The Social Insects

Their Origin and Evolution

By

WILLIAM MORTON WHEELER

Ph.D., Sc.D., LL.D., Professor of Entomology at Harvard University, Dean of the Bussey Institution for Research in Applied Biology

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Le destin des fourmis, des abeilles, des termites, si petit dans l'espace, mais presque sans bornes dans le temps, c'est un beau raccourci, c'est, en somme, tout le nôtre que nous tenons un instant, ramassé par les siècles, dans le creux de la main. C'est pourquoi il est bon de le scruter. Leur sort préfigure le nôtre, et ce sort, malgré des millions d'années, malgré des vertus, un heroisme, des sacrifices qui chez nous seraient qualifiés d'admirables, s'est-il amélioré ? Il s'est quelque peu statilisé et assuré contre certains dangers, mais est-il plus heureux et le pauvre salaire paie-t-il l'immense peine ?

MAETERLINCK, "La Vie des Termites."

PREFACE

THE twelve lectures which make up the present volume were delivered during the spring of 1925 at the University of Paris while I was occupying a Harvard exchange professorship established by Mr. James Hazen Hyde, and were published by Gaston Doin & Co., during the summer of 1926 under the title " Les Sociétés d'Insectes, leur Origine, leur Evolution " in the " Encyclopédie Scientifique," edited by Professor M. Caullery. The following year the prix Dollfus was conferred on the work by the Societé Entomologique de France. In preparing this English edition I have retained the original lecture form, but several passages, which had to be omitted in order to bring the volume within the requirements of the French publisher, have been restored to the text, a number of typographical and other errors have been corrected and a small amount of new material has been added. I have also introduced several new illustrations and have omitted a few of those in the French edition. In its present form the work has been brought up to date so far as this was possible without unduly expanding the text and the bibliography.

I am greatly indebted to Professor Caullery for the care and labour he devoted to seeing the French edition through the press. For typing the English manuscript my thanks are due to Miss Julia C. Foley and Miss Frances R. Rust. Mrs. Francena Taylor has given me much aid in revising the manuscript and the references to the bibliography and illustrations.

FOREST HILLS,
Boston, Mass.

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I

THE SCOPE AND MEANING OF THE SOCIAL AMONG THE INSECTS

THE evolution of the social insects was selected as the topic of this course of lectures for several reasons: First, because lectures on an important group of insects seemed to me to be eminently appropriate for a laboratory founded by the illustrious Giard for the study of the evolution of organic beings. Second, I could think of no subject more interesting to the young biologists of a country which has produced a Réaumur, a Latreille, a Lepelletier de St. Fargeau, a Dufour, a Fabre, a Pérez, a Ferton, a Paul Marchal, and a Bouvier, not to mention a host of other brilliant hymenopterists. Third, having myself devoted more than a quarter of a century to the study of a single family of the social insects, with ample opportunities for travel, and as the recipient of much aid from enthusiastic entomologists in all parts of the world, it seemed to me that I might be able to suggest or emphasize some lines of thought worthy of your consideration. Fourth, it occurred to me that you could not be expected to be familiar with all the work that has been accomplished by my countrymen in entomology, and that by briefly presenting as much of it as it pertinent to my subject, I might be furthering to a slight degree that intellectual *entente cordiale*, which we are so desirous of maintaining between France and the United States. Fifth, I believe that the study of the social insects has, at the present time, a peculiar interest to the serious student of philosophy, sociology, and animal behaviour. Since we ourselves are social animals—I had almost said social insects—the philosophically inclined cannot fail

to find food for thought in the strange analogies to human society, which continually reveal themselves among the wasps, bees, ants and termites, and the behaviourist will note that they suggest a bewildering array of fascinating facts and problems. Moreover, the very elaborate social behaviour of the insects, in that it is almost exclusively determined by the reflexes, tropisms, and the so-called instincts and not by intelligence, assumes great theoretical significance, when we contemplate the present anti-intellectualistic and relativistic tendencies and currents of European and American thought. We are beginning to see that our social as well as our individual behaviour is determined by a great background of irrational, subconscious, physiological processes. Any doubts in regard to the existence of this substratum will be dispelled by a perusal of Pareto's " Treatise of General Sociology " (1917), the first volume of which is devoted to these " residues " which condition our social activities.

For much that I have to say I shall have to draw on materials accumulated while I was preparing my Lowell lectures on " Social Life Among the Insects." In that work I endeavoured to stress the fundamental rôle of nutrition in the development of the various insect societies, but in the present lectures I wish to treat the insect societies in a different and somewhat more technical manner, and to dwell on certain matters which were merely suggested in my former course.

Before descending very far into details, I feel that I ought to attempt at least partial answers to four very general questions :

(1) What are the social insects ?

(2) Can they be shown to have had an evolution ?

(3) If so, what are the peculiarities of this evolution, and to what methods must we resort for their elucidation ?

(4) To what general causes or conditions may we assign this evolution ?

What are the social insects? The words "social" or "associative" are, of course, rather vague, and tinged with anthropomorphism. Their vagueness is due to the extraordinary multiplicity and Protean character of the phenomena, even among the insects, not to mention the various classes of Vertebrates. These phenomena range all the way from a feeble gregariousness or collectivity or the mere temporary union of the sexes to permanent and highly integrated societies remotely analogous to our own.' The anthropomorphism attaching to the word "social" is easily explained and may be condemned or condoned according to the general philosophical convictions of the critic. I can only record my belief that in the discussion of matters psychological—and the phenomena in question are in part psychological—we can scarcely avoid a certain amount of anthropomorphism or teleology.

Recently Deegener (1918) has made a bold and rather unsatisfactory attempt, in a tome of 420 pages, to classify and describe all the various forms of association in the animal kingdom. He distinguishes some ninety-two different categories, fifty-three of which are represented among the insects. They are all supplied with scientific names, mostly of Greek derivation, some of which, like "heterosymphagopædium", "amphoterosynhesmium", and "heterosynepileium", have a truly Germanic ponderosity. The ninety-two different categories are divided into two groups, accidental societies or associations, in which the congregation of the organisms has no intrinsic value, i.e., serves no useful purpose for the individual, and essential societies or associations, in which the congregation has an intrinsic value or subserves in part a useful purpose. Each of these leading categories is subdivided according as the association comprises individuals of the same or of different species. The finalistic *principium divisionis* of the main groups is very dubious, to say the least, since even the most highly integrated animal associations are frequently confronted with situations in which membership in the

society inevitably involves the destruction of the individual. And apart from the fact that the same animal (e.g., the sexton-beetle, Necrophorus) is cited by Deegener as belonging to several different categories, some of the latter border on the humorous as e.g., his " heterosymporium ", which comprises the insects of different species brought together by a freshet, or the various animals fleeing from a prairie fire, or his " symphotium ", which comprises the miscellaneous assortment of insects attracted by a lamp.

The classification of social forms adopted by Alverdes (1925) into associations and societies is both more logical and more useful than that of Deegener. Associations are aggregations of organisms brought about by extraneous factors whereas in societies the individuals are held together by a mutual attraction, or peculiar social appetency. In associations the single individual is oriented primarily towards stimuli emanating from its environment apart from the other individuals of its species, but in societies the stimuli are furnished by the latter and orientation towards the remaining environment is secondary. In true societies, therefore, an individual may exchange a favourable for an unfavourable environment merely in order to satisfy its craving to remain with other individuals of its kind.[1]

[1] Rabaud (1927) has rather captiously criticized Bouvier (1926) and myself on the basis of some observations on males of Halictus and on general principles. Since he adopts a strenuously physiological view of biology and seems to be unable to accord any value to the historical, or phylogenetic aspect of the science, discussion of his general position would be unprofitable. So far as his observations are concerned, it is difficult to see that he has added anything of importance to what has long been known in regard to a great many insects that form aggregations, or associations, such as the Ipid, or Scolytid and Plalypodid beetles, hibernating Coccinellids and many solitary Aculeates which make their individual nests in close proximity to one another (Bembix, Philanthus, Synagris, Andrena, etc.). At the same hour and especially in the evenings of several consecutive days he observed males of *Halictus latipes* and *nigricornis* congregated in compact clusters on a few dry grass stems in two localities, and concludes from several experiments that the insects were attracted to these particular spots as if they were nesting sites. He believes, however, that the initial attraction was due to interindividual stimuli and was not therefore merely gregarious, or associational, but social. I have myself seen very similar daily agglomerations of males of our North American *Chloralictus albipennis*

Now it seems to be obvious that the behaviour of every animal, figuratively speaking, revolves about two axes, one of which is aggressive and individualistic, the other co-operative, or social. The Darwinians took the former behaviour largely for granted and greatly stressed it, so that the latter appeared to be exceptional and in need of a special explanation. At the present time one might more properly require an explanation of the solitary mode of life, so deeply are all who study animals in their complicated living environment impressed by their social or associative proclivities. This is apparent even in the biocœnoses, since every organism, no matter how egocentric, predatory or parasitic, is social or co-operative at least to the extent of being a member of some biocœnose.

The truth of the foregoing statement was so long ago and so admirably expressed by Espinas in the introduction to his "Des Sociétés Animales" (1877) that I cannot refrain from quoting the pertinent passage: "No living being is solitary. Animals, especially, sustain multiple relations with the organisms of their environment, and without mentioning those that live in permanent intercourse with their kind, nearly all are impelled by biological necessity to contract, even if only for a brief moment, an intimate union with some other individual of their species. Even among organisms devoid of distinct and separate sexes, some traces of social life are manifested, both among the animals that remain, like plants, attached to a common stock and

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on particular corymbs of *Aster corymbosa*, but have attributed it to an impregnation of the flowers with odours, left either by virgin females which had previously visited them, or by the males after they had once congregated on the spot. These possibilities are not considered by Rabaud. Furthermore, as will be shown in the fourth lecture many species of Halictus are really social bees, so that Rabaud is not dealing with a simple or incipient tendency to social life. Finally Bouvier and I were not concerned with the universal phenomena of the social in its broadest sense, but with the true *genetic* societies of insects, and Rabaud seems to overlook the fact that these societies have a definite ontogeny traceable to definite physiological relations between parent and offspring.

among the lowly beings which, before separating from the parental organism, remain for some time attached to it and incorporated with its substance. Communal life, therefore, is not an accidental fact in the animal kingdom; it does not arise here and there fortuitously and as it were capriciously; it is not, as is so often supposed, the privilege of certain isolated species in the zoological scale, such as the beavers, bees and ants, but on the contrary—and we believe we are in a position to prove this statement abundantly in the present work—a normal, constant, universal fact. From the lowest to the highest forms in the series, all animals are at some time in their lives immersed in some society; the social medium is the condition necessary to the conservation and renewal of life. This is, indeed, a biological law which it will be expedient to elucidate. Moreover, from the lowest to the highest stages in the series, we detect in the development of social habits a progression which if not uniform is at least constant, so that each zoological group carries the perfecting of these habits a little farther in one or another direction. Finally, social facts are subject to laws and these are the same everywhere where such facts appear, so that they constitute a considerable and uniform domain in nature, a homogeneous whole thoroughly integrated in all its parts."

Perhaps, if we were asked to point to a group of typically solitary animals, we should select the spiders, but when we study them in the tropics, we find that many of the species are decidedly gregarious or vaguely social. Recently, in Panama, Mr. Nathan Banks and I were impressed by the habits of several of these arachnids. One of the largest and commonest of the orb-weaving spiders, *Nephilla plumipes*, during the wet season, regularly builds its webs in such a fashion that those belonging to different females run together so that huge and elaborate structures are sometimes formed. One compound web, which we observed among the trees on the summit of Ancon Hill near the City of

Panama, was fully twenty feet broad and more than twenty-five feet high. In it were suspended at least 200 female and nearly as many male Nephillæ, besides a considerable number of *Argyrodes nephillæ*, a small parasitic Theridiid spider which lives only in the webs of Nephilla. We also encountered several species of Theridion and Uloborus which unite their webs in a similar manner, and a peculiarly social species, apparently undescribed, but allied to *Anelosimus socialis* Simon, in the webs of which dozens of females of all ages moved about freely and in all probability fed in common on at least the larger prey. Many of these spiders bore on their abdomens the larvæ of a parasitic Hymenopteron (probably Polysphincta). Even alien insects may live unmolested in the webs of some of these Panamanian spiders. On Barro Colorado Island we found numerous red nymphs and black adults of a small, ant-like Nabid bug (*Arachnocoris albomaculatus* Scott) resting or moving about in the webs of Uloborus and Theridion and apparently feeding on the prey abandoned by the spiders (see Myers (1925)). On two occasions we observed dozens of small Cecidomyid flies resting peacefully on the webs of Nephilla and Uloborus. When the webs were shaken, the tiny insects flew off only to return at once to their former station.

In 1891, Simon made similar observations on the social habits of spiders in Venezuela and cites numerous examples in other tropical countries. He gives an excellent account of *Epeira bandelieri*, *Anelosimus socialis* and *Uloborus republicanus*. On ordinary occasions *E. bandelieri* is solitary, but when the egg-laying season approaches several females congregate and together construct a large elliptical capsule in which they conceal themselves and make their egg-cocoons. *A. socialis* lives in colonies of several thousand individuals which construct a common web. " The spiders walk about on it freely, meet one another and exchange greetings with their palpi, as ants do with their antennæ, and sometimes devour the more voluminous pieces of prey

in common." The association of *U. republicanus* is "far the most perfect, since it presents both a web constructed by all the associates working together and single webs constructed by individual spiders. Several hundred Ulobori live together. They spin among the trees an immense structure, consisting of a central web with rather dense meshes on which numerous individuals of both sexes, but mostly males, are stationed. This web is suspended by long threads, radiating in all directions and attached to surrounding objects. In the intervals of these stout strands, other Ulobori weave orbicular webs with radii and circles, and inhabited only by single individuals. Mating takes place on the central web, if we may judge from the number of males which we found congregated on it. . . . It is certainly the place where the eggs are laid. All the females of the colony seem to lay almost simultaneously. At this time the males have disappeared and the females, having ceased to spin regular webs, are attached to the central web, a few centimetres apart and each guarding her cocoon in complete immobility."

According to Bouvier (1918), "Semichon (1909) has observed the same fraternal sharing (of the prey as in *U. republicanus*) in a Mexican social spider, *Cœnothele gregalis*, brought to the Museum in Paris by Leon Diguet (1909a, 1909b). In order to capture insects, this species constructs on the trees great concentric webs consisting of carded strands. Thousands of individuals live in harmony in this immense alveolar sac and never leave it, except after the rainy season, when they emigrate, or rather swarm, to leave room for the young. These webs may be divided and are hung from the ceiling and used as fly-traps in certain parts of Mexico. One of them, exhibited in the galleries of the Museum, is several meters long". Diguet has the following notes on two interesting commensals which he found living in these nests of Cœnothele. "In all the internal portions of the nest very great numbers of a Latridiid of the genus Melanophthalma are found living as commensals. The

rôle assumed by this minute beetle seems to be the cleaning of the nest, i.e., transporting and doing away with the detritus which may encumber or soil the galleries; its principal food seems to be the remnants of the spiders' repasts. . . . Another commensal also found living in perfect harmony with the 'mosquero' colony is a wandering spider which has become a guest in this lodging and there finds an easy and assured existence". This spider was identified by Simon (1909) as *Pœcilochroa convictrix* Simon.

In 1926, I published some notes on a couple of social spiders, *Cyrtophora citricola* and *Argyrodes argyrodes*, which I observed in the Canary Islands (Teneriffe, Palma and Gran Canaria). There is much the same relation between these two species as between the Panamanian *Nephilla plumipes* and *Argyrodes nephillæ* mentioned above. The webs constructed by the Cyrtophora are spread over trees and shrubs and are sometimes of great dimensions. At Puerto de la Luz I found a dense hedge of Opuntia cactus fully one hundred feet long and six or eight feet wide, covered by a single web estimated at more than 1,000 square feet and containing many thousands of spiders. The web consists of two parts, a very irregular structure or frame work of long, coarse, yellow and somewhat glutinous threads, running in all directions and attached to the plants, and a variable number of suborbicular, horizontal webs suspended side by side or one above the other in the frame work. These webs are three to eight inches in diameter and made of very even square meshes, of the size of those of mosquito netting, but consisting of exceedingly delicate, whitish silk. The Cyrtophoras rest on the lower, convex surfaces of these webs. Individuals of all ages live together amicably and seem to feed in common on the prey that is caught in the webs, but the adult females (15 mm. long), which are gray, with large, paired, silver spots on the dorsal surface of the abdomen, are usually few in number. The egg-cocoons are elliptical, about 15 to 20 mm. long, made of dense, coarse, gray-green

silk, and are suspended vertically in or near the center of the whole structure. They vary from one to five in number and are attached to one another in a series, so that they resemble a string of minute sausages. The mother spider is usually found resting at the end of the lowermost cocoon. The Argyrodes, which are black, with pale legs and extensive silver spots on the abdomen and are very much smaller than the adult Cyrtophoras (adult female only 4.5 mm., adult male 3.5 mm.), were also present in all the webs which I examined. They seem to make no webs of their own but live in the coarse framework of the structure spun by the larger species. Like the latter, they are present in considerable numbers, of all sizes and of both sexes. They were seen to feed on small insects caught in the coarse yellow strands. When disturbed they quickly drop to the ground by letting out a thin silken filament, but the Cyrtophoras run off to the side and hide in the foliage of the plant supporting the web. The egg-cocoons of the Argyrodes resemble certain seed-capsules and are of the peculiar type seen in other species of the genus, being small subspherical or pear-shaped, yellowish brown, papery-walled structures. One pole of the capsule is prolonged into a stiff stem, or pedicel by which the capsule is suspended from the threads of the web and at the opposite pole there is a small circular, protruding rim.[1]

Probably most of us would agree with Petrucci (1906) who reviewed the various forms of societies among the vertebrates and pointed to their polyphyletic derivation,

[1] Interesting accounts of the habits of the social spiders of the genus Stegodyphus, represented by several species in South Africa and India are given by Simon (1892-5), Distant (1898), Marshall (1898), Pocock (1903) and Jambunathan (1908). Walsingham (1903), Marshall and Pocock also describe a peculiar Tineid moth (*Batrachedra stegadyphobius*) which lives in all its stages in the webs of these spiders. Mr. J. H. Emerton informs me that some of our New England spiders may build closely continuous webs, e.g. *Dictyna muraria* and *Amaurobius ferox*, and that he has seen more than a hundred small midges resting peacefully on the web of *Linyphia marginata*. Recently Prof. C. T. Brues has made some observations on *Uloborus republicanus* which is common near the Harvard Tropical Laboratory, at Soledad, Cuba. Sae elso Schwarz (1904) and Banks (1904).

when he says: "There is no inheritance in the social activities of animals, except a tendency to association, a tendency manifested in a predominant fashion throughout the domain of biology and realized in concrete phenomena whenever and wherever external conditions permit of its manifestation". Petrucci naturally traces his "tendance associative" to such phenomena as the cellular constitution of the Metazoa and Metaphyta and even to atomic equilibria and molecular associations in the inorganic world. But the conception, though not devoid of interesting philosophical implications, thus becomes very vague. I should prefer for the purpose of making the matter more concrete and intelligible, at least in the biological field, to regard the "tendance associative" as an "appetition" in the sense in which that term has been employed by the French thinker Fouillée and the British and American psychologists Drever (1917), Craig (1918) and Thurstone (1924). It thus takes its place with the other appetitions like hunger and sex, though it is feebler, more continuous, i.e., less spasmodic and, therefore, less obvious. It is most strikingly displayed, however, in the restless behaviour of the higher social animal when isolated from the continuous, customary stimuli of its kind.[1]

That this social appetition is clearly and very generally manifested in certain insects admits of little doubt, but it will be advantageous to narrow the conception still further by the introduction of other considerations if we are to make any use of it in the very special field which I have marked out for treatment in these lectures. There are authors, who like Fabre have hinted that even the societies of ants and bees may have arisen phylogenetically by chance associations of female insects of the same species, but this was before the actual constitution and genesis of insect societies were known. It is now

[1] I do not, of course, wish to imply agreement with the views of Becher (1917), who postulates a distinct altruistic *penchant* in certain plants and animals to serve other and quite unrelated organisms. This view has been adequately criticized by Bequaert (1924), A. Meyer (1926), and others.

unanimously admitted that all insect societies worthy of the name, and no matter how populous, are families, i.e., affiliations of the parents and, in most cases, of the mother alone, with the offspring. This view is abundantly supported by the study of the ontogeny of existing insect societies and by such fragmentary indications as we can obtain in regard to their phylogeny.

There has evidently been a very long evolution through numerous stages of constantly increasing intimacy of the mother with her progeny from the most rudimentary stage of complete or almost complete indifference to one of mutual and abiding co-operation. We may construct, e.g., such a series as the following, without stopping to enumerate concrete examples, many of which will at once occur to you.

(1) The insect mother merely scatters her eggs in the general environment in which the individuals of her species normally live (*atrophaptic* insects). In some cases the eggs are placed near the larval food (*dystrophaptic* insects).

(2) She places her eggs on some portion of the invironment (leaves, etc.) which will serve as food for the hatching larvæ (*eutrophaptic* insects).

(3) She supplies her eggs with a protective covering. This stage may be combined with (1) or (2).

(4) She remains with her eggs and young larvæ and protects them.

(5) She deposits her eggs in a safe or specially prepared situation (nest) with a supply of food easily accessible to the hatching young (mass provisioning).

(6) She remains with the eggs and young and protects and continuously feeds the latter with prepared food (progressive provisioning).

(7) The progeny are not only protected and fed by the mother, but eventually co-operate with her in rearing additional broods of young, so that parent and offspring live together in an annual or perennial society.

The insects included in categories (1) to (5) may be designated as " infrasocial " ; those of (6), which are more interesting for our purposes may be called " quasi- " or " subsocial ". Only the last category (7) comprises social forms *sensu stricto*. This final stage in the series is reached primarily through the development of an increased interest on the part of the mother in the later instars of her offspring and is, of course, made possible by a lengthening of her individual life-span. Had the students of human sociology been conversant with this very obvious inference we might have been spared some speculations which are constantly repeated in sociological literature. John Fiske in his " Cosmic Philosophy " (1874) maintained that the lengthening of human infancy and childhood has led to the definitive association of the parents with the offspring. He conceived this to be a new interpretation of the origin of the family, but Lovejoy (1922) has recently shown that the notion was familiar to many eighteenth century thinkers. He mentions particularly the poet Pope, and the philosophers Locke and Rousseau, and shows that Rousseau demolished Locke's argument, which was essentially that of John Fiske, in 1755, in his " Discourse on the Origin of Inequality " by pointing out that if the habit of family life had not been established by primitive man during the months preceding the birth of the first child, the human male would hardly have come to the aid of the female after the " accouchement ". " Why should he aid her to rear an infant which he does not even know to be his, and the birth of which he has neither purposed nor foreseen ". At the present day we should, of course, turn to a study of the Anthropoids for light on the remote and nebulous origins of the human family.