

THE COMPOUND AND MIXED NESTS  
OF AMERICAN ANTS

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AMERICAN ANTS.

WILLIAM MORTON WHEELER.

PART III. SYMBIOGENESIS AND PSYCHOGENESIS.

“Eine Psychologie in Spencer-Darwin'schem Sinne auf Entwicklungslehre gegründet, aber auf positiver Detailforschung fussend, verspricht reichere Resultate als alle bisherigen Speculationen.” — E. MACH.

ALL writers on the behavior of ants have been deeply impressed with the cases of social symbiosis, more especially with those of an extreme type like *Polyergus* and *Anergates*. The deadly animosity of the members of a formicary, not only towards ants of another species but even towards ants of the same species belonging to different colonies, is so striking and so nearly universal that an extraordinary explanation seems to be demanded to account for the cases of amicable consociation of two species. In the presence of such phenomena, instinct and consentience, or sense-experience, have been abandoned as inadequate, and the existence in ants of some higher form of intelligence, like understanding and ratiocination, has been postulated without further ado. At the same time the evolutionist has been stimulated to broach a phylogeny of social

symbiosis. Both the stress laid on the psychical manifestations of ants and the attempts at establishing a phylogeny of the compound and mixed nests have been clearly apprehended and set forth in considerable detail by Wasmann ('91). While my own observations lead me to agree with this able investigator in many respects, I must, nevertheless, dissent from his attitude towards the genetic method as applied to the study of the compound and mixed nests. It is necessary, therefore, to attempt a critical revision of this matter so far as this is possible within the limits of the present paper. I shall deal first with phylogeny as applied to the cases of social symbiosis and conclude with a very brief consideration of some of the pertinent psychical problems.

Darwin was the first to attempt an explanation of the origin of dulosis in the European ants. In a well-known passage in the "Origin" ('61, p. 244) he says: "By what steps the instinct of *Formica sanguinea* originated I will not pretend to conjecture. But as ants, which are not slave-makers, will, as I have seen, carry off pupæ of other species, if scattered near their nests, it is possible that such pupæ originally stored as food might become developed; and the foreign ants thus unintentionally reared would then follow their proper instincts, and do what work they could. If their presence proved useful to the species which had seized them — if it were more advantageous to this species to capture workers than to procreate them — the habit of collecting pupæ originally for food might by natural selection be strengthened and rendered permanent for the very different purpose of raising slaves. When the instinct was once acquired, if carried out to a much less extent even than in our British *F. sanguinea*, which, as we have seen, is less aided by its slaves than the same species in Switzerland, natural selection might increase and modify the instinct — always supposing each modification to be of use to the species — until an ant was formed as abjectly dependent on its slaves as is the *Formica rufescens*."

Apart from the statement that the English and Swiss *sanguinea* differ in their behavior — a statement which has been since disproved — Darwin's views have been accepted by Forel

('74, p. 440), who has also called attention to the fact that the frequent occurrence of pupæ without cocoons in the nests of *F. fusca* would add to the plausibility of Darwin's hypothesis, for such free pupæ would be able to hatch without the assistance of the enslaving species.<sup>1</sup>

Pursuing Darwin's line of thought, Forel ('74, p. 443) called attention to the following series, which seems to have been previously in great part suggested by von Hagens ('67): "1. Working ants pure and simple; 2. ants dwelling in abnormal mixed colonies; 3. *F. sanguinea* (sometimes without slaves); 4. *Polyergus rufescens* (here the working instinct, which is merely diminished in *F. sanguinea*, disappears completely and the slave-making instinct attains its apogee); 5. *Strongylognathus huberi* (the slave-making instinct is certainly still alive); 6. *S. testaceus* (the slave-making instinct no longer exists except in the form of derisory vestiges, the worker is on the road to atrophy and tends to disappear); 7. *Anergates atratulus* (the worker has disappeared; only parasitism is admissible). This last ant, it seems to me, is a remarkable example of reversion to ancestral traits (incomplete societies, without workers) through parasitism; its genealogy is explicable through *S. testaceus*, the workers of which have become so rare in comparison with the females and males." Essentially the same series of cases was adopted by Lubbock ('94, pp. 88, 89). At the present time it could be still further perfected, as Wasmann suggests, by the insertion of *Tomognathus sublævis* between *F. sanguinea* and *Polyergus*.

The views initiated by Darwin have not been allowed to pass unchallenged. The first to take up the cudgels was McCook in the concluding paragraphs of his paper on *Polyergus lucidus* ('80, pp. 383, 384). After presenting Darwin's views he writes: "Whatever credit we may give to this ingenious hypothesis, it must be said that in the case of our *F. schaufussi*, natural selection has not operated to degenerate the soldierly courage and faculty, and remand the duty of defense to those associates in whom the military faculty

<sup>1</sup> The American slaves of *F. sanguinea* and *Polyergus*, viz., *F. fusca*, vars., *subsericea* and *subnescens*, and *F. nitidiventris* also often have free pupæ.

has been specialized. In other words, if *Lucidus* has become specialized as a warrior, dropping an original disposition and ability to labor, her slave has not become specialized as a worker, nor dropped her combative faculty, but seems to be possessed in all respects of the normal habits and nature of ants of her species. At least I could trace in her no effects of slavery, other than the strange association with and care of her abductor. One, therefore, who accepts Dr. Darwin's suggestion, must allow that natural selection has wrought toward specialization in one section of the colony, but has been suspended in its operations upon the other section. It is doubtful if the anomalous conditions thus raised by Dr. Darwin's explanation be not more difficult to explain than the original conditions to which the hypothesis was applied."

Assuredly, if all the arguments against natural selection were as easily refuted as the one here produced by McCook, Darwin's followers would have occasion for great rejoicing. The refutation is equally easy whether we consider the colonies of the auxiliary species with which *Polyergus* wars, or only the larvæ and pupæ which it abducts from these colonies and rears as its slaves. So far as the latter are concerned, McCook has completely overlooked the very obvious fact that *Polyergus* rears only the workers of the auxiliary species, and these have never been known to reproduce in the mixed nests. But even if we suppose, for reasons to be given below, that these workers may often reproduce normally, the difficulty is not removed, since they would not only have to be able to transmit characters acquired in their imaginal stage, — and the possibility of this has by no means been demonstrated, — but they would have to transmit these characters to male or female offspring if there was to be any permanent modification of the species. Now this is impossible, because *Polyergus* will not permit the winged sexes of the auxiliary species to reach maturity. Hence the detached auxiliaries cannot impart any modifications to the species to which they belong, no matter what peculiarities they may take on in the *Polyergus* nests.

Though the fallacy in McCook's argument is very obvious, Wasmann still contends that it involves "einen vorzüglichen

Gedanken," which he puts in the form of the following question: "If natural selection can bring about such a peculiar development of the instincts in the dominant species, why has it not exercised a corresponding influence over the enslaved species?" Wasmann is evidently bent on rescuing that portion of the argument not expressly stated by McCook, *viz.*, the necessity of a change of character in the ants of the colonies attacked by *Polyergus*. But closer inspection shows this attempt to be unsuccessful, for he has not considered the question of the relative abundance of the dominant and auxiliary species. That this is a matter of some moment in a discussion of this kind is seen from a general survey of parasitic and predaceous organisms. These must of necessity live on that margin of surplus vitality and reproductivity so characteristic of all animals and plants; for it is obvious that organisms which depend very decidedly for their sustenance on special hosts or prey must endanger their own existence to the extent that they endanger the existence of the species on which they depend. The serious injury or death of the host species implies the death of the parasitic species in all cases where the relations between the two are of a highly specialized character. This argument could be adduced if the *Polyergus* were more abundant or quite as abundant as the auxiliary species. But it is quite unnecessary to make use of it, because *Polyergus* is a rare ant of local occurrence, and the various forms of *F. fusca* and *F. pallide-fulva* which it enslaves are widely distributed and vastly more abundant both in colonies and individuals. In fact, no other insects are as common in our Northern States as the varieties of these two ants, and even in Texas, near the southernmost limits of the distribution of *F. fusca*, a form very closely related to *F. subsericea*, *viz.* (*F. gnava* Buckley, is the most prolific of ants. Its nests often contain upwards of thirty fertile queens, and the number of eggs, larvæ, and pupæ which are reared between the end of February and the first of June is enormous. Why, then, should these very prolific and widely distributed species exhibit a special development of valor or a particular defensive form of nest architecture in adaptation to a rare predaceous

ant of sporadic occurrence? As well might we expect the human dermis and its appendages to present hereditary modifications in adaptation to occasional parasites like *Pediculus capitis*. The advantages that would result from the development of a courageous disposition and specially protective forms of nest architecture in *F. fusca* and *pallide-fulva* are more than outweighed by those derived from their unusual powers of reproduction. These species run to offspring, not to valor. That the survival and even the predominance of species does not necessarily depend on the development of moral and psychic endowment is demonstrated on a grand scale in the vegetable kingdom.

This defense of McCook's argument is, however, only a small portion of Wasmann's criticism of the position held by Darwin, Forel, and Lubbock in regard to the phylogeny of the mixed colonies ('91, pp. 214-254). Wasmann sees in these same facts irrefutable arguments against the theory of indeterminate variation and natural selection, and arguments equally strong in favor of tracing the modicum of physical and psychical development which is acceptable to him to "innere gesetzmässig wirkende Entwicklungsursachen." In my opinion, he has succeeded — if indeed he has really succeeded — only in showing that the genetic method has been somewhat awkwardly applied to the cases of compound and mixed nests. On the whole, I believe that he has neither invalidated the principle of natural selection, nor made it perfectly clear that we must forthwith deliver ourselves up to anything so impalpable as "innere gesetzmässig wirkende Entwicklungsursachen." In support of these statements the following remarks on some of Wasmann's arguments are offered.

Wasmann seems to regard it as an established fact that worker ants do not reproduce, or do so only under unusual or even pathological conditions. He is also inclined to emphasize the differences between the instincts of the queens and those of the workers. Hence the workers are debarred from transmitting their peculiar characters, either congenital or acquired, and the instinct modifications, so characteristic of different species of ants, must be explained as arising from determinate,

internally regulated variations. The premises to these conclusions I cannot accept, since they do not appear to me to be indefectibly established. They are based on a rather limited study of a few species of highly specialized European ants, and cannot, therefore, lay claim to great generality. My own observations, still incomplete, to be sure, on several Texan ants representing both the most primitive and the most specialized subfamilies (Ponerinæ and Camponotinæ) convince me that worker ants not only very frequently lay eggs in considerable numbers, but that these produce perfectly normal offspring. When workers are properly fed in the artificial nests, they seem to have no more desire to devour their own eggs than to devour those which are deposited in their keeping by the queens. During February last a carefully isolated lot of workers and soldiers of a handsome *Camponotus* (*C. texanus* n. sp.) laid dozens of eggs in my Fielde nests. By the first week in June many of the larvæ were mature, and a few of these had spun their cocoons before I was compelled to leave my laboratory for the summer. These cocoons were found to contain perfectly normal male pupæ, thus adding fresh evidence for the generally accepted belief that the parthenogenetic offspring of worker ants are males. Similar observations were made on workers of *Camponotus marginatus* n. var. and *Pachycondyla*, except that in these cases I did not follow the larvæ quite to the pupal stage. I am, moreover, convinced that numerous eggs are laid (probably by the soldiers) and reared in the frequently queenless nests of a gall-inhabiting *Colobopsis* (*C. etiolata* n. sp.) from Texas. In fact, for aught we know to the contrary, every well-developed ant colony may contain one or more fertile workers. Where the worker caste is dimorphic the soldiers probably have the greatest tendency to lay eggs. Judging by analogy with other Hymenoptera, like *Polistes* among the wasps, it is also probable that the older and more vigorous the ant colony, the greater the tendency for workers to take on the reproductive powers of the queen. That these conditions clearly imply the possibility of the inheritance of worker characters through the male offspring goes without saying. The comparatively frequent development of



the reproductive power in worker ants makes it possible to account for the conditions presented by *Leptogenys* and *Tomognathus*. In these genera worker forms (ergatoids) have usurped the functions of the winged queens, which have completely disappeared.<sup>1</sup>

The statements of Wasmann and other authors concerning the differences between the instincts of the queens and workers seem to me to require some qualification. This difference is rather quantitative than qualitative, for the recently fertilized queen, even in highly specialized ants, during the establishment of her colony displays nearly all the worker instincts, even to excavating and defending the nest and caring for the first brood of young. In some species (*Ponerinæ*?) she may even exhibit the foraging instinct so characteristic of the workers, for aught we know to the contrary. It is true that in the more highly specialized ants like *Formica*, these instincts lapse into desuetude as soon as the workers make their appearance in the nest, but it is equally true that they may be retained throughout life as in the queens of the *Ponerinæ*, *Leptothorax*, and probably also many other ants. While I do not wish to lay unwonted stress on these fragmentary observations and reflections, they are, nevertheless, quite sufficient to bid us hesitate in the use of arguments which start from the assumption that the worker ants reproduce only under pathological conditions and present instincts essentially different from those of the queens.

Wasmann encounters the gravest difficulties in the genetic explanation of dulosis. His remarks are mainly confined to the two well-known cases, *Formica sanguinea* and *Polyergus*, the former, in the opinion of most writers, an incipiently, the latter a perfectly, dulotic species. He attempts to show that dulosis could not have arisen in *sanguinea* by selection, since flourishing or medium-sized colonies of this species could have derived no advantage from the possession of a small number of slaves, while the advantage that would accrue to a small colony

<sup>1</sup> Silvestri ('01), in a paper received while these paragraphs are going through the press, expresses some very similar views concerning the fecundity of worker Termites.

would be more than outweighed by the difficulty such a colony would experience in obtaining slaves.<sup>1</sup> And even if the dulotic habit had manifested itself repeatedly as a chance variation, and had proved useful, there would still be lacking the hereditary basis for the instinct, since this is exhibited only by the workers. Wasmann states the difficulty in the following words ('91 p. 236): "Before the inclination to rear slaves had proved itself permanently beneficial during many generations, it could not have been established by natural selection as an hereditary Anlage; but the possibility of inheriting the Anlage must exist before the incipient inclination could be transmitted from one colony to another — *ergo* natural selection lacks the very point of departure for the development of an hereditary slave-making instinct from the accidental forms of mixed colonies. We must leave natural selection like Baron von Münchhausen to drag itself out of the morass by its own hair."

Surely natural selection, however numerous its shortcomings, deserves better treatment at our hands. A careful perusal, however, of the above-quoted passage from the "Origin" and a consideration of the facts brought to light since its publication leave little cause for anxiety. Wasmann assumes that *sanguinea* robs the pupæ of other ants *for the sake* of rearing slaves. This is scarcely borne out by the facts. The young of the auxiliary species are sought for and appropriated to serve as food, in obedience to an ancient and widespread formicid instinct that emerges to view very clearly in many often distantly related species of ants. Thus Adlerz has shown ('96a) that on exceptional occasions even *Lasius niger* robs the larvæ and pupæ of *L. flavus*, and these may hatch and function as slaves in the nest of the dark-colored species. Wasmann, too ('99a), has observed a colony of *L. fuliginosus* appropriating the larvæ and pupæ of a neighboring colony of *Myrmica lævinodis*. I have repeatedly observed the same instinct in Mexican and Texan Ecitons ('01; *E. crassicornis*, *schmitti*, *pilosum*).<sup>2</sup> It is also probable that many cases

<sup>1</sup> This latter statement is disproved, at least so far as the American *sanguinea* is concerned, by the above-quoted observation of Forel.

<sup>2</sup> Although these ants often store the larvæ and pupæ in their nests for some time, they are probably never allowed to develop; but even if some of them

of synclerobiosis (especially those of *F. exsectoides* with *subsericea*) are due to a sporadic outcropping of this ancient instinct.<sup>1</sup> In view of the further facts that *sanguinea* can get on perfectly without auxiliaries, that it is the young colonies which usually contain the greatest number of slaves, and that the number of these is often highly variable in different colonies even in the same localities, we are certainly justified in demanding more stringent proof that *sanguinea* really robs for the sake of rearing slaves.<sup>2</sup> Laying most stress on the fact that the booty serves as food, —and of this Forel's observations contain sufficient evidence ('74, p. 258),<sup>3</sup> — we may regard the imaginal auxiliaries in the *sanguinea* nests as a *mere by-product*, as it were, of the colonial activities. The *sanguinea* often appropriate more food than they can devour, and the residuum merely adds workers to the colony, which are not harmful and may even be advantageous. This is evidently the interpretation intended by Darwin, who does not pretend to invoke the principle of natural selection in his genetic explanation of the *sanguinea* stage of dulosis, so that Wasmann has taken unnecessary pains to refute an imaginary argument. With

should hatch, the nomadic habits of the Ecitons and their poorly developed deportation instinct would prevent the formation of permanent mixed colonies, since the larvæ and pupæ which they kidnap belong to home-loving species.

<sup>1</sup> At Colebrook, Conn., I recently found three cases of synclerobiosis in addition to those enumerated in the second part of this paper: (1) a colony of *F. exsectoides* with *F. subsericea*, similar to the mixed colonies of these species observed by Forel and Schmitt; (2) *F. nitidiventris* with *F. rufa* var. *obscuripes* Forel; (3) *F. nitidiventris* with *F. rufa* var. *difficilis* Emery. All of these colonies were small, and in none of them could I find the queens of either of the consociating species.

<sup>2</sup> Wasmann believes ('91, p. 198) that in *sanguinea* the perception of the pupæ and the idea of their abduction are intimately connected by association with the idea of the auxiliaries to be bred from them, and he concludes: "Hieraus dürfte sich die Neigung der *sanguinea* zum Sklavenraub und zur Aufzucht fremder Hilfsameisen am leichtesten begreifen." This is one of the cases in which I am inclined to believe that Wasmann has greatly overestimated the power of association in ants. His statement, however, as he himself would probably admit, can hardly be regarded as proof of the point under discussion.

<sup>3</sup> "The *F. sanguinea* rarely rear all the cocoons of *F. pratensis* which they are given. Of these they often devour a great portion. One *sanguinea* formicary to which I gave a fabulous number of *F. pratensis* cocoons during the course of the summer failed to rear a single one. The same was true of several other formicaries to which I gave fewer cocoons."

*F. sanguinea*, however, there is already given the generalized condition required as a starting point for the action of natural selection and the development under its guidance of cases like *Polyergus*, as Darwin suggests. In *Polyergus* the predatory instincts have been developed to a highly specialized condition, while the domestic instincts have retrograded *pari passu* as a natural result of the survival of the prey, till the presence of slaves in the nest has become a *conditio sine qua non* of existence. This correlation of instincts has involved the corresponding correlation of structure which we find so beautifully exhibited in *Polyergus*.<sup>1</sup> In the predatory instincts every slight variation in advance would be beneficial to the species, while slight retrogressions would not under the circumstances be disadvantageous. I cannot, therefore, agree with Wasmann when he says ('91, p. 247): "Natural selection could only maintain and augment useful instinct variations: but the development of slavery up to the *Polyergus*-, *Strongylognathus*-, and *Anergates*-stage is beneficial neither to the masters nor the slaves — *ergo* natural selection cannot have produced the instincts of the slave-holding ants." As good an answer as I can conceive to an argument of this nature is a reference to the cases of extremely specialized parasitism like the *Cestode* and *Sacculina*, both of which are connected by tolerably complete series of intermediate forms with the more generalized, non-parasitic members of their respective phyla.

The symbiotic sequence suggested by Forel and Lubbock is objected to by Wasmann on fairly good grounds. It is by no means clear that the development has passed successively through the stages represented by these forms. Indeed, as Wasmann shows, the problem of symbiogenesis is much more complicated than it appeared when the above sequence was suggested. It now seems evident that several lines of development have proceeded independently from cases of plesio-biosis (and possibly also parabiosis), which constituted the necessary initial stages of symbiogenesis. Thus it is probable that cleptobiosis, xenobiosis, and dulosis represent at least three

<sup>1</sup> In accounting for this development of instincts and structures, it is, of course, necessary to regard the whole mixed colony as a single evolutionary unit.

discrete lines of development, the two former starting from conditions of plesiobiosis, the latter from the widespread instincts of ants to prey on the offspring of other Formicidæ. Other cases which obviously resemble true dulosis may have arisen from xenobiosis. This appears to be true of cases like *Leptothorax emersoni* and possibly also of the species of *Strongylognathus* and *Tomognathus*. On the other hand, the cases of colacobiosis may be conceived to have originated either from xenobiotic conditions like that of *L. emersoni* or from dulotic conditions like that of *Strongylognathus testaceus*. I cannot believe that Forel or Lubbock really intended their sequence as anything more than a rather general attempt in concrete language to account for the phylogenetic derivation of the remarkable cases of social parasitism (Anergates) from the simpler forms of mixed nests. It is therefore superfluous to waste many words for the sake of showing that the ants of the Forel-Lubbock series are not phylogenetically related. It is not only easier to sketch the phylogeny of the compound and mixed nests in bold outlines than to fill in the details, as Wasmann somewhat reproachfully suggests, but this is the only available method of procedure at the present time. Still even the attempt at detailed speculation in this direction scarcely merits our disapproval as it does Wasmann's, for free and open speculation is necessary to the advancement of a scientific subject, if only as furnishing the necessary incentives and guides to the attainment of profounder insight. Mere fact-culling is not and never can be science.

Another argument on which Wasmann lays some stress is drawn from the supposed immutability of instinct.<sup>1</sup> The instincts of *F. sanguinea* and *Polyergus* are regarded as identical both in Europe and America, and these instincts must therefore have remained unchanged for a very long period of time ('91, p. 249). "Huber's amazons of 1804 fought and

<sup>1</sup> It is unnecessary in this place to deal with the doctrine of the immutability of instinct so brilliantly advocated by Fabre ('79-'00). That it is quite untenable has been demonstrated by Dr. and Mrs. Peckham ('98), Whitman ('99), and others. It could, in fact, be demonstrated to be false from Fabre's own magnificent observations. The genus *Leptothorax*, considered below, furnishes additional evidence, if this were needed.

conquered exactly like Forel's amazons of 1870, and proved themselves to be quite as dependent on their slaves as their modern descendants; and there can be no doubt, that if Adam had studied and described the habits of the amazons, his account would agree very accurately with Huber's and Forel's." Similarly, Wasmann stresses the long-existing fixity of instinct in *Formicoxenus* and *Leptothorax* (p. 226). No issue can be taken with him on this point — but what phylogenist would not take it for granted? If structure can remain stable during æons of geological time, certainly instinct may also remain relatively unchanged. It is, however, equally true — and this point seems not to have been considered by Wasmann — that structure may undergo little change as compared with instinct. In support of this statement I would include in this place a series of facts which may have arrested the attention of the reader in the previous portions of this paper, viz., *the remarkable differences of instinct exhibited by the species of the single genus Leptothorax*. Morphologically, this very large and widely distributed genus has been justly styled "homogeneous" by Forel ('74, p. 339), since the numerous species are closely related to one another and often separable only on rather trivial characters. Even the subgenera *Dichothorax* and *Temnothorax* are based on relatively slight differences. In their habits, on the other hand, the species of *Leptothorax* are singularly diverse. Many of the forms have no tendency to consort with ants of other species, but differ considerably in the stations which they inhabit. Some prefer to live under stones, others in moss, others under bark or in dead wood, and still others, like one of the Texan species, in cynipid galls, or, like our New England *L. longispinosus* Rog., in worm-eaten hickory nuts among the dead leaves under the trees. Many species, however, have a pronounced *penchant* for entering into more or less intimate symbiotic relations with other Formicidæ, as shown in the following conspectus:

1. The European *L. muscorum* often lives in plesiobiosis with *Formica rufa* (see pp. 519, 520).
2. A similar tendency is undoubtedly exhibited by our

American *L. canadensis* Provencher,<sup>1</sup> which I have had occasion to observe since the second part of this paper was written. June 21, I found at Cudahy, near Milwaukee, Wis., two nests of this *Leptothorax* compounded with a large nest of *Cremastogaster lineolata* Say in an old oak stump. The galleries of the *Cremastogaster* extended far into the dry rotten wood and contained numerous worker larvæ and pupæ. The two *Leptothorax* nests, which together scarcely contained more than sixty to seventy ants, were about twenty inches apart. Each was a simple chamber one-half to three-quarters of an inch in diameter excavated in the thick bark, and each communicated by means of a slender passage with the subcortical space, which was used as a common runway by the workers of both species. When the bark was stripped off, several of the *Leptothorax* were seen running on the surface of the wood and mingling with the *Cremastogasters*, which they closely resembled in coloration and sculpture, though differing in size, shape, and movement. The *Leptothorax* were very timid, and when touched with the fingers or tweezers, at once curled up and "feigned death," after the manner of *Myrmecina*. One of the nests contained several mature larvæ and pseudonymphs. These the workers and the single dealated queen were hastily removing to a place of safety. Rain began to fall soon after I had opened this interesting compound nest, and I was obliged to continue my observations on some living specimens of both the species hurriedly confined to a small vial. When the two species met, as they often did in these narrow quarters, the *Cremastogaster* stroked the *Leptothorax* with its antennæ. On such occasions the latter at once crouched motionless and folded its antennæ along the sides of its head. Then sometimes the *Cremastogaster* would stand over the little ant and lick its rugose head and thorax; at other times it would pass on without bestowing these attentions on the *Leptothorax*, which at once sprang to its feet and ran away. This performance was repeated so often during the remainder of the day that there could be no doubt

<sup>1</sup> According to Emery ('94, p. 318) this ant is perhaps only a subspecies of the European *L. acervorum*.

concerning the friendly relations of the two species. By the following morning the *Leptothorax* and most of the *Cremastogasters* were either dead or dying, having been suffocated by the pungent exhalations of the latter species. Thus the little I could observe of the relations of the two species resembled those which I have recorded for *L. emersoni* and *Myrmica brevinodis* — only reversed, the *L. canadensis* behaving like the *Myrmica*, while the *Cremastogaster* behaved somewhat like *L. emersoni*.<sup>1</sup>

3. *L. pergandei* lives, probably as a guest, in the nests of *Monomorium minutum* var. *minimum* (see p. 539).

4. The single colony of the Mexican *L. petiolatus* which I have seen was living in parabiosis with species of *Cryptocerus* and *Cremastogaster* (see p. 527).

5. *L. tuberum* var. *unifasciatus* lives with the European *Formicoxenus ravouxi*, the relations between the species being, perhaps, the same as those which obtain between *Formica rufa* and *Formicoxenus nitidulus* (see p. 538).

6. *L. muscorum*, *L. acervorum*, and *L. tuberum* live as slaves or auxiliaries with the European *Tomognathus sublaevis* (see pp. 70, 71).

7. *L. curvispinosus* probably performs the same rôle in the nests of *T. americanus* (see p. 715).

8. *L. tuberum* has been found associated with *Strongylognathus testaceus*. Here, too, the *Leptothorax* probably acts as the slave of the dulotic species (see p. 710).

9. *L. emersoni* lives with *Myrmica brevinodis* as described in the first part of this paper. The compound nest resembles that of *L. canadensis* with *Cremastogaster* and of *Formicoxenus nitidulus* with *Formica rufa*, but the relations between the two species of ants are like those existing in mixed nests. In one sense *L. emersoni* is the dominant species and the huge *Myrmicas* are its auxiliaries, or slaves; in another sense the

<sup>1</sup> At Colebrook, Conn., July 22, I again encountered *L. canadensis*. In this instance the workers were running about on some stones which covered a very extensive nest of *Formica rufa* var. *difficilis* Em. The *Leptothorax* nest, which was probably compounded with that of the *rufa*, was not found. This fact is of some interest in connection with the remarks on *L. muscorum*, recorded at p. 519.



Leptothorax is a guest or social parasite resembling *Anergates*, though still retaining intact its own household and its domestic instincts. *L. emersoni* may therefore be said to combine in itself the instincts of ants belonging to several categories of mixed and compound nests.

The range of habits clearly indicated in this brief survey of our very fragmentary knowledge of *Leptothorax* species is still further enlarged if we include the genera *Tomognathus* and *Formicoxenus*, both of which are closely allied to *Leptothorax*. In fact, *Tomognathus* is indistinguishable from *Leptothorax* in the male sex and larval stages (Adlerz, '96). That the three myrmicine genera under consideration must have had a common origin is evident from their morphology. Nevertheless the habits of the various species are so diverse as to represent all the forms of social symbiosis except colacobiosis of the extreme type found in *Anergates*. It is evident, furthermore, that the ants of these genera must have originally possessed certain traits which made it especially easy for them to enter into symbiotic relations with other species of *Formicidæ*. I believe that we may still recognize in many of the species of *Leptothorax* several of these traits, such as the following:

1. The genus has a very wide geographical distribution, a prerequisite to the establishment of such numerous and varied relations with other ants.
2. The species are all of small size. This must undoubtedly facilitate their association with other ants.
3. The colonies consist of a relatively small number of individuals. This, too, must greatly facilitate life as guests or parasites in the nests of other ants.
4. Most of the species are rather timid, or at any rate not belligerent. They are, therefore, of a more adaptable temperament than many other ants even of the same size (*e.g.*, *Tetramorium cæspitum*). Forel ('74, pp. 339, 340) has shown that *L. tubero-affinis* will rear pupæ of *L. nylanderi* and even of *Tetramorium cæspitum* and live on good terms with the imagines when they hatch.
5. There is no very sharp differentiation in habits between the queens and workers of *Leptothorax*. This, too, should

facilitate symbiosis. The queens, as I have shown in the case of *L. emersoni*, may retain the excavating instinct and the instincts which relate to the care of the larvæ. Wasmann ('91, p. 219, footnote) saw the queen of *L. tuborum* var. *nigriceps* removing the larvæ and pupæ when the nest was disturbed, and I have recorded above a similar observation on *L. canadensis*. More recently I have seen both the winged and dealated queens in a nest of *L. longispinosus* carrying away the larvæ quite as busily as the workers. It is as Forel says ('74, p. 339): "Les ♀ vivent presque comme les ♂; elles sont seulement moins aptes au travail."

6. The similarity in instinct between the queens and workers of *Leptothorax* finds its physical expression in the frequent occurrence of intermediate, or ergatogynous, forms. So-called microgynic individuals, or winged queens no larger than the workers, have been frequently observed by Forel ('74, p. 341) and Wasmann ('95, p. 618) in *L. acervorum*. Those observed by the latter author also showed color transitions between the normal queens and workers. Adlerz ('86, p. 77) found microgynic individuals in *L. acervorum*, *muscorum*, and *tuborum*. Still other ergatogynous forms, which may be called ergatoid queens, are represented by the large ocelligerous workers of *L. emersoni* described and figured in the first part of this paper (pp. 434, 436). These individuals bear a striking and suggestive resemblance to the ergatoid queens of *Tomognathus sublævis* described and figured by Adlerz. Wasmann ('95, p. 619) also records the occurrence of what he calls "ergatogyne Mischformen," or individuals completely transitional between the queens and workers, in colonies of *L. acervorum* and *Formicoxenus nitidulus*.

It is possible to draw still further inferences from the heterogeneous instincts exhibited by the genus *Leptothorax* and its allies. Viewed as a whole, these different symbiotic relations cannot be said to bear the ear-marks of internal developmental causes operating in a perfectly determinate manner. Indeed, appearances are quite otherwise and seem rather to point to indeterminate variations which have been and are still in process of being seized on and fixed by natural selection. It

must also be admitted that the same appearance is presented by the whole complex of conditions in compound and mixed nests, but the demonstration is more cogent when it can be shown that we have relations as different as those of dominant species (*L. emersoni*) and slaves (*L. acervorum*) not only in the same genus but among closely allied forms. *This fact also suggests that the instincts of the same species may be so generalized as to enable it to function like man, either as a slave or master, according to the circumstances.*

Although these considerations may seem to lack precision they certainly show that we cannot dogmatize on the inadequacy of natural selection from a study of a few highly specialized ants like *F. sanguinea* and *Polyergus rufescens*. The complicated phylogeny of the mixed nests can only be established after a patient study of genera like *Leptothorax* and *Tomognathus*. Another even more neglected group of small ants which promises to throw some light on this subject comprises the species of *Monomorium* with the allied genus *Xenomyrmex*. At present so very little is known concerning the habits of these genera that it must suffice merely to call attention to them in this connection.

✓ It is necessary in conclusion to consider very briefly the psychological problems suggested by the phenomena of social symbiosis, since, as above stated, the cases of dulosis have led authors to postulate unusual mental powers in ants. The accounts of sane and critical workers like Forel have been distorted by the "popularizer," till one almost believes that the *ante-bellum* Southerner might have learned many things in the management of his slaves from a conscientious observance of Proverbs vi. 6. Wasmann in his numerous writings ('91, '97, '99, '99b, etc.) has undoubtedly done much, at least in Germany, towards the exposure of this pseudo-psychology and a more rational conception of ant behavior. His long familiarity with these animals and their guests has given him a singularly lucid insight into their activities. My own more limited observations on our North American species lead me to agree with him so far as the facts are concerned and many of the inferences which he has drawn from them. I am constrained to say, however,

that I cannot adopt either his psychological definitions or his psychogenetic reservations.

Wasmann seems to me unduly to expand the conception of instinct in one direction, while circumscribing it rather too narrowly in another. It is true that he distinguishes instinct *sensu stricto*, the equivalent of the term as employed by many comparative psychologists to designate the purposeful, automatic, or stereotyped hereditary activities which are performed prior to all experience and without awareness of their object, and instinct *sensu lato*, which embraces also the activities depending on the sense-experience of the individual, and all that this implies, — adaptation and choice, associative memory, etc., — activities which have come to be very generally designated as “intelligent.” But he does not appear to regard these differences as sufficiently important to merit sharp distinction. Indeed, he even attempts ('99, p. 12 *et seq.*) to show that the presence of an element of experience in the associative process of an animal is not of sufficient moment to merit distinction from purely hereditary associations. This, I believe, few psychologists will admit. The detection of such a difference, however difficult it may be in practice, is surely not beyond the possibility of carefully devised experimentation and induction. And theoretically the two kinds of activity should certainly be distinguished and separately designated. Wasmann traces the non-stereotyped activities depending on choice to a “*sinnliches Erkenntniss- und Begehrungsvermögen*,” which he regards as being the distinguishing trait of instinct. Thus he comes to include under instinct both the instinct and intelligence of other authors. I believe with Emery ('93, '98) and Bethe ('98) that Wasmann has overshot the mark and attempted to include too much in his conception of instinct. I should continue, therefore, to emphasize the difference between activities which are compelled by inherited mechanism and those which imply choice on the part of the individual organism. For the latter the term “intelligence” has been so very generally used that it seems both hopeless and idle to try to restrict it, as Wasmann so emphatically desires, to the ratiocinative process in its clearest manifestations.

That instinct activities and activities implying choice should not be included under the same name is also evident from the difficulties which we experience when we attempt to show how the former could pass over into the latter; although the ingenious hypothesis of Spencer, James, Morgan, and Whitman ('99, p. 333 *et seq.*) may indicate where we are to seek for this transition, which these authors find in the progressive complication and mutual interference of instincts. Such conditions, it is claimed, must lead to a diminution in the automaticity of instinct and the supervention of a state of hesitancy and choice on the part of the organism.

While on the one hand, as above stated, Wasmann improperly expands the conception of instinct by including in it also the simpler manifestations of intelligence, he narrows it in another direction when he attempts to distinguish rather too sharply between reflex action and instinct. His criterion that reflex action depends essentially on the function of subordinate ganglia, whereas instinct depends on the activity of a brain, or sensorium, can only be maintained if the conception of instinct is restricted to the Metazoa and understood as including intelligence (*sensu auctorum*). But with the rejection of this definition of instinct we must also reject such a distinction between reflex action and instinct.

It may be said in this connection that the attempts of others to distinguish between instinct and reflex action are almost equally unsatisfactory. This is true, *e.g.*, of the distinction emphasized by Romanes, when he says ('95, p. 12): "I endeavor to draw as sharply as possible the line which *in theory* should be taken to separate instinctive from reflex action; and this line, as I have already said, is constituted by the boundary of non-mental or unconscious adjustment, with adjustment in which there is concerned consciousness or mind." It is well that Romanes has stamped his distinction as a theoretical one, for its application in comparative psychology is obviously impracticable, since it must fluctuate with our opinions concerning the presence or absence of consciousness in different animals. It is not at all certain that consciousness is present in the cases of pure instinct; or, if present, it may exist as a

mere epiphenomenon as Morgan explains ('00, p. 208) : "An organism — if such exists — in which all the activities are throughout life purely automatic and purely instinctive, might indeed be conscious, but its consciousness would be of no practical value ; for all the activities being, *ex hypothesi*, automatic, there would be no conscious guidance or control. Consciousness might be present as a spectator of the activities, but it would be a mere spectator without power of guidance, since, in so far as guided by intelligence, activities cease to be instinctive. It should be clearly grasped that, in so far as an activity is guided by individual control towards more complete accuracy, just so far does it cease to be instinctive, as the word is here used, and become intelligent. And when an instinct is, as so often is the case, modified and adapted to meet new circumstances, the modification and adaptation is no part of the instinct as such, but is due to intelligent control.

"I repeat, then, that in instinct as such consciousness is an epiphenomenon or adjunct. But this does not, of course, imply that it is absent. Only in so far as consciousness accompanies the performance of instinctive activities can intelligence get a hold on them for the purpose of control and guidance. The performance of automatic activities affords to consciousness data, which form a foundation upon which the psychical structure reared by intelligence is based."

Finally, the distinction noted by Spencer, Morgan, and others that reflex action is "localized response involving a particular organ or a definite group of muscles initiated by a more or less specialized external stimulus," whereas "instinctive activity is a response of the organism as a whole, involving the coöperation of several organs and many groups of muscles," implies only a difference in degree as Marshall ('98, p. 100 *et seq.*) and Loeb ('00, p. 77) have pointed out ; for when we extend our view to simple as well as complex organisms, and forget for the moment the staple experiments of neuro-muscular physiology, we must agree with James when he says ('90, p. 384) that the "actions we call instinctive all conform to the general reflex type," and with Marshall ('98, p. 100) when he says : "All

instincts appear as modes of that simplest of all forms of activity, the reaction of a living cell to the stimulus received from its environment." And we are led to conclude with Loeb ('00, p. 177) that "the discrimination between reflex and instinctive actions is chiefly conventional." The work of this last author, above all others, is of great value in freeing us from some of the traditional misconceptions of instinct. He has succeeded in tracing a number of instincts to simple tropisms (or taxes) and has shown good reasons for maintaining that many of the more complicated instincts are only catenary reflexes (*Kettenreflexe*). These, however, have not yet been sufficiently analyzed.

Loeb's conception is also fruitful in another direction, for as Mach says ('00, p. 64) it throws light on the relations between development and instinct. Numerous "instincts" of ants, such as their reactions to moisture, heat, light, and contact, are evidently simple reflexes and may, I believe, be treated as cases of hygro-, thermo-, helio-, and thigmotaxis. The first and last of these reactions are especially striking. Similarly the olfactory reactions, which are such an extremely important factor in the lives of ants, are probably not essentially different from the chemotactic reactions of simpler organisms. The consociation of ants in mixed and compound nests is undoubtedly dependent to a very considerable extent on olfactory reactions. The young auxiliaries that hatch from stolen pupæ are at once adopted in the mixed nests because they have acquired the nest odor of the dominant species. Moreover, the fact that these intimate relations are established only between ants of rather close taxonomic affinities is probably due to their having very similar odoriferous secretions to begin with. The animosity of ants seems to be at once excited by species which emit peculiar or unfamiliar odors. While I accept Loeb's conception as simplifying to a considerable extent the problem of instinct, I cannot suppose with Bethe ('98, '00) that the behavior of ants and bees is entirely of a reflex nature; I can only indorse Wasmann's ('99b) and Forel's ('00-'01) comments on this author's extreme views.

Wasmann ('91, p. 179 *et seq.*) has shown in detail why it is

quite unnecessary to assume the existence of anything beyond instinct and simple intelligence in the ants which form compound and mixed nests. I should even be inclined to place a more moderate estimate than Wasmann on the psychical endowments of these animals. The manifestations of intelligence are very feeble, as any observer who tries to free himself from anthropomorphism will surely find. There are distinct traces of associations with indications of some permanence of these associations, or what might be called animal memory as restricted in its meaning by Thorndike ('98, pp. 98, 99). Imitation is clearly manifested, but in a form which does not necessarily imply the existence of consciousness. There is a certain ability to profit by experience, and considerable power of adaptation to new circumstances, both remarkably developed as compared with these powers in other insects. There is evidence of choice and of that which it necessarily presupposes, *viz.*, will, but there are no evidences of anything resembling abstract thought, cognition, or ratiocination as manifested in man. Nor are there the slightest grounds for postulating the existence of these powers, which would be a hindrance rather than a help in the activities of ants under existing conditions.

Having arrived at the same conclusion as Wasmann that there are no evidences of ratiocination in ants we have reached the limits of our brief inquiry. This conclusion, however, even if it be extended so as to exclude all animals except man from a participation in this faculty, does not imply the admission of a qualitative difference between the human and animal psyche, as understood by Wasmann. Surely the sciences of comparative physiology, anatomy, and embryology, not to mention paleontology, distribution, and taxonomy, must have been cultivated to little purpose during the nineteenth century if we are to rest satisfied with the scholastic definition of ratiocination as an adequate and final verity. And surely no one who is conversant with modern biological science will accept the views that the power of abstract, ratiocinative thought, which is absent in infants and young children, scarcely developed in savages and highly developed and generally manifested only in the minority of civilized men, has miraculously sprung into



existence in full panoply like the daughter of Jove. Such conceptions recall the rhetorical figure which Houzeau ('72, Vol. II, p. 264) aptly uses in his discussion of this same matter: "The spark," he says, "which we draw from a rod of wax is analogous to that from the Leyden jar and we attribute it to electricity. Had we from the very first sought to liken it to the thunderbolt, the difference of proportions, the quantitative inequality might have been such that we should have been scandalized by the comparison." But we need not dwell on mere opinions respecting the status of ratiocination in the animal kingdom. That the task of tracing reason to more generalized and primitive psychic processes is not impossible is shown by Binet's recent investigations ('01), the gist of which is included in the following quotation (p. 159): "There is no decided difference between perception and logical reasoning; the two operations are both reasonings, transitions from the known to the unknown. The analogy is so close that we were able to compare perception with formal reasoning, and to show that perception contains all the essential elements of a peripatetic syllogism (see p. 88). In short, perception and logical reasoning are only the two extremes of a long series of phenomena, and when we place ourselves in the middle of the series we find inferences which belong to both at the same time (see p. 70). Further, we have shown that a kind of filial relationship exists between perception and the reasonings of conscious logic. Thus when we make systematized anæsthesia, which has been developed in a patient relatively to a certain person, gradually disappear, the thing which appears first of all is the perception of the person as species; and it is only afterwards, by a kind of ascending evolution, that the recognition of the person as individual takes place; now, we know that recognition is a complex operation which touches closely upon reasoning properly so called. All these reasons lead to the belief that perceptive reasoning and logical reasoning imply the same mechanism (see p. 77)." A somewhat similar conclusion respecting the derivation of ratiocination is reached by Wundt ('01, pp. 342, 395).

However doubtful we may be of the complete success of attempts like that of Binet, we may be confident, nevertheless,

that they contain the germs of promise, for the consensus of the biological sciences leads us at last to one point of view: "We are prepared," as Mach says ('98, p. 235), "to regard ourselves and every one of our ideas as a product and a subject of universal evolution; and in this way we shall advance sturdily and unimpeded along the paths which the future will throw open to us."

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