

# Some Remarks on Temporary Social Parasitism and the Phylogeny of Slavery among Ants.

By

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## Some Remarks on Temporary Social Parasitism and the Phylogeny of Slavery among Ants.

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In a paper covering nearly one hundred pages and occupying a prominent place in several recent numbers of the „Biologisches Centralblatt“, Father E. Wasmann of the Society of Jesus has embodied his latest views on the origin and development of slavery among ants<sup>1)</sup>. This paper, which contains many valuable observations, is written in such a manner as to produce the impression that its author discovered temporary social parasitism and its significance in the development of slavery, and that my work on the

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1) Ursprung und Entwicklung der Sklaverei bei den Ameisen. Biol. Centralbl. Bd. 25, Nr. 4—9. Feb. 15, May 1, 1905. pp. 117—127; 129—144; 161—169; 193—216; 256—270; 274—292.

same subject is largely an American confirmation of his own. The bulk of the paper is increased by numerous observations on myrmecophiles, observations which are quite irrelevant and serve to befog the whole matter at issue, so that future students may find the historical development of our ideas obscured if not completely falsified. This has led me to offer the following comments on Wasmann's paper.

My own contributions to the subject of temporary social parasitism and the development of slavery among ants are contained in three short papers published in the "Bulletin of the American Museum of Natural History", a periodical of somewhat limited circulation even in America, and perhaps one of the last in which the student would look for ethological work. In the first paper of the series, published Nov. 21, 1903<sup>1)</sup>, I called attention to the fact that the females of some of our North American species of *Formica* belonging to the *rufa* group are aberrant in color and pilosity or in being of diminutive stature. I was unable to explain these aberrations, but decided to study the habits of some one of the species at the earliest opportunity. This presented itself during the summer of 1904 when I found among the Litchfield Hills of Connecticut a number of colonies in all stages of growth of *F. difficilis* var. *consocians*, a new variety of a form in which Emery had previously noted the occurrence of diminutive fulvous queens. I was able to establish the fact that the female of this variety, after her nuptial flight, regularly enters a depauperate and probably queenless colony of *F. schaufussi* var. *incerta* Emery, an ant belonging to the *pallide-fulva* group, for the purpose of starting her own family. A series of mixed colonies of the two species demonstrated to my satisfaction that the *incerta* workers, after adopting and caring for the *consocians* queen and nursing her offspring to maturity, eventually die and leave the *consocians*, now able to provide for themselves, to increase apace till they form a populous and pugnacious colony, which shows no traces of its lowly parasitic origin. The tiny stature of the queen is thus seen to be correlated, in all probability, with deficient or very tardy fertility and an inability on the part of the insect to establish a colony by herself alone like the females of the vast majority of ants. This singular phenomenon I designated as temporary social parasitism in order to distinguish it from the permanent social parasitism of the slave-holding or dulotic species and of such abjectly inquilinous forms as *Anergates atratulus*. In glancing over the known mixed colonies among European and American ants I

1) Extraordinary Females in Three Species of *Formica*, with Remarks on Mutation in the Formicidae. Bull. Am. Mus. Nat. Hist., Vol. 19, Nov. 21, 1903, pp. 645—649, 3 Fig.

arrived at the conclusion that a number of these which have been known for years as „abnormal“ or „accidental“ consociations of two species, were in all probability merely cases of temporary parasitism, and I predicted that the various *Formica* of the *rufa* group on both continents (*F. rufa*, *pratensis*, *truncicola*, *exsecta*, *exsectoides*, *pressilabris*, etc.) would be found to establish their colonies in the same way as *F. consocians*, namely, with the aid of workers of another *Formica*, presumably *F. fusca* or some one of its varieties. These views were first published Oct. 1, 1904, as a brief preliminary note in the Journal of the American Museum of Natural History and some days later in more detailed form in the Bulletin of the same institution<sup>1</sup>).

While writing these papers I could hardly fail to see that young colonies of *F. sanguinea* and *Polyergus rufescens*, our typical slave-making ants, must also conform to the earlier colonial conditions of temporary social parasites like *F. consocians*, but I was much hindered in developing my ideas by a statement in one of Wasmann's earlier works<sup>2</sup>) where he says: „Eine befruchtete Königin von *Formica sanguinea* kann allein, ohne Mitwirkung eigener oder fremder Arbeiterinnen, eine neue Kolonie gründen.“ In support of this assertion he cites observations by Blochmann, long known to me as a conscientious worker. When I looked up the pertinent passage, however, I found that Wasmann had overstated a possibly inaccurate and certainly inadequately recorded observation<sup>3</sup>).

1) A New Type of Social Parasitism among Ants. Bull. Am. Mus. Nat. Hist., Vol. 20, Art. 30. Oct. 11, 1904, pp. 347—375.

2) Die zusammengesetzten Nester und gemischten Kolonien der Ameisen. Münster, Aschendorff'sche Buchdruckerei, 1891, p. 201.

3) Wasmann makes no allusion to this matter in his latest paper. He says, however, that he has been unable, during the more than twenty years he has been studying *F. sanguinea* under what appear to be exceptionally favorable circumstances, to find a female of this species in the act of establishing her formicary, either alone or with the aid of *F. fusca* workers. Like myself he now accepts the latter alternative as the more probable, so I am led to believe that he would endorse my interpretation of Blochmann's observations.

A number of experiments on artificial colonies of *F. sanguinea* subsp. *rubicunda* Emery, performed during the past July, have given me an insight into the method in all probability adopted by this insect while founding its colonies under natural conditions. A detailed account of these experiments will be published in the near future, but the results may be here briefly stated. When a dealated female *rubicunda* is confined in an artificial nest with as many as twenty workers of *F. fusca* var. *subsericea* and their brood, she is received with great hostility. At first her conduct is patient and insinuating, or even somewhat timid, but the persistent pulling and tweaking to which she is subjected by the workers, soon throws her into a frenzy of rage. She falls upon her tormentors, drives them from their brood and, when they persevere in returning, kills them one by one. With feverish haste she then appropriates the brood, secretes it in some corner and carefully guards it, ever on the alert with open mandibles to attack any intruder, till the pupæ are ready to hatch. She deftly frees the pale drab callows from

The inference that the slave-making ants are social parasites which differ from *F. consocians* in keeping up a mixed condition of the colony by kidnapping the young of the host species from time to time, was an easy one to draw from my observations. It was, in fact, at once drawn by several correspondents to whom my paper on *F. consocians* was sent, among others by my friend Prof. Emery of Bologna. As soon as I could satisfy myself of the dubious nature of Blochmann's observation, I decided to publish my views on the phylogenetic development of the slave-making instincts in a separate paper. This was completed during October, 1904, but owing to the printer's making a mistake in the size of the Bulletin pages, which were enlarged for the twenty-first volume, the article<sup>1)</sup> was much delayed, and instead of appearing very early in January, did not leave the press till Feb. 14, 1905.

Beginning with the number of the „Biologisches Centralblatt“ for Feb. 15 and ending May 1, 1905, Wasmann published the article above cited<sup>2)</sup>. It contains views in surprisingly close accord with those published by myself on temporary social parasitism and the phylogeny of the dulotic instincts. The inferences on the latter subject must have been reached by Wasmann independently, because they appear in the very first installment of his paper published Feb. 15, a day after the publication of my paper on the same subject. But as any one familiar with the facts of temporary social parasitism could have drawn these inferences, I am willing Wasmann should have whatever credit he may claim for this independent discovery — if such it can be called — although in this matter, as in that of temporary social parasitism, there can be no question about the priority of publication. It was not „gleich-

their pupal indusia, and immediately adopts them, thus quickly surrounding herself with the means of nourishing both herself and her progeny as soon as the latter are brought forth. The immediate result of these tactics is to produce a small mixed colony consisting of a female of one species of *Formica* and a number of workers of another, exactly as in the *consocians-incerta* colony, but with the interesting and important difference that in this case the *incerta* workers are effete or moribund, or, at any rate, older than the queen, whereas the *subsericea* workers in the case of *rubicunda* are younger than the queen and have before them a lease of life amounting to three or four years. Moreover, the result in the case of *rubicunda* is not achieved passively, by adoption of the queen, as in *consocians*, but actively, by conquest and abduction. Of course, none of these differences is apparent from mere inspection of an incipient mixed colony of *consocians* or *rubicunda*; they can be ascertained only through studying the behavior of the queen during the period that elapses between the nuptial flight and the establishment of her colony.

1) An Interpretation of the Slave-Making Instincts in Ants. Bull. Am. Mus. Nat. Hist., Vol. 21, Art. 1, pp. 1—16, Feb. 14, 1905.

2) Das Ms. dieses Artikels lief am 14. Dez. 1904 in Erlangen ein und wurde am 16. Dez. der Druckerei übergeben. Die Arbeit konnte aber, da ältere Manuskripte vorlagen, erst vom Februar 1905 ab erscheinen. Anmerkung der Redaktion.

zeitig“ as Wasmann states. Wasmann, however, manifestly desires to create the impression that he likewise discovered temporary social parasitism independently. I propose to show that he can have no adequate ground on which to rest such a claim.

A separate of my paper on temporary parasitism was, of course, sent to Wasmann, who courteously acknowledged its receipt in two postals dated Oct. 21 and Oct. 23, 1904. In his article he claims that the manuscript of his „Ursprung und Entwicklung der Sklaverei bei den Ameisen“ was half finished when mine was received (l. c. p. 267): „Die Ausarbeitung des vorliegenden Manuskriptes war schon zur Hälfte vollendet, als ich eine neue Arbeit von Wheeler zugesandt erhielt mit dem Titel „A New Type of Social Parasitism among Ants.“ Ich war nicht wenig erfreut, als ich bei Durchsicht dieser Arbeit fand, dass die daselbst beschriebenen temporär gemischten Kolonien von *Formica consocians* mit *F. incerta* das getreue Ebenbild unserer europäischen *truncicola-fusca*-Kolonien sind, deren Stadium 1—3 ich bereits 1902 als „Adoptionskolonien *truncicola-fusca*“ in der Allgem. Zeitschr. f. Entomologie beschrieben hatte. Nur der Name für jene Form der Symbiose ist verschieden, die Sache dieselbe. Wheeler's Beobachtungsmaterial über *F. consocians* ist jedoch reichhaltiger als das meine über *truncicola*. Auch hat er zuerst ausgesprochen, dass jene temporär gemischten Kolonien eine gesetzmäßige Form der Symbiose darstellen, obgleich sie wesentlich dasselbe sind wie die von mir 1902 beschriebenen „Adoptionskolonien“. Ich war zwar im Laufe der letzten zwei Jahre durch meine obenerwähnten Beobachtungen an der im Zimmer gehaltenen *truncicola-fusca*-Kolonie schon lange zur Überzeugung von der Gesetzmäßigkeit dieser gemischten Kolonien gelangt, wurde aber zur Veröffentlichung der Resultate erst durch die Aufzucht von *fusca*-Sklaven in jener Kolonie (August und September 1904) veranlasst, da hierdurch das Problem des Ursprungs der Sklaverei bei den Ameisen sich lösen ließ.“

If not slightly disingenuous this paragraph is, to say the least, somewhat misleading. In the first place, is it not a little strange that Wasmann in his postals merely acknowledged the receipt and „interesting“ contents of my paper without stating that he had found my predictions in regard to *truncicola* and other European forms of *rufa* to be in full accord with his own observations? True, he was not bound to make this admission, even if his manuscript was at that time half finished, but it would have been evidence of frankness and candor, would have given me great pleasure and would, perhaps, have been conducive to that „ruhige sachgemäße Erörterung derartiger Fragen“ which he rather unctiously recommends in the concluding paragraph of his paper.

In the second place, although he admits that I was the first to give expression to a general law, his words, nevertheless, produce the impression that I have simply renamed or revamped certain facts to which he was the first to call attention. Now it is well known that Forel and not Wasmann was the first to explain certain mixed colonies of *Formica*, etc., as the result of the adoption of a queen of one species by workers of another. Colonies of precisely the same nature as the *truncicola-fusca* colonies mentioned by Wasmann were, in fact, made known by Forel in his magnificent „Fourmis de la Suisse“ long before Wasmann's time. There is, however, a great difference between observing and recording isolated phenomena or even collecting and classifying similar phenomena and discovering the law which pervades them. And in this case the difference was the greater, because Wasmann had regarded the phenomena as exceptions, as „abnormal“ or „accidental“; in other words, he had not left them isolated and unexplained, but had saddled them with a misleading interpretation<sup>1</sup>).

Let us now endeavor to estimate the observations said by Wasmann to have furnished him „long ago“ with the conception of temporary social parasitism. During all the years that European ants have been under observation, only four mixed colonies of *F. truncicola-fusca* seem to have been recorded. One of these, found near Loco, Switzerland, was described by Forel in his „Fourmis de la Suisse“ (1874, p. 372); a second was found in 1903 in Saxony by Zur Strassen (*teste* Wasmann l. c. p. 130) and two have been found by Wasmann in Luxemburg (1900 and 1901). Both of these colonies were in a stage corresponding to the earliest I have described for *F. consocians-incerta*, and in both cases Wasmann mistook the *truncicola* female for a female of *rufibarbis* till the middle of August, 1902. One of these colonies has been kept in an artificial nest since April 8, 1901, and the observations on it are the basis of Wasmann's implication that he independently discovered temporary social parasitism as well as the phylogenetic origin of slavery. Twenty pages are required to relate these observations. They are doubtless very valuable, but they are nearly all on myrmecophiles (*Atemeles*, *Lomechusa*, etc.) and to that extent irrelevant to the question under discussion and merely useful in inflating a few very simple and, in certain respects, inconclusive inferences. The facts concerning this colony may be briefly, and I believe adequately, stated as follows:

1) The words „abnormal“ and „accidental“ are frequently used by Wasmann when his writing would gain in clearness by their avoidance. Thus I am said to believe that slavery in ants had a „rein zufällige Entstehung“ (p. 289), when such a conception never crossed my mind. The presence of *fusca* workers even as a „byproduct“ in a *sanguinea* nest is not due to „pure chance“.

When found the colony comprised a *truncicola* queen and about a hundred *fusca* workers. The queen and fourteen of the *fusca* were confined in an artificial nest. She commenced laying during May, 1901, and by June a few *truncicola* workers had been reared by the *fusca*. Later some pupæ of the latter species were added for the purpose of strengthening the colony. During the year following (1902) a number of *truncicola* workers were reared from eggs laid by the queen and by August the colony contained about fifty *fusca* and as many *truncicola*. In 1903 the queen began to lay as early as March, and, during the early part of the summer the *fusca* bore the brunt of nursing the brood. Fifty to sixty *truncicola* workers were reared. Then the *fusca* workers began to die off till all had perished by August 25, so that necessarily a pure *truncicola* colony remained. During 1904 cocoons of *sanguinea*, *rufibarbis* and *fusca* were placed in the nest, but the *truncicola* workers adopted the *fusca* workers only, so that the colony again became a mixture of *truncicola* and *fusca*. The adoption of *fusca* and the rejection of the other species is very plausibly attributed by Wasmann to habit association: *fusca* being the species with whose aid the *truncicola* colony was started and reared and therefore a familiar species from the outset.

Now I venture to maintain that no impartial reader will for a moment admit that these observations, either alone or taken in connection with the other cases of what Wasmann has for years been in the habit of calling „abnormal“ or „accidental“ mixed colonies, are sufficient to accredit him with the independent discovery of temporary social parasitism as a general and regular phenomenon among certain Formicidæ. There is absolutely nothing in the behavior of this *truncicola-fusca* colony that could not have been predicted of any mixed colony of similar composition, that is, consisting of a fertile female of one and several workers of another species. It is perfectly clear that, under the circumstances, the *fusca* must some time have died off and left a pure *truncicola* colony. Moreover, the observations prove next to nothing in regard to the phylogeny of slavery, since a colony of ants that appropriates pupæ dumped into its nest, is not exhibiting true dulotic instincts even when the young are allowed to develop and thereby give rise to a mixed colony. In the case under discussion it could readily be predicted that the *fusca* pupæ would stand a much greater chance of survival than the pupæ of *sanguinea* and *rufibarbis*.

I am far from denying that the above observations on a single *truncicola-fusca* colony may have suggested to Wasmann the conception of temporary social parasitism, but they assuredly do not establish it as a regular occurrence. In order to do this many more observations on wild colonies were needed and these were



first supplied in my paper on a „New Type of Social Parasitism among Ants“. Wasmann should not, therefore, treat my work on *F. consocians* as a sequel and confirmation, or even as „das getreue Ebenbild“ of his own on *F. truncicola*, but his own work as acquiring through mine whatever significance and validity it may possess. It is not I who have been approaching Wasmann's point of view, as the reader of his paper may be led to believe, but the reverse.

In stating what I believe to be the truth in regard to the discovery of temporary social parasitism, I have no desire to arrogate to myself any great amount of credit and much less do I wish to belittle the splendid work of Forel, Wasmann and other European myrmecologists who had hitherto failed to note this interesting occurrence among the ants that have been so long the objects of their attention. Compared with the ant-fauna of North America, that of Europe is in many respects very meagre, not to say monotonous. Hence it is easy to see how during the nearly forty years of diligent observation on the part of Forel and the more than twenty years devoted by Wasmann to similar studies, temporary social parasitism as a regular occurrence in species of *Formica* of the *rufa* group, should have passed unobserved. I am convinced that had these savants been able to study our much richer American *Formica*-fauna they would long since have detected not only the regularity of the parasitism I described as occurring in such species as *F. consocians*, *F. microgyna*, etc., but also many other interesting facts which have hitherto escaped my observation.

Colebrook, Litchfield County, Connecticut, July 20, 1905. [78]