thought. Hence, it is best to write *Herpetomonas drosophilae*, *mesnili* and so on.

To return to the discussion of the parasite from *Culex pipiens*, I have referred above to the reasons which particularly influenced me in continuing to regard it as a "*Crithidia*". I think now that I did not attach sufficient weight perhaps, to the occurrence, in the infections which I studied, of certain forms which can hardly be regarded as other than Leptomonads (ante Herpetomonads) (cf., for example, my fig. 31). It is true that these individuals are very scanty in number, most of the elongated forms being, as I pointed out in my previous note, not typical Leptomonads, but differing in having the anterior end of the body more or less tapering, the flagellum being consequently attached to the body for a greater or less distance, this depending also, of course, on the exact position of the kinetonucleus (cf. my figs. 16, 17, 29, 32, 33 and also the American workers' fig. 4 pl. 8 of a rosette). Many of these forms resemble certain which develop in cultures of Avian Trypanosomes (e. g. *T. fringillinarum*), which I have distinguished in my first memoir on Avian Haemoprotozoa (8) as "pseudoherpetomonad" forms (I prefer to term them in future "semi-leptomonad" forms). It is just in such a case, of course, that it is difficult to decide whether to regard a parasite

as crithidial or leptomonad. It is entirely a question of degree; for such a condition is transitional between a typical *Crithidia* and a typical *Leptomonas*, and may be quite as readily connected with the one type as with the other — if anything, indeed, more readily with the former.

On the other hand, so far as I have been able to ascertain from a comparison of the different species described, no "*Crithidia*" shews a true leptomonad phase, that is to say, of course, in the elongated, monadine condition. I think this is a most important point, and one to be borne in mind when we try to distinguish a generic type, *Crithidia*. While one would not go so far as to say that all Crithidiæ entirely lack such a phase, (remembering that the crithidial type is derived from a leptomonad one), still, its absence appear to be a very general feature. As already indicated, I have no reason to suppose that the few Leptomonad individuals which I found represent a form distinct from the other phases; everything points to their belonging to the life-cycle of one and the same parasite. It seems best, therefore, to regard this parasite from *Culex pipiens* for the time being as a *Leptomonas*, its name becoming *L. fasciculata* (= *Crithidia* f. N. McN., and T., nec Léger). This implies, of course, that it does not really possess any undulating membrane². I find that Patton, in the two papers already referred to (3 and 4), has also expressed the same opinion with regard to the form studied by the American workers³.

Before leaving the subject of the flagellate parasites of *Culex*, a few observations may be noted with regard to certain other forms which have been described. As mentioned above, Novy, McNeal and Torrey gave at the same time an account of another parasite from *C. pipiens* and other sp. which they called *Trypanosoma* (*Herpetomonas*) *culicis*, n. sp. As Patton has also pointed out, a typical *Crithidia* as now understood (with well-developed membrane) is concerned here; in this case the authors' description and figures leave no doubt upon the matter. This form is certainly not a *Herpetomonas* (*Leptomonas*) at all. Of course, in the phase described, it is not a true Trypanosome, because the kinetonucleus and the origin of the flagellum are not near the aflagellar end of the body. But for all that, it is quite likely that this

² This certainly renders it less likely that this parasite is connected with a Trypanosome; but does not, of course, affect the question of "*Crithidia*" *fasciculata*.

³ I may add, however, that I had come to the conclusion indicated quite independently, as a result of my own work, and before reading Patton's earlier remarks on this parasite. As will be apparent from what has been written above, one had not sufficient evidence, from a consideration of Novy, McNeal and Torrey's account alone, to regard this form as a Leptomonad rather than a *Crithidia*, any more than one has to say that the small forms of Léger's "*C.*" *fasciculata* do not belong to the same parasite as the larger (monadine) individuals.

parasite is really the Insectan phase of some Trypanosome⁴. Patton considers that this form is identical with Léger's "*C.*" *fasciculata*. I am rather inclined to regard it as a distinct parasite, whether one associates it with a Trypanosome or not; because Novy, McNeal and Torrey did not find in connection with it the characteristic "grain d'orge" phaseshewn by Léger's form and by various other Crithidia. (This is assuming, of course, that the American workers were correct in separating their crithidial parasite from the small forms above discussed.) Hence I prefer to retain the name "*C.*" *culicis* (N., McN. and T.) for this parasite for the present.

Patton has recently given a detailed account (9) of a Leptomonad parasite from *C. fatigans* in India; this is a quite typical *Leptomonas* (or unflagellate *Herpetomonas*, as hitherto understood). I must say that, in this paper, Patton appears to have done his best to thoroughly confuse the subject of "*Crithidia*" and *Leptomonas*, as occurring in mosquitoes. Patton actually refers his parasite to Novy, McNeal and Torrey's form, *Herpetomonas culicis*, although he himself has previously recognized that this latter form is a typical *Crithidia*! Until I had looked through his earlier papers I was quite at a loss to imagine whatever he meant. One can only suppose that Patton has calmly transferred the specific name of the *Crithidia*, viz. *culicis*, to the Leptomonad form of the American workers, in utter disregard of the established rules of nomenclature, according to which the parasite to which the name *culicis* has been given must retain that specific name, even though it be a *Crithidia*, and not a "*Herpetomonas*" as the American authors considered; just as, similarly, the Leptomonad form must still bear the specific name *fasciculata* bestowed upon it by the American writers. But there is no mention of this juggling with specific names in Patton's paper. Readers are left entirely under the impression that he is dealing with the parasite described as *Herpetomonas culicis* by Novy, McNeal and Torrey. In summarizing their observations he uses throughout the terms *H. culicis* and *Crithidia fasciculata* just as the Americans used them, saying, for instance, that they found so many mosquitoes to be infected with *Crithidia*, so many with *Herpetomonas*, and so on; (the latter generic name should certainly read *Crithidia*, and the former preferably *Leptomonas*). In the whole of his detailed account, I can find no mention whatever of the fact that he is not dealing actually with Novy, McNeal and Torrey's *Herpetomonas culicis* at all, which is a *Crithidia*, but with a quite different parasite. One can scarcely imagine

⁴ It must be remembered that all the *Culex* investigated by the American authors were "wild", i. e. caught individuals.

anything more liable to mislead others upon the already sufficiently confused and difficult subject of the nomenclature of these forms.

I consider this parasite from *C. fatigans* is most probably a species distinct from *Leptomonas fasciculata* of *C. pipiens*. In the first place, the two hosts have a quite different distribution, and this is a factor which I have always maintained must be taken into account. Again, the elongated, monadine individuals of Patton's parasite are considerably larger than any of *fasciculata* which I have found, or which are described and figured by the American authors. Moreover, although both parasites appear to be of the same general type, the monadine forms of the parasite from *C. fatigans* are more typically leptomonad than are, for the most part, those of *fasciculata*, as I have discussed above. On these grounds, therefore, the two are best regarded as separate species, and Patton's form should bear the name *L. culicis* n. sp. Patton (nec Novy, McNeal and Torrey).

It remains to add a few remarks upon the question of *Crithidia* as a generic type. We have, on the one hand, crithidiform (as well as herpetotrypaniform) phases occurring very generally in the life-cycle of *Herpetomonas*; on the other hand, crithidial (or, as they are conveniently termed, trypanomonad) forms occur as a developmental phase in the life-cycle of most — perhaps all — Trypanosomes. Is there, therefore, a separate and independent generic type, *Crithidia*, which can be distinguished and characterized? While it is evident from the above facts that there is much to be said in favour of the view that crithidial forms represent only a phase in a life-cycle of one or other of the above types, I think, nevertheless, that there is sufficient evidence to make it at any rate very convenient to continue to recognize a distinct type, *Crithidia*. Leaving aside the many instances of crithidial forms occurring in blood-sucking Insects and the question of the connection of such parasites with some Trypanosome — a question which, I may point out, still remains in statu quo — there are a few forms which, it seems to me, may be regarded as furnishing the nucleus of such a genus. We have, for example, *C. campanulata*, *C. cleti* and *C. gerridis*. All these forms are parasitic in non-bloodsucking hosts. They possess the typical crithidial characters (undulating membrane, proximity of the two nuclei, etc.); and in neither is anything like a leptomonad phase (i. e. of course, in the elongated, monadine forms) described. This last point seems to me to differentiate such a parasite from the crithidiform phase of a *Herpetomonas*. So far as I gather from the accounts of various species of *H.*, when the crithidial forms are found, there is no difficulty in finding not only herpetotrypaniform individuals, but also the ordinary leptomonad forms; and Miss Robertson, for instance, in commenting

upon an infection of certain African bugs with a *Herpetomonas*, says (10) expressly that while the herpetomonad (or leptomonad) forms of the parasite were met with unaccompanied by crithidial forms, the converse was never observed. I think it is quite likely that many Crithidia may shew a semi-leptomonad phase, just as the crithidial forms of a Trypanosome may pass into such, either in cultures, or in the Invertebrate host; but that either the one or the other has a true leptomonad phase, comparable to that of a *Leptomonas*, seems to me to be doubtful; at any rate such a phase remains to be described. Provisionally, therefore, a *Crithidia* may be characterized as a form which possesses the typical crithidial features, enumerated above, which has not developed a trypaniform phase and which in most cases no longer possesses a typical leptomonad phase.

The relationships of the different generic types above discussed to one another are best indicated, it appears to me, not by representing the different forms in one phylogenetic line or series (thus, *Leptomonas* → *Herpetomonas* → *Crithidia* → *Trypanosoma*, or *Leptomonas* → *Crithidia* → *Herpetomonas* → *Trypanosoma*), but rather as comprising two distinct branches from a Leptomonad stock. For one can hardly suppose *Crithidia* to be derived from *Herpetomonas* by the loss of the herpetotrypaniform phase, only to give rise to *Trypanosoma* by the re-development of a similar phase again; and on the other hand, it is not likely that *Herpetomonas* with its well-marked, persistent leptomonad phase, has been developed through *Crithidia*. *Herpetomonas* most probably represents one branch or line of development from *Leptomonas*, *Crithidia* and *Trypanosoma* together, another. The idea may be expressed diagrammatically as in the accompanying text-figure 1.

References.

- 1) C. R. soc. biol. 54. 1902. p. 354. text-figs.
- 2) J. inf. diseases. 4. 1907. p. 223. 7 pls.
- 3) Arch. Protistenk. 12. 1908. p. 131. pl. 9.
- 4) Arch. Protistenk. 15. 1909. p. 333. pl. 30.
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- 6) Arch. Protistenk. 31. 1913. p. 1. 3 pls.
- 7) C. R. soc. biol. 71. 1911. p. 578.
- 8) Q. J. micr. sci. 55. 1910. p. 641. 5 pls.
- 9) Sci. Mem. med. Ind. No. 57. 1912. 21 pp. 1 pl.
- 10) Proc. Roy. Soc. 85. 1912. p. 234. text-figs.

3. Einige kritische Bemerkungen zu neueren Mitteilungen über Trichoplax.

Von Franz Eilhard Schulze.

eingeg. 6. Januar 1914.

Das im Erscheinen begriffene vortreffliche »Handwörterbuch der Naturwissenschaften«, welches zweifellos auf Jahre hinaus über den

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Zeitschrift/Journal: [Zoologischer Anzeiger](#)

Jahr/Year: 1914

Band/Volume: [44](#)

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