FOIBLES
OF INSECTS AND
MEN

Translated and Annotated

by

WILLIAM MORTON WHEELER

THE NATURAL HISTORY OF ANTS

By

RENÉ ANTOINE
FERCHAULT DE RÉAUMUR

FOIBLES OF INSECTS AND MEN

by

WILLIAM MORTON WHEELER
Professor of Entomology, Harvard University

NEW YORK
ALFRED · A · KNOPF
19 28

21382

Manufactured in the United
States of America

To My Friend

DAVID FAIRCHILD

in Memory of Many Happy Excursions

in the Jungles of Panama and the Mountains of Morocco

PREFACE

For some time friends have been urging me to republish in book form some of my papers which have appeared in various scientific journals. The continued demand for these parerga long after the exhaustion of my supply of off-prints suggests that they may, perhaps, be of interest to readers who do not habitually consult scientific journals.

For permission to republish the article on the "Physiognomy of Insects" I am indebted to my friend Dr. Raymond Pearl, editor of the "Quarterly Review of Biology." Dr. Robert C. Cook has kindly granted my request to reproduce the article on insect courtship and Professor J. M. Cattell has generously allowed me to use the remaining articles which appeared in his journals, "Science," "The Scientific Monthly" and "The American Naturalist." Very few changes have been introduced into the articles apart from the insertion of several foot-notes and in two of them the addition of several pages of new matter. The paper on Leptothorax emersoni *has been rewritten and considerably expanded.*

Forest Hills, Mass.,
June 28th, 1927

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

INTRODUCTION

Et je songeai que la grande vertu de l'homme est peut-être la curiosité. Nous voulons savoir; il est vrai que nous ne saurons jamais rien, mais nous aurons du moins opposé au mystère universal qui nous enveloppe une pensée obstinée et des regards audacieux; toutes les raisons des raisonneurs ne nous guériront point, par bonheur, de cette grande inquiétude qui nous agite devant l'inconnu.

ANATOLE FRANCE

Ne nous fions qu' à nous; voyons tout par nos yeux;
Ce sont là nos trépiéds, nos oracles, nos dieux.

VOLTAIRE, "OEDIPE"

The title of this volume seems to call for an explanation. According to the lexicographers, the word 'foible' is derived from 'faible' (feeble) and signifies "a special weakness of character; a failing; a weak point; a fault of a not very serious kind." The word might seem, therefore, to be inapplicable to many of the miscellaneous activities discussed in the following pages. Since, however, character is revealed only in behavior, and behavior is always positive, we should, perhaps, stress the word 'special' in the dictionary definition and take it in the sense of 'peculiar' or 'unusual.' Foibles would then be peculiar trends of individual behavior. When in the human species they become general, or social, we call them fashions, fads or cults. I can see no objection to expanding the meaning of the word to include both such ontogenetic behavior as habits and specializations of appetencies and such phylogenetically or racially stabilized and standardized behavior patterns as are commonly called 'instincts' and 'mores.' All these activities may be regarded as potential weaknesses to the extent that they are more or less highly specialized, or organized, and may therefore endanger the life of the individual or species if the environment happens to change. This danger to the species is diminished or avoided in many very highly specialized lower organisms like the insects by a great increase in fecundity. In the higher animals, which have developed a much more pronounced individual flexibility, or amplitude of response to the environment, the number of offspring may be greatly reduced without danger to the race. The greater stability of specialized, or more highly organized as compared with less organized behavior patterns accounts, moreover, for certain characteristics of the individual and social foibles, since as Richards[1] admirably remarks, "The element of sacrifice exacted by any stable system explains to a large extent the tenacity with which custom is clung to, the intolerance directed against innovations, the fanaticism of converts, the hypocrisy of teachers and many other lamentable phenomena of moral attitudes. However much an individual may privately find his personality varying from hour to hour,

---

[1] "Principles of Literary Criticism," Harcourt, Brace & Co., 1926.

he is compelled to join in maintaining a public façade of some rigidity and buttressed with every contrivance which can be invented. The Wills of Gods, the Conscience, the Catechism, Taboos, Immediate Intuitions, Penal Laws, Public Opinion, Good Form, are all more or less ingenious and efficient devices with the same aim—to secure the uniformity which social life requires."

Our attitude towards our own foibles is, of course, notoriously and fatuously charitable, but it may be very different towards the foibles of animals and of our fellow men. We usually regard the peculiarities of human behavior, when harmless, as laughable or pathetic, but when injurious to their possessors or to others, and especially if we happen to be afflicted with the reformer's itch, we are apt to stigmatize them as abnormal or vicious. This is clearly shown by the attitude of the general public to the cultivation of entomology during the past three centuries. Intense curiosity in regard to the behavior, life-histories and classification of insects and other lower organisms is still regarded as a foible, or weakness, and the entomologist is still depicted as a pitiable or ludicrous figure in novels and comedies.[2] For this reason many a sensitive entomologist, especially in new countries like the United States, prefers to do his field and laboratory work where he cannot be annoyed by the public. He is sure that his activities will excite mirth or contempt or be misinterpreted. When he digs little holes in the soil, fingers the foliage or beats it over an inverted umbrella, peers under stones or bark, scrutinizes the dung or carcasses of animals or pursues insects with a net, he is commonly supposed to be prospecting for oil or minerals, hunting for food, drugs or buried treasure, or amassing showy butterflies for ornamental or commercial purposes. But the foible of entomologizing was much more seriously regarded in the seventeenth century, if we may judge from the comments of contemporaneous writers. Moses Harris, who in 1766 published a well-known book on British Lepidoptera,[3] after his description of Glanville's fritillary (*Melitæa cinxia*), cites the following incident from the latter part of the previous century: "This fly took its name from the ingenious Lady Glanville, whose memory had like to have suffered for her curiosity. Some relations that were disappointed by her will, attempted to set it aside by acts of lunacy; for they suggested,

---

[2] A serious study of curiosity by the psychologists is long overdue. The only work I have seen on the subject is a little volume by F. Queyrat, "La Curiosité, Etude de Psychologie Appliquée" (2nd edit. Paris, Alcan, 1920). He distinguishes and discusses three forms of this mental appetency, the "frivolous," the "malign" and the "fecund." The last is considered under two heads, the practical, or useful, and the disinterested, or scientific. My remarks are concerned, of course, only with Queyrat's "curiosité féconde."

[3] "The Aurelian or Natural History of English Insects namely Moths and Butterflies," in fol. London, 1766.

that none but those who were deprived of their senses, would go in pursuit of butterflies. Her relations and legatees cited Sir Hans Sloane and Mr. Ray to support her character; the last gentleman went to Exeter, and on the trial satisfied the judge and jury of the lady's laudable inquiry into the wonderful works of the Creation; and established her will." And Kirby and Spence[4] referring to the status of entomology in England as late as 1815, find that "though in this country things are not now quite so bad as they were when Lady Glanville's will was attempted to be set aside on the ground of lunacy, ... yet nothing less than line upon line can be expected to eradicate the deep-rooted prejudices which prevail on this subject."

The following passage in the preface to Faguet's "History of the Eighteenth Century"[5] gives a concise view of French opinion in regard to the investigation of nature in general and of insects in particular during the preceding century: "The causes of the disappearance of the Christian idea are probably many and confused. The principal is very probably what is called the 'scientific spirit,' which scarcely existed in the twelfth century and in France certainly dates from 1700. This spirit is the same as the 'philosophy' of the eighteenth century, and when the writers of the latter speak of the 'philosophical spirit' we must always interpret their words as meaning the scientific spirit. The seventeenth century had shown the scientific spirit little favor, and had even disdained it, for this century was mathematical and 'geometrical,' not scientific in the proper sense of the term. It was mathematical and geometrical, that is to say, it countenanced only a purely intellectual science and one which the mind alone was capable of creating; it was unfavorable to realistic science, which requires objects for its development and has its source in the observation of reality. "Men are not made to consider gnats," said Malebranche, "and we do not approve the pains some people take to teach us how certain insects are constructed, the transformation of their larvæ, etc. One may be permitted to amuse oneself with such things when one has nothing to do and is in search of diversion." Nor was such occupation even a "permissible diversion" for the more austere and philosophical intellects. It was regarded as a form of concupiscence, a *libido sciendi*, a *libido oculorum*, a veritable sin and a subtle and deadly temptation. It was, according to Jansenius, a "forever restless curiosity, parading under the name of 'science.' Hence has arisen the investigation of the secrets of nature, which are none of our business, which it is useless to know and which men wish to know merely for the sake of knowing."[6]—Literature, art,

---

[4] "An Introduction to Entomology," London, 1815, Vol. I, p. XIX.

[5] Faguet, E. "Dix-Huitième Siècle. Etudes Littéraires, 19th ed." Paris, 1901.

[6] Jansenius is here simply repeating the sense of the following passage from a more eminent theologian, St. Augustine (Confessions X, 35): "Upon this, another form of temptation assails me; and that many ways more dangerous. For besides that concupiscence of the flesh, which

philosophy, metaphysics, theology and a thoroughly intellectual mathematical science, these are the various directions of French thought during the seventeenth century."

If Faguet has correctly depicted the attitude of the French intellectuals of this century towards the concrete world of nature, we can imagine what it was in the Middle Ages, or "Muddle Ages," as they have been facetiously called. The lack of curiosity was, indeed, even more marked in those earlier centuries, which constituted the "Age of Faith," of which Brewster[7] writes: "The general idea that one can secure information about the world around him merely by looking at it is something quite outside the ken of the entire learned world. Thus, for example, century after century, the learned world repeats the story that the common salamander exudes an icy cold that puts out flame. But nobody after Pliny's day thinks to test the poor little creature at the kitchen fire. Up to the time of Vesalius, who died in 1564, all men supposed that all the sons of Adam had one rib short on one side, the missing member having gone into making Eve. For more than a thousand years, no man thought to notice his own ribs or to count another man's. The only thing that the Age of Faith did not believe was its own eyes." Mediæval writers were convinced that all that was worth knowing about nature had been ascertained by the ancients and that all that was required was to keep on copying the crazy statements of people who for the most part were as blind and childish as themselves. But there were other more recondite reasons for discouraging all interest in insects and for regarding their study as an evidence of insanity or sin. They were, of course, included among the "creeping things," and Noah had not permitted them to enter his famous ark. This was, in fact, unnecessary, because they were supposed to arise by ubiquitous and spontaneous generation from the earth, water, air or vegetation and not like the higher animals from preexisting individuals of their own kind. And since values were supposed to inhere in objects and not in the mind, and many insects seemed to behave like incarnate implets, it was natural to regard them as the offspring of Eeelzebub.

---

lurketh in the delight of all our senses and pleasures, (wherein those the slaves of it, who go far from Thee, waste and perish;) there is conveyed into the soul by the same senses of the body, a certain vain and curious itch; not of delight taking in the flesh, but of making experiments by help of the flesh; which is masked under the title of knowledge and learning, which, because it is sealed in the appetite of knowing, and that for the attaining of knowledge the eyes be the principal of all the senses, is in Holy Writ called the lust of the eyes." (Transl. by William Watts, 1631.) St. Augustine, of course, is here merely paraphrasing the remarks on the *ἐπιθυμία τῶν ὀφθαλμῶν*, or "*concupiscentia oculorum*" in I John 16. This dog-in-the-manger attitude towards curiosity not only retarded the development of true science for many centuries but has even prevented the theologians from developing their own spurious science, or addled metaphysics.

7 "Creation, a History of Non-Evolutionary Theories," Indianapolis, Bobbs-Merrill Co. 1927.

He was, therefore, their 'patron,' the "lord of rats and eke of mice, of flies and bed-bugs, frogs and lice," as Goethe calls him in Faust (1, 3). The supposed origin of the insects is clearly revealed in the second part of the poem, when Mephistopheles shakes Faust's fur mantle and the vermin tumble out with the song:

"Welcome, and hail to thee!
Patron, to-day;
We're flying and humming
We hear and obey.
Singly and silently
Us thou hast sown;
Hither by thousands
Father, we've flown.
The imp in the bosom
Is snugly concealed;
But lice in the fur coat
Are sooner revealed."

Naturally, to investigate such spawn of the Devil, if conceivable, was no common foible, but downright dementia or depravity.

This, however, does not go to the root of the matter, which is clearly not so much the diabolical character of the insects themselves as the concupiscence and "lust of the eyes," that stimulate the investigator. So much is clear from the language of Malebranche and Jansenius. It seems inconceivable that the active, investigative curiosity to which we owe the whole glorious development of modern science and technology, could seem so sinful, but when we examine it more closely we find that it is a very complex, cognitive and affective attitude involving perception, interest, wonder, attention, expectancy, scrutiny, exploration, doubt, apprehension, indecision, suspension of judgment and critical caution. While most of these would seem to be prerequisites to any adequate understanding of the infinite reality in which we are immersed and of which we are a part, doubt, suspension of judgment and critical caution, especially, have always and for obvious reasons aroused the qualms of the devout and the ire of theologians. Nor is this a peculiarity of Christians. There is a very similar avoidance and disdain of investigative curiosity among devout Mohammedans, Jews and Buddhists, and it has not been lacking among philosophers, who are so often merely camouflaged pietists and theologians.

After Redi (1626–1697) and his successors had proved that the "creeping things" are engendered in the same manner as higher organisms it was no longer possible to father them on Satan, and it had to be admitted that they must have shared in the one and original Creation. The social status of those interested in these creatures should therefore have undergone some improvement, but the inertia of popular opinion was not so easily overcome. We find that the entomologists, like other naturalists, had to resort to more efficacious means not only of neutralizing the venom of theologians like Malebranche and Jansenius, but of enhancing their own prestige as well as that of insects. The means consisted in harping on their exquisite structure and beauty as proofs of the ingenuity, power and goodness of the Creator. Throughout the seventeenth, eighteenth and first half of the nineteenth century, the writings of entomologists, therefore, read like sermons. How far this method of presentation may have been sincere and how far it was merely an expedient, it is now impossible to ascertain. Much of the writing has the superficial air of the conventional religiosity which the clergy are forever condemned to accept at its face value as the price of their dogmatic insistence on a mystical orientation towards reality. The entomologists of the time, being unable to prove that man was made to consider gnats, since they could point to no spectacular triumphs like the modern sanitary control of tropical countries, had no other means of securing an open field for the exercise of their investigative curiosity. It will be noticed that the eminent naturalist, John Ray, did not dwell on Lady Glanville's activities as an entomologist, but "fixed" the judge and jury by calling attention to her "laudable inquiry into the wonderful works of the Creation." Of course, many country clergymen with abundant leisure have indulged in the study of insects during the past three centuries, and being both theologians and entomologists were doubly inclined to record their appreciation of their Diety's tender solicitude for the Insecta—now estimated at four to five million species![8] The same device still succeeds in Jesuit colleges, where if a professor allows his *concupiscentia oculorum* to tempt him to investigate some queer group of insects he can slide his manuscript past the censor by providing it with a mendacious scholastic motto, like "*nulla umquam inter fidem et rationem vera dissentio esse potest*" and appending a few exalted paragraphs on his personal Diety's concern with the particular species under

---

[8] This estimate is cited from Karl Holdhaus, who opens his article on the geographical distribution of insects in Schröder's "Handbuch der Entomologie," 2, 1927, p. 592, with the following paragraph: "The number of described species of insects has now risen to 500,000, and yet no limit to their number is anywhere discernible. It is not even possible to reach any conclusion from the number of described to the number of actually existing species. Within the tropics only those insect families that contain many large and showy forms have been investigated in their main features, the microfauna of extensive tropical areas being very imperfectly known. Whymper vividly describes how one day in Ecuador, on a hill near Quito, he knocked the insects from the low vegetation into his hat and thus secured 30 species; all 30 species proved to be new and there were two new genera among them. In the less investigated families of insects the number of existing species must be estimated as being at least ten times as great as that of the described species. The number occurring on the whole earth is therefore probably four to five millions, and perhaps considerably more."

discussion. The censor may be familiar with A. S. Packard's "Half Hours with Insects," but unless he has spent whole nights with them in a tropical jungle or a metropolitan lodging house he will be willing to stretch a point in favor of the Divine Beneficence and affix his *nihil obstat*.

Yet the Church, in its official capacity, seems never to have abandoned the belief that insects and other noxious animals may be possessed by evil spirits, a belief which probably long antedates the most ancient European civilizations and still prevails among savage and barbarous people. "For hundreds of years this idea of diabolical possession was steadily developed. It was believed that devils entered into animals, and animals were accordingly exorcised, tried, tortured, convicted and executed. The great St. Ambrose tells us that a priest, while saying mass, was troubled by the croaking of frogs in a neighboring marsh; that he exorcised them, and so stopped their noise. St. Bernard, as the monkish chroniclers tell us, mounting the pulpit to preach in his abbey, was interrupted by a cloud of flies; straightway the saint uttered the sacred formula of excommunication, when the flies fell dead upon the pavement in heaps, and were cast out with shovels! A formula of exorcism attributed to a saint of the ninth century, which remained in use down to a recent period, especially declares insects injurious to crops to be possessed of evil spirits, and names among the animals to be excommunicated or exorcised, mice, moles and serpents. The use of exorcism against caterpillars and grasshoppers was also common. In the thirteenth century a Bishop of Lausanne, finding that the eels in Lake Leman troubled the fishermen, attempted to remove the difficulty by exorcism, and two centuries later one of his successors excommunicated all the May-bugs in the diocese. As late as 1731 there appears an entry on the Municipal Register of Thonon as follows: '*Resolved*, That this town join with other parishes of this province in obtaining from Rome an excommunication against insects, and that it will contribute *pro rata* to the expenses of the same.' Did anyone venture to deny that animals could be possessed by Satan, he was at once silenced by reference to the entrance of Satan into the serpent in the Garden of Eden, and to the casting of devils into swine by the Founder of Christianity himself."[9] In certain parts of Canada crop-pests are still exorcised by the Church, and I am informed that there is a very mysterious specialization among the parish priests, some being most successful in suppressing cut-worms while others are more deadly to potato-beetles. Quite recently the priests have hit upon an ingenious device. They carefully consult the bulletins and calendars of the government entomological bureaux and set the dates of exorcism just before the annual dates of pupation of the insects. This combination of hocus-pocus and up-to-date science is as impressive as

[9] A. D. White, "A History of the Warfare of Science with Theology in Christendom," 1910, Vol. II, p. 113.

it is efficacious, because the pests are sure to vanish with amazing and edifying promptitude immediately after their excommunication.

Notwithstanding all the investigation and whitewashing of the "Mediæval mind" by certain recent historians, we may still doubt the sanity of some of the great scholastics and theologians who, like Duns Scotus Erigena, assert that "to admire nature is a sin comparable with adultery." Even the saints occasionally found it advisable to consider the gnats, albeit those of supernatural dimensions and biting powers. Thus it is recorded that St. James, Bishop of Edessa, in defending Nisibis from the attack of the Persians, had to call up an army of mosquitoes to sting the trunks of the elephants and drive them away in confusion! [10] But opinions like those of Duns Scotus, Malebranche and Jansenius are revealed in all their naked ineptitude when we consider the benefits we owe to their utter rejection in the modern world. I have seen no more concise statement of these benefits than the following by J. A. Thomson,[11] though its last sentence might have been made even more emphatic without departing from the truth: "A few years ago zoologists were laughed at who solemnly counted the hairs on the backs of flies and quarreled over the specific distinctions between one gnat and another. And could there be for able-bodied men a waste of time more scandalous than cutting sections of the entrails of ticks? Yet it has been this sort of knowledge of flies and gnats and ticks that has made it possible to open up Africa and complete the Panama Canal."

The preceding discussion may seem to have led us far from the 'foibles' with which we started, but it has really guided us to what might be called one of the grand foibles, or peculiar weaknesses of our species. At the same time it must have become clear that curiosity, in the sense in which I have been using the word, is not a foible, but, as Anatole France says, "perhaps the great virtue of man." It is surely essential to investigation and therefore to the development of scientific knowledge, whereas our grand foible turns out to be a very different activity and one of which the preceding pages contain several examples, namely, the facile and hasty reference of natural phenomena to mystical bogus entities, or to emotionally associated and whimsically selected "causes." We are coming to see that there are two very different types of thinking, one characteristic of a small portion of mankind, the scientists, when functioning as such, and one which is the only type indulged in by most humans and also by the scientists when they are off duty.[12] The former is a disciplined type of thinking, objective in that it

[10] J. Rhys, "Shaken Creeds: The Resurrection Doctrines," London, Watts & Co., 1924, p. 227.

[11] "The Control of Life," N. Y., Henry Holt, 1921, p. 14.

[12] "Even in the minds of trained scientists," as Bernard says ("Instinct, a Study in Social Psychology," N. Y., Henry Holt, 1924, p. 14), "especially outside of their immediate specialties, judgments and attitudes are determined largely with little or no rational analysis, and primarily on the basis of preconception or subconscious mental organization and suggestion."

submits reality to controlled observation and experiment, as impersonal and unemotional as possible and therefore fraught with renunciation. The latter called by Bleuler[13] autistic and undisciplined thinking, is described as follows: "It has its own peculiar laws which differ from those of realistic logic, and does not seek truth but wish-fulfilment. Chance associations of ideas, vague analogies and above all emotional needs largely supplant the associations of experience which enter into strict, realistic, logical thinking, and whenever such associations are utilized, it is in an inadequate and careless manner." Other writers have called this 'emotional,' 'irrational' or 'wishful thinking,' or 'rationalization,' and recently Henshaw Ward has dubbed it 'thobbing.'[14] Some psychoanalysts prefer to describe it as thinking in the service of the pleasure principle (*Lustprinzip*), as opposed to the disciplined thinking which is dominated by the reality principle (*Realitätsprinzip*). Savages, children, theologians and many philosophers are inveterately addicted to autistic thinking and when, as commonly happens, this is compounded with the grand foible of verbalism, we get those astonishing aberrations of mythomania, superstition and metaphysics from which the race has been suffering ever since it began to think. Autistic thinking is essentially magical and fails utterly to attain its aim, which is a control, without a knowledge, of phenomena; scientific thinking, however, has shown that it can secure both a knowledge and a control of phenomena and that the latter cannot be secured without the former. In other words, experience has demonstrated that the explanations reached as a result of emotional thinking—i.e., thinking hobbled by fear, desire, aspiration, exaltation, etc.—are intellectually and in practice nugatory, sterile, misleading or even harmful, while those resulting from scientific thinking, though it has been seriously tried for only three centuries and by a very small fragment of the race, has proved to be fruitful beyond our wildest expectations. To quote Richards (*loco citato*), "Emotional satisfaction gained at the cost of intellectual bondage is unstable. When it does not induce a partial stupor it breaks down." In an interesting recent volume, Essertier[15] has therefore called the explanations due to autistic thinking 'inferior,' in order to distinguish them from the 'superior' explanations of science. This, of course, contradicts the theologians and philosophers, who always take it for granted that the various mystical, spiritual, primal, absolute, divine, psychical, virtual, essential, noumenal, metaphysical, vitalistic, entelechial, etc., etc., "causal" agencies which they excogitate

[13] E. Bleuler, "Autistisches Denken." Jahrb. psychoanalyt. u. psychopatholog. Forschungen 4, 1912, and "Das autistischundisciplinierte Denken in der Medizin und seine Ueberwindung," 4. Aufl. Berlin, J. Springer, 1927.

[14] "Thobbing, A Seat at the Circus of the Intellect," Bobbs-Merrill Co., 1926.

[15] "Les Formes Inférieures de l'Explication," Paris, F. Alcan, 1927.

have a very superior explanatory value; in which opinion they are merely deluded by the 'magical' properties and emotional resonance of the word-symbols they are constantly employing.[16]

It would be interesting to consider our varying attitudes towards the universal foible of autistic thinking and the overt behavior in which it finds expression, were the task less discouraging in its magnitude. Wishful thinking on matters of no vital importance to the community or the individual may excite our mirth or sense of the pathetic, as when a priest excommunicates the potato-beetles of his parish, but such excessive departures from reality as witchcraft, which during its long and ghastly course is said to have destroyed no less than ten million lives, and the religious persecutions and nationalisms, which have destroyed many more millions, certainly represent no common foible but belong to the domains of insanity and crime. It was, in fact, the study of the hypertrophied autistic thinking of the insane and the criminal which first led psychoanalysts to detect the feebler, normal forms of the process in all of us. One might, in fact, maintain that human life would be impossible without a certain amount of emotional or wishful thinking and there is no likelihood that education will ever eradicate it. And "even if it were possible," as Martin[17] says, "to convert the public to belief in the mechanistic universe of science, the conversion would be external and formal; the old mysteries and sanctities, and refuges, and taboos, and unctions, and dreads, and hopes, and consolations, would persist somehow, and we should find that a pseudo-scientific jargon would soon come into existence as an instrument for expressing and justifying the old religious attitudes. In fact, something like this commonly happens even now. It may be seen in attempts to reconcile science and faith; again it is not infrequent among those new and so-called up-to-date religious movements and cults which thrive among the half-educated." The lapse of scientific into more primitive autistic thinking as described by Martin may be clearly witnessed even during the ontogenies of some of our aging physicists and biologists. After a youth and manhood devoted to splendid contribution to their respective sciences, these individuals "regress," as the psychoanalysts would say, to the autistic thinking of their childhood and naively spend their old age manufacturing argumentative ammunition for the Fundamentalists, spiritualists, anti-evolutionists and other confusionists with whom our modern world is so richly provided.

---

[16] For a lucid analysis of these very significant peculiarities of words see C. K. Ogden and I. A. Richards, "The Meaning of Meaning," Harcourt, Brace & Co., 1923.

[17] "The Mystery of Religion, a Study in Social Psychology," Harper Bros., 1924.

THE PHYSIOGNOMY OF INSECTS

FROM THE *Quarterly Review of Biology*, VOL. II, NO. I, 1927

Ante omnia scire convenit naturam corporis, quia alii graciles, alii obesi sunt; alii calidi, alii frigidiores; alii humidi, alii sicciores; alios adstricta, alios resoluta alvus exercet. Raro quisquam non aliquam partem corporis imbecillam habet.

CELSUS, LIB. I, CAP. III

I am convinced that if our souls were visible to the eye, we should see clearly that, strange as it may seem, every individual of the human species corresponds to one of the species in the animal creation; and we could easily recognize what has hardly been suspected by thought, that, from the oyster to the eagle, from the pig to the tiger, all the animals are in man, and each of them is in some particular man—sometimes even, several at once.

VICTOR HUGO, "LES MISERABLES"

An entomologist no less interested in his fellow men than in the insects may with increasing years of observation find increasing resemblance between the two—some insects seeming almost human and some humans behaving very much like insects. This may be due in part to the fact—if indeed it be a fact—that the entomologist may come to resemble the objects with which he is so constantly occupied. If we can trust the statements of some observers, he may even take on some of the physical peculiarities of the group in which he specializes. We have all known entomologists who looked like grasshoppers, cockroaches, bumble-bees or Histerid beetles. The confusion is increased by the fact—and this has not escaped the cartoonists—that there is a certain resemblance between the human and insect body, with its division into head, thorax, and abdomen. And though the insect body has too many appendages and certainly too many wings to suit any human being this side of Paradise, nevertheless the face, head, and eyes of some Orthoptera, Coleoptera, Hymenoptera, and Diptera are very suggestive of certain physiognomies which we daily encounter in the streets and trolley-cars of our great cities. In some ancient entomological works, purporting to be of a serious character, for example in Johnston's *Theatrum Universale Omnium Animalium* (1718), the heads of insects are often drawn with the obvious intention of accentuating their resemblance to human countenances.

HUMAN TYPES

Those who devote all their attention to our own highly polymorphic species, which Linnæus, I suspect, somewhat sarcastically called *Homo sapiens*, have repeatedly endeavored to group its various individuals in categories according to their temperaments and physical peculiarities. As a result, a number of human types have been distinguished and named by a long series of investigators, most of whom agree that the pure types are best studied among the young adult males of the species. Two of the types, which have been recently called the "asthenic"[1] and the "pycnic" by Kretschmer (1922),

[1] In his "Rasse und Körperbau" (Berlin, J. Springer, 1927) Weidenreich gives a most inter-

stand out conspicuously and will be recognized at once by the following diagnoses:

The asthenic is pale, scrawny, long-limbed, with narrow head and face ("hatchet-faced"), long, narrow, straight nose, small, often receding chin, narrow chest and abdomen, deficient development of fat and musculature, reduced pilosity on the body but often with abundant cranial thatch, abstemious, dyspeptic, with a tendency to tuberculosis, and when insane, schizophrenic, *i.e.*, prone to fixed ideas, ideas of persecution, etc. This type is active, intense, intellectual, self-centered (introverted), often deficient in a sense of humor, fond of reforming, dogmatic or fanatical, and not infrequently detestable when claiming a too intimate knowledge of the Almighty's plans for making the world safe for democracy. The pycnic—so called, not because he likes picnics, though no other type is so fond of them—but from the Greek word *πυκνός*, meaning compact or thickset—is rubicund, rotund, large-bodied, short-limbed, broad through the chest, but broader through the abdomen, with round or pentagonal face, pug or thick nose, moderately pilose, fond of eating and drinking, eupeptic, with a tendency to apoplexy and arteriosclerosis; on the mental side cyclothymic, *i.e.*, predisposed to the recurring, circular or manic-depressive forms of insanity, such as melancholia; extroverted, socially easy-going, tolerant in morals and religion and often very lovable because claiming no inside information in regard to the Almighty's designs.

These two types in their purity are sufficiently frequent among our American population. Kretschmer seems to have found the pycnics very common among the Swabians, who are generally characterized by the Germans as "gemütlich" or "gutmütig." The popular distrust of the asthenic and fondness for the pycnic is indicated by the fact that Satan, or Mephistopheles is usually represented as an asthenic while the favorite gods and saints of China and Japan are depicted as fat pycnics. When the belief in Satan was more vigorous than it is at present, he and his demons were often represented as belonging to the athletic type. [See the pictures from the twelfth to the sixteenth century and especially the frontispiece from Didron's *Christian Iconography* in Bonner (1913).] Why the people should have chosen a symbol like Uncle Sam to represent the United States and one like John Bull to represent England was not altogether clear till the passage of the Volstead Act. Among historical figures the reader will recall Cassius (as depicted by Shakespeare), Dante, Savonarola, Torquemada and

---

esting discussion of Kretschmer's types among the various races of mankind and adduces excellent reasons for preferring the terms 'leptosome' and 'eurysome' to 'asthenic' and 'pycnic.' Had the volume appeared before this article was written I should have used Weidenreich's terms. For an excellent account of the physical types of man see also E. Miller, "Types of Mind and Body," New York, W. W. Norton & Co., 1927.

John Calvin as asthenics and Falstaff (as conceived by Shakespeare), Martin Luther and ex-President Taft as pycnics. In fiction Don Quixote and Sancho Panza are good examples of the two types. Bud Fisher's creation of Mutt and Jeff may also be cited in this connection.

The great mass of human individuals, however, may be regarded as blends or mosaics of the two types in varying proportions. Even during the lifetime of the same individual, the asthenic may predominate at one time, the pycnic at another. Often the young are asthenic and become pycnic with advancing years, and we have all seen examples of the reverse transformation of pycnic youngsters into asthenic oldsters. Undoubtedly the endocrine glands, and especially the thyroid, pituitary and interstitial glands, are concerned in the production of both the extreme and the intermediate types.

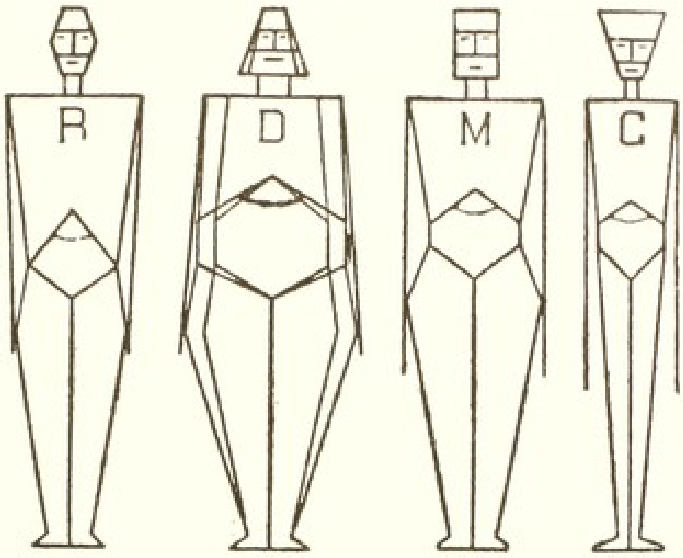

Figure 1. The Four Human Types of Claude Sigaud, Schematized by Pierre Robin.

Among the latter Kretschmer recognizes several categories. One of these is the "athletic," which I need not describe as the reader is familiar with its physical and mental peculiarities from the football and baseball field, the gymnasium, vaudeville stage and movies. Kretschmer further distinguishes "dysplastic" types, which show more or less pathological defect- or excess-development (hypoplastic or hyperplastic development) in certain characters, but I shall pass over these distinctions and for the sake of brevity and clarity call all the intermediates athletic.

The same or similar types have been recognized by other investigators and have been reviewed by Bauer (1924). The asthenic, athletic and pycnic types of Kretschmer evidently correspond to the phthisic, athletic and plethoric habitus of de Giovanni and to Beneke's microsomatic, microplastic, microskelic, longilineus, or longitypus and megalosomatic, euryplastic, brachyskelic, brevilineus, or brachytypus, with the intermediate normosplanchnic, normosomatic, mesoplastic, normolineus, normotypus. The two extreme types correspond to Viola's microsplanchnic, or phthisic habitus and megalosplanchnic, or apoplectic habitus, to Bryant's carnivorous and vegetarian types, Bean's hypermorph and mesomorph types, Stockard's linear and lateral types, etc. Obviously the pycnic type is that of the human infant. According to Stockard (1923) "the linear type is the faster growing, high metabolizing, thin but not necessarily tall group, while the lateral type is slower in maturing and is stocky and rounder in form."

The French school, following Sigaud and including his pupils Chaillon, MacAuliffe and other contributors to the very interesting *Bulletin de la Société d'Etude des Formes Humaines*, recognize four human types, the respiratory, digestive, muscular and cerebral (fig. 1). The digestive corresponds to the pycnic, the cerebral to the asthenic, the muscular and respiratory to

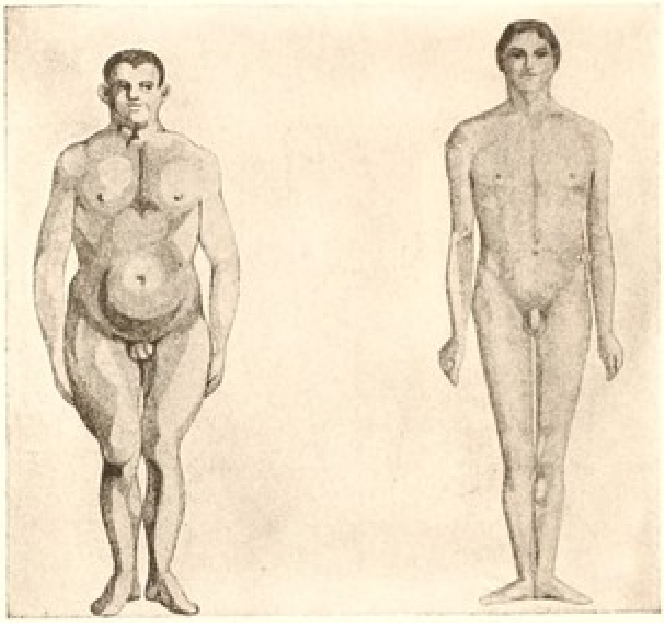

Figure 2. Idealized "Round" and "Flat" Colloidal Human Types, According to MacAuliffe. (Taken from A. Thooris: "La vie par le Stade.")

the athletic type of Kretschmer. In a recent paper MacAuliffe (1925) distinguishes a "round" and a "flat" type (fig. 2), which correspond to the pycnic and asthenic respectively, and refers their differences to differences in the colloidal state of their tissues, the former consisting of strongly, the latter of feebly hydrophilous gels. The cells of the bibulous pycnic have great osmotic powers, those of the asthenics a feeble surface tension. "The flat type functions more economically than the round. It is also probable that the electric polarization of the cellular surfaces is higher in this latter human category."

Bauer studied the distribution of Sigaud's four categories among 2000 male Viennese and found the following proportions of pure type: respiratory 18 per cent, muscular 9 per cent, cerebral 3.9 per cent, digestive 3.8 per cent. Taking the mixed forms in which one of the types predominates, he found: respiratory 43.1 per cent, muscular 23.8 per cent, cerebral 18 per cent, digestive 6.6 per cent. The remaining 8.5 per cent could not be included in any one of the categories. Zweig, one of Bauer's students, studying the same material, disproved Sigaud's view that the types do not change with age, although it was clear that each is fixed in youth in its general characters. The digestive type increases with age. Sigaud's schema is not easily applicable to females. Bauer divides them according to the distribution of fat on their bodies into (1) "Reithosentypus" (with fat on hips); (2) fat on arms, breast and neck, but with thin legs; (3) fat on thighs and legs, but poorly developed on trunk; (4) fat on breasts and gluteal region (steatopygous type).

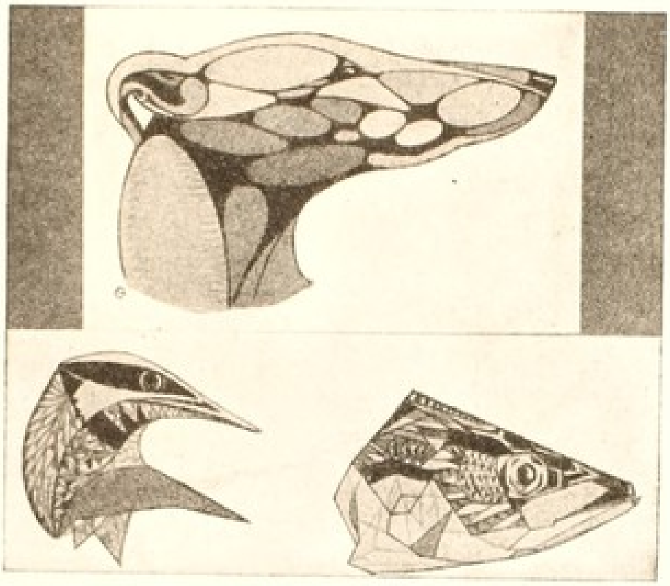

Figure 3. Heads of Greyhound, Bittern and Pike to Illustrate the "Flat" Colloidal Type of MacAuliffe. (Taken from A. Thooris: "La vie par le Stade.")

ANALOGUES OF HUMAN TYPES AMONG ANIMALS

Now it is interesting to note that all the main types exhibited by the single species *Homo sapiens* have their analogues in most groups of animals and even among the plants. As examples of the asthenics and pycnics I mention only the following: among our domestic animals the greyhound and King Charles spaniel (figs. 3 and 4) and among other mammals the giraffe and armadillo, among the birds the herons and finches (figs. 3 and 4), among reptiles the tree-snakes and box-tortoises, among the amphibians the coecilians and toads, among fishes the eels and box-fishes; among crustaceans such forms as Caprella and the crabs; among Echinoderms the brittle-stars and the sea-urchins; among myriopods Geophilus and Glomeris and among plants the vines and the melon-cacti. Between the extremes in each case we find the great majority of species, the athletes, which exhibit a more nearly average development of their organs.

Of course, the insects, which are represented on our planet by such a bewildering number and variety of highly specialized species, may be expected to show the asthenic and pycnic types in a very pronounced form.

There are, in fact, in all the principal orders, whole genera or even families of the two types. For purposes of illustration I have brought together a series of these insect Mutts and Jeffs in the accompanying figures (figs. 5 and 6). As the reader is familiar with them or with similar forms I shall not stop to designate the various tenuous walking-sticks, grasshoppers,

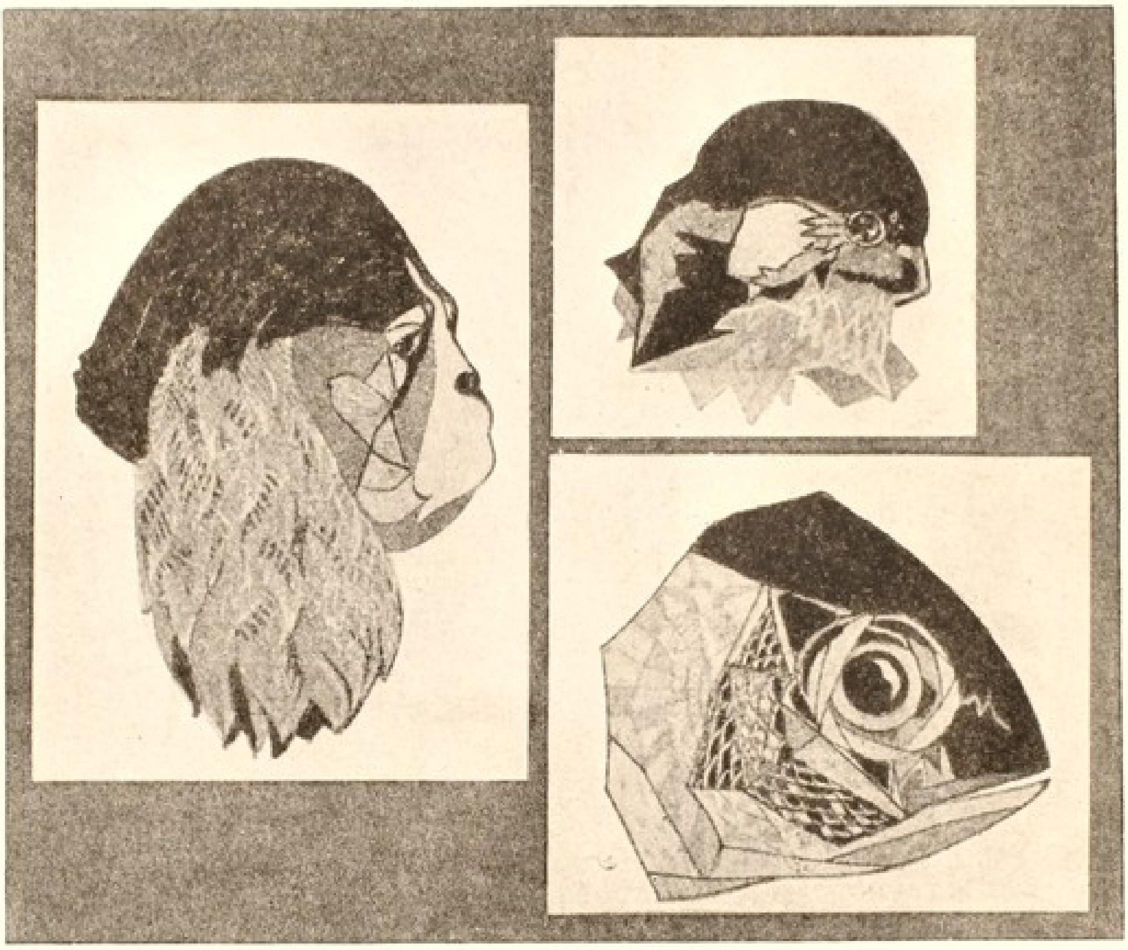

Figure 4. Heads of King Charles Spaniel, Finch, and Bream, to Illustrate the "Round" Colloidal Type of MacAuliffe. (Taken from A. Thooris: "La vie par le Stade.")

ants, dragon-flies, crane-flies, mosquitoes, ant-lions, Panorpids, etc., nor the many chunky bugs, beetles, moths, etc. The reader will notice that the latter insects, like some human pycnics, have large rotund bodies and rather short, slender legs, and will recall certain cases of both types occurring in succession in the same species, as, *e. g.*, in the ant-lion, which has a pycnic larva and an asthenic adult, and the flea which has an asthenic larva and a rather pycnic adult. Among the insects, too, the great majority of species are intermediate, and if I designate this group as "athletic" the economic entomologists, who spend their lives ardently and often unsuccessfully wrestling with them, will certainly not object.

The general impression produced by the insect asthenics and pycnics is that of mutations which have somehow managed to survive among the great mass of athletic species, but it is doubtful whether they have arisen as such saltatory variations. The asthenics are more archaic or at least more

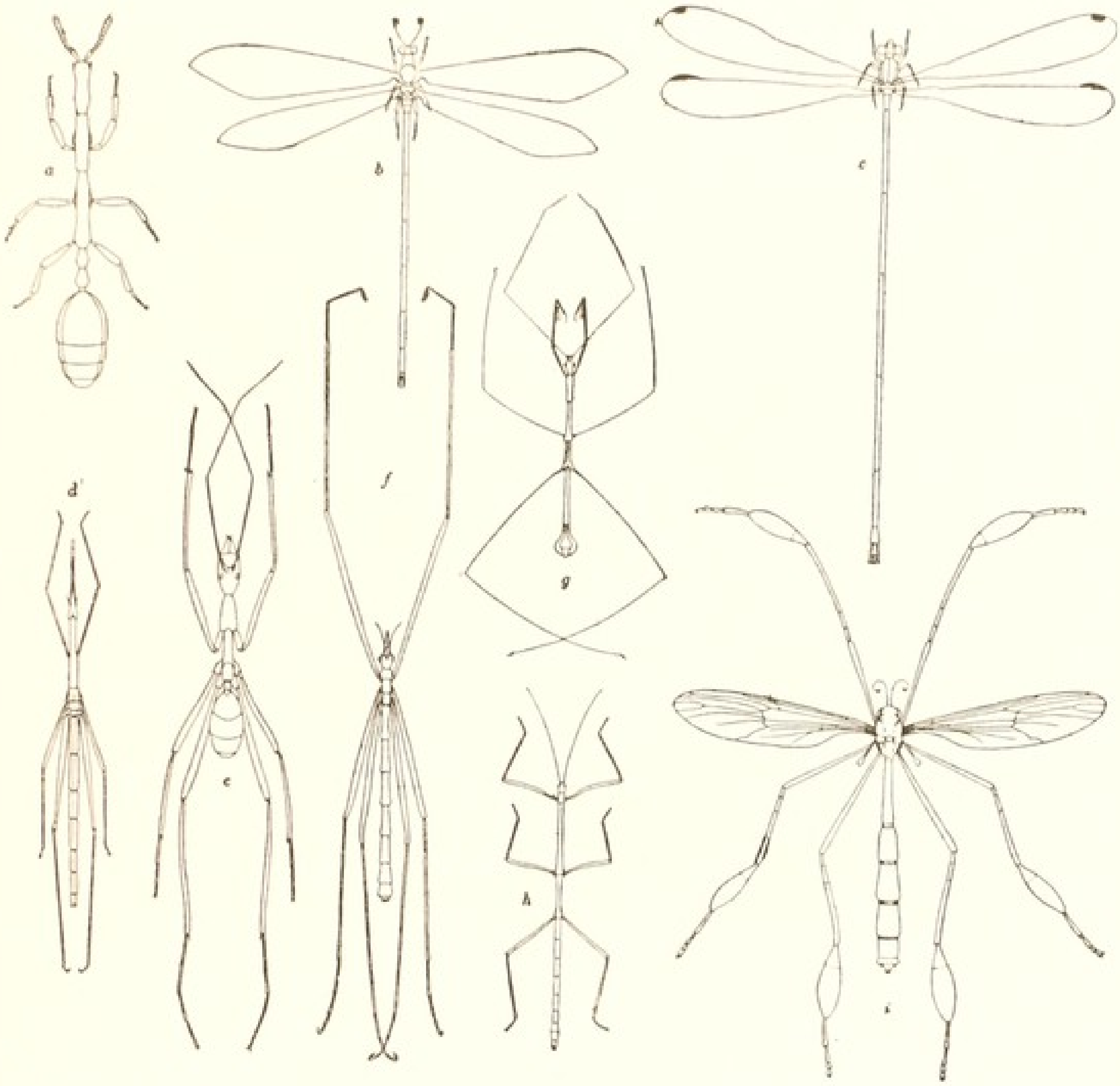

Figure 5. Examples of Asthenic Insects Belonging to Various Orders. a, *Staphylinid Myrmecophile (Coleopteron);* b, *Ant-Lion (Neuropteron);* c, *Dragon-fly (Odonate);* d, *Grasshopper (Orthopteron);* e, *Ant (Hymenopteron);* f, *Panorpid (Mecopteron);* g, *Bug (Heteropteron);* h, *Phasmid (Orthopteron);* i, *Crane-fly (Dipteron).*

frequent in ancient and primitive orders or suborders, and, with the exception of the mosquitoes and Chironomids, seem often to belong to rather rare, recessive or evanescent species. The differences between the two types cannot be due to the quality of the food, because there are predatory and phytophagous species in both groups. That they differ in metabolism is probable. The pycnics, like their human analogues, are certainly great feeders compared with the asthenics—compare, *e. g.*, the appetite of a dung-beetle with that of a walking-stick insect. And structurally there is a great difference in musculature, the muscles of the asthenics being long and slender

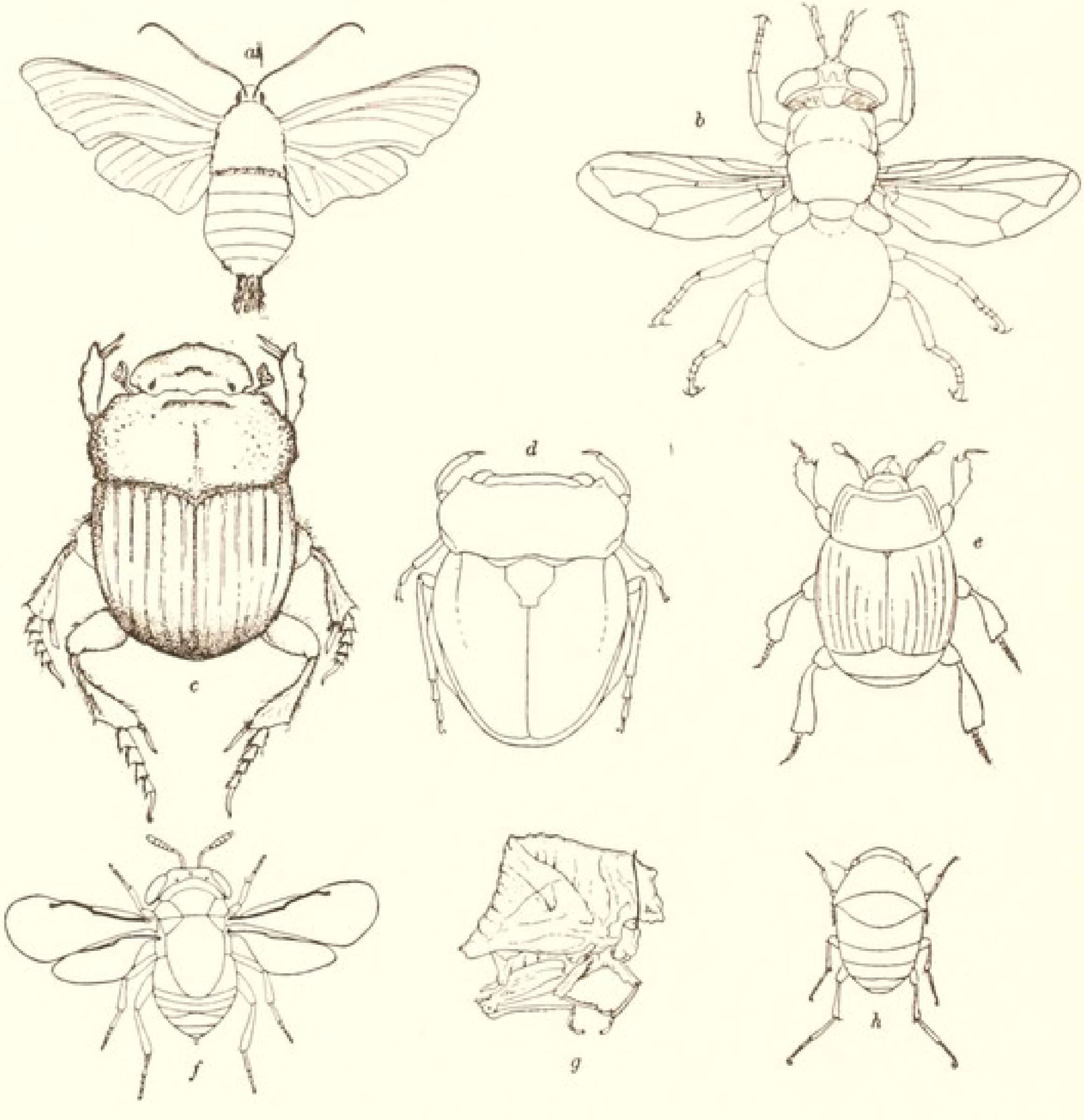

Figure 6. Example of Pycnic Insects Belonging to Various Orders; a, *Sphingid Moth (Lepidopteron);* b, *Syrphid Fly (Dipteron);* c, *Lamellicorn Beetle (Coleopteron);* d, *Bug (Heteropteron);* e, *Histerid Beetle (Coleopteron);* f, *Chalcidid Fly (Hymenopteron);* g, *Grasshopper (Orthopteron);* h, *Phorid Fly (Dipteron).*

while those of the pycnics are short and voluminous. This matter of the musculature in these and other insects—a matter as much neglected by recent insect morphologists as it was emphasized by those of former times—I should like to place in the center of the following discussion, because, as we shall see, it is the musculature that mainly determines the physiognomy of insects.

PRINCIPLES OF INSECT PHYSIOGNOMY

The reader is familiar with the fact that in insects, as in other Arthropods, the musculature is inside the skeleton to which it is attached and that the shape and size of the various elements of the skeleton depend on the volume and arrangement of the muscles. Here the skeleton and integument are one, whereas in vertebrates the muscles which move the skeletal elements are external to them and immediately beneath the very flexible integument. Hence in vertebrates that are not too scaly, feathery or hairy the play of the musculature is visible from the outside, whereas in insects we are presented with a rigid envelope capable of movement only at well-defined, preformed articulations. Hence, also, the very limited and mechanical expression of the emotions in insects as compared with the wonderful range and subtlety of expression in the human face and body, a range and subtlety so extraordinary that from our earliest years it constitutes a means of inter-communication among us second only and very often superior to articulate speech. Moreover, although the powers of facial and bodily expression of the human infant are very limited compared with those of the adult, as we should see if we could follow the development of some great actor from his birth to his highest triumphs on the stage, the insect's expression throughout each of its instars is extremely uniform and circumscribed. Of course, if we could look beneath the rigid chitinous integument of such insect busybodies as ants, bees or solitary wasps we should probably witness an astonishing wealth of expression in the finer play of the smaller muscles, especially of those belonging to the viscera.

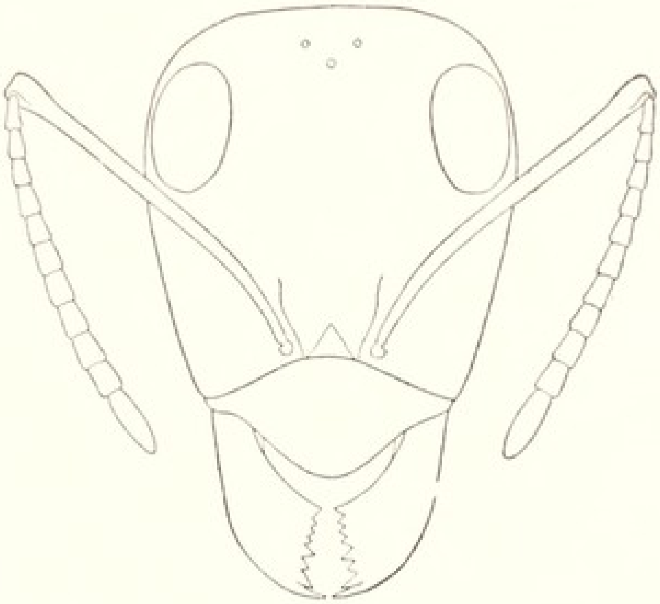

Figure 7. Head of Worker of the Common Circumpolar Formica fusca *L. from Above, Showing Eyes, Ocelli, Antennæ, Clypeus and Mandibles.*

To trace the correlations between the development of the various muscles and that of the skeletal elements throughout the insect body would prove to be an undertaking as formidable as it would be wearisome. I shall therefore discuss at length only the most interesting region, the head, and confine myself still further very largely to a consideration of the ants. This will be best for two reasons: first, because I have been peering for nearly thirty years into the countenances of so many thousands of these insects that I have acquired some familiarity with their idiosyncrasies, and second, because they are unusually favorable for physiognomic studies, owing to the extraordinary morphological and functional differences between the sexes and castes of the same species. The reader will have no difficulty in testing the

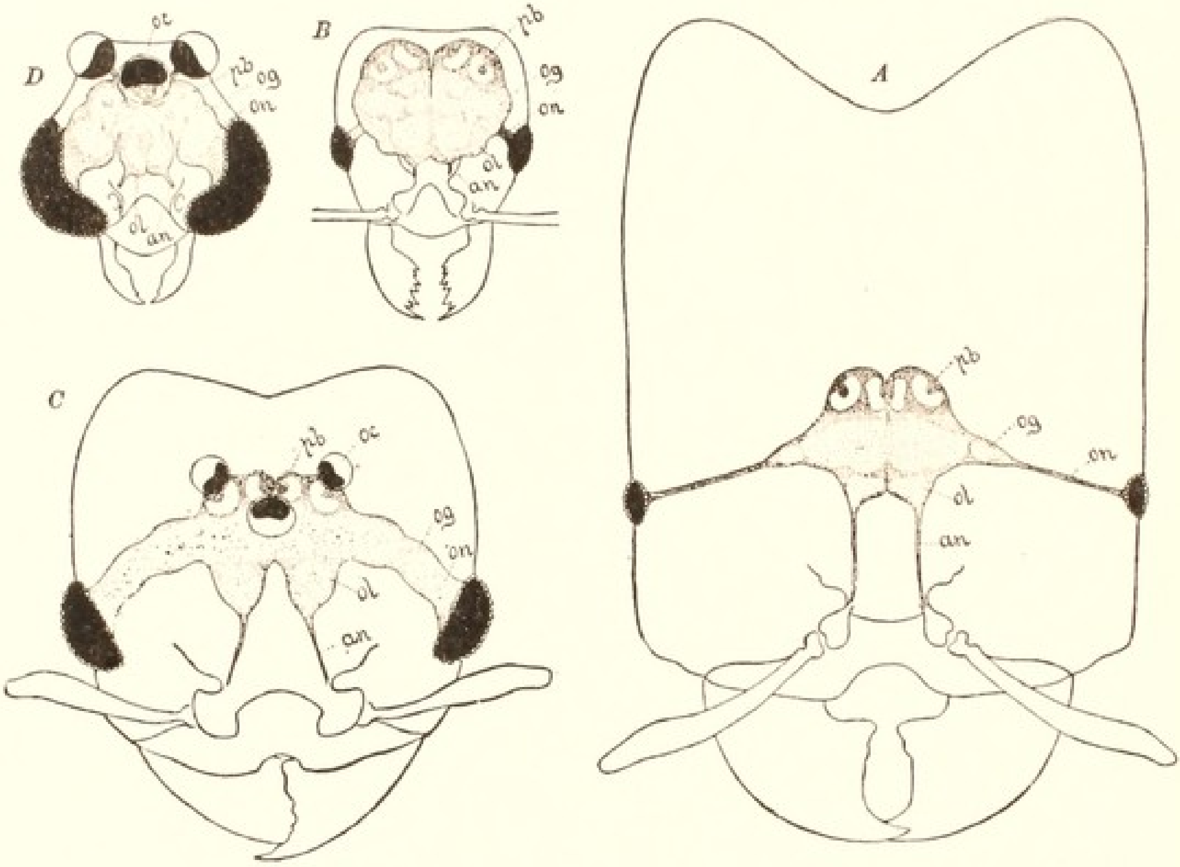

Figure 8. Heads and Brains of the Four Castes of Pheidole instabilis *Emery from Texas, Drawn to the Same Scale.* A, *soldier;* B, *Worker;* C, *Female;* D, *Male.*

general validity of my conclusions by extending them to the insects of other families with which he may be acquainted.

The following are the main points which I should like to establish:

1. The form of the head and face is very largely determined by the size and shape of the flexor muscles of the mandibles and in turn the functional or adaptive peculiarities of these organs are closely correlated with the character of their flexor muscles.

2. In certain species, at least, the development of the antennal muscles seems to be correlated with the convexity of the front, or forehead.

3. The antennæ are also responsible for the development of certain adaptive structures in the configuration of the head, such as the scrobes.

4. The eyes are of little importance in determining the shape of the head

in the workers and females of most ants, but these organs, when large, as in male ants and especially in certain other insects with haustellate mouthparts (Diptera, Lepidoptera, Homoptera, Heteroptera, etc.) have considerable physiognomic value.

5. Certain head-forms are very largely determined by direct adaptation to the cylindrical cavities in the hard plant tissues or soil inhabited by the insects.

Let us begin with the head of our common *Formica fusca*, an ant of the true Nordic type, the *beau idéal* of the family, with chaste, well-balanced features and beautifully rounded forehead (fig. 7). To a slightly stretched imagination this head will not appear so very inhuman, especially if we let the clypeus represent the nose. The mouth is rather large, to be sure, and its upper lip is hidden away under the clypeus. The antennæ and mandibles, however, are decidedly inhuman. But if we imagine our hands and arms split into two pairs of appendages, and one pair thin, mobile, covered with exquisite, intermingled tactile and olfactory organs and inserted just above the base of our nose, and the other, shortened till only the rigid hands remain and inserted in the corners of our mouth, we should be equipped very much like an ant. And, no doubt, we should find the whole arrangement delightfully convenient. We could do very rough work with our inferior, or oral pair of hands without in the least impairing our sense of touch in the superior, or nasal pair, and the intimate combination of touch and smell in this pair would enable us to gain a very satisfactory knowledge of our immediate environment. We should move through the world like ants, continually topochemorecepting the various objects in our path, and we should probably speak of strawberries as soft, rounded-conical odors, of

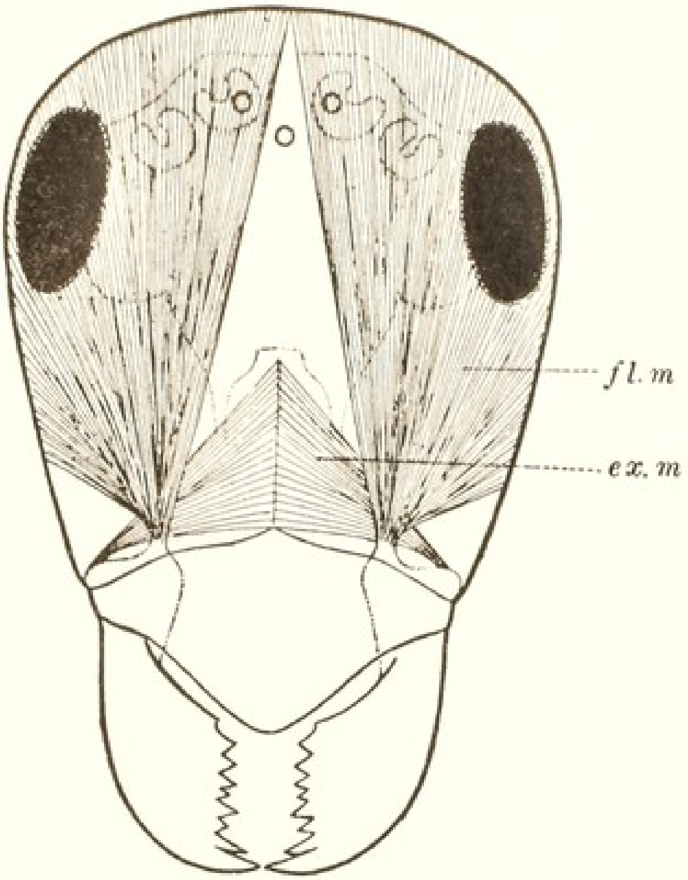

Figure 9. Head of Worker Formica fusca L.; fl. m., *Flexor Muscle of Mandible;* ex. m., *Extensor Muscle of Same.*

cigarettes as harder, cylindrical odors, table-tops as very hard, smooth, oblong odors of a certain quality, etc.

Judging by superficial appearances we might be tempted to extend the old phrenology of Gall and Spurzheim to the ant and regard the size and shape of its hard cranium as indications of the size and shape of its brain, but when we open its head we see at once that the brain is separated by a considerable space from the cranial wall and that the greater part of the

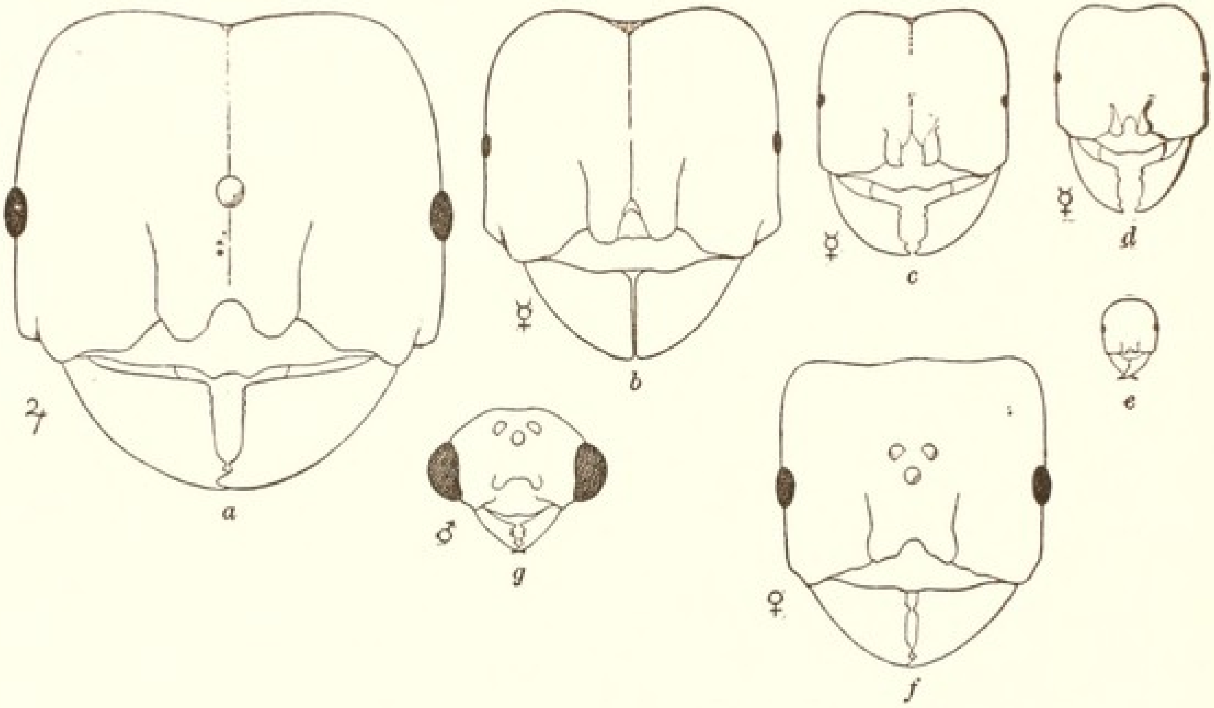

Figure 10. Heads of the Various Castes of an East Indian Harvesting Ant, Pheidologeton diversus *Jerdon.* a, *Soldier;* b *to* d, *Intermediate Forms between the Soldier and Worker Minima*, e; f, *Female;* g, *Male. Note Rounding of Occiput Correlated with Feeble Mandibular Development in the Male and Minima.*

cranial cavity is filled with muscular tissue. The brain varies greatly in different species and even in the different castes of the same species. Roughly speaking, the brain seems to vary inversely as the size of the individual ant. This is clearly seen in the heads of the four castes of a common Texan Pheidole (*Ph. instabilis*) (fig. 8). When the eyes are small or of moderate size, therefore, the head is an index to the muscular powers and not to the intelligence or sensory development of the insect.

CORRELATION OF HEAD SHAPE AND MUSCULATURE OF MANDIBLES

Returning to the head of *Formica fusca* (fig. 9) which has an unusually large brain, and removing the dorsal wall, we observe that on each side of the median line its contents consist very largely of a huge pyramidal muscle, which is attached proximally by a short, stout tendon to the inner corner of the base of mandible, while the gradually expanding fibres are attached distally to a very large area comprising much more than the posterior half of the cranial wall. In some ants this muscle, the contraction of which closes the mandible, really consists of two muscles, but as both have the same mandibular tendon and the same function, I shall treat them as a unit. It has been called the adductor, or flexor mandibulæ. The muscle which opens the mandible, the abductor, or extensor, is very much smaller. It is flattened

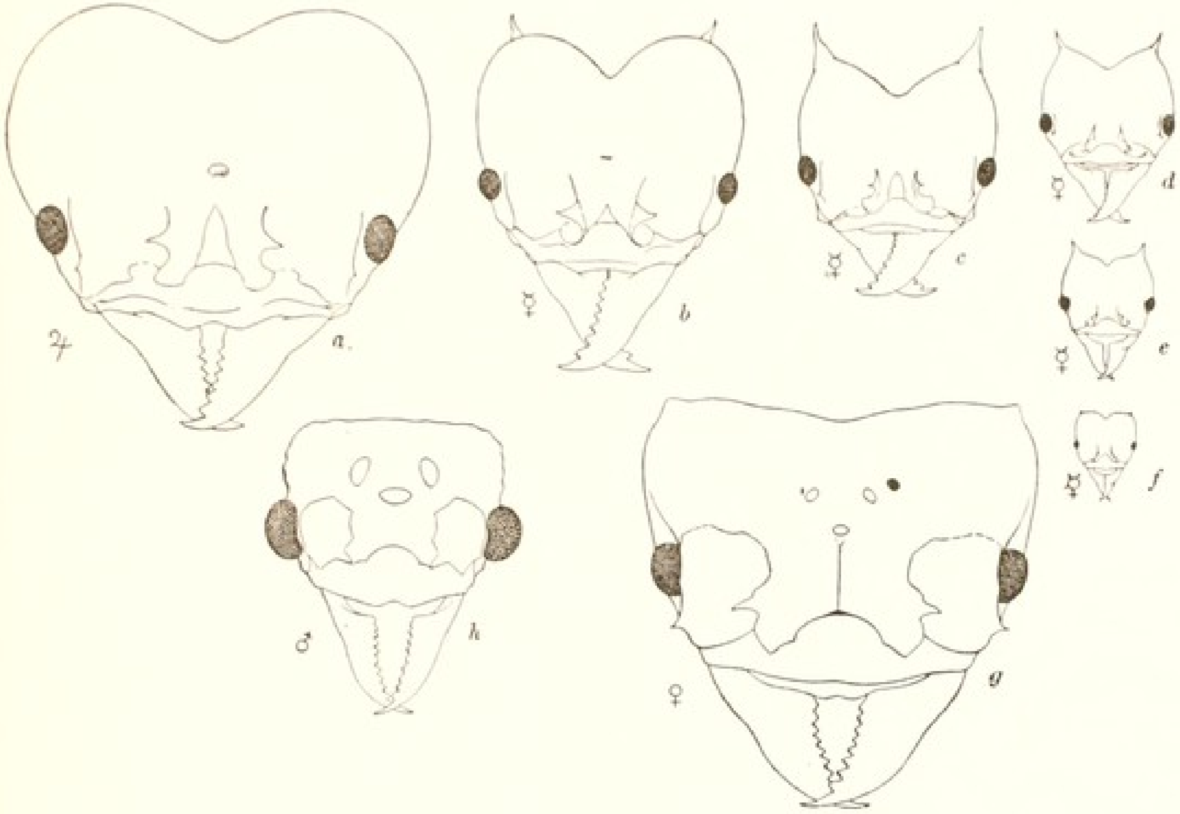

Figure 11. Heads of the Various Castes of a Large Leaf-Cutting Ant, Atta cephalotes *L. from the Neotropical Region.* a, *Soldier;* b *to* f, *Series of Workers from the Major to the Minima;* g, *Female;* h, *Male. The Strong Mandibles in All the Forms Are Correlated with Prominent Occipital Lobes or Angles.*

and fan-shaped, inserted by a short, stout tendon on the outer corner of the extreme base of the mandible and runs ventrally under the tendon of the flexor to spread out and become attached to a thin, chitinous plate, or apodeme, which rises in the middle line from the floor or ventral wall of the cranium, the gula.

The great differences in the volume of the mandibular flexors and extensors is, of course, correlated with differences in their functions. The extensors have merely to open the mandibles, but the flexors have to perform the much more arduous task of seizing, holding, biting, gnawing or crushing the prey or the wood or soil in which the ants' nests are made. We may, therefore, concentrate our attention on this pair of more important muscles, whose development in the various species and castes intimately depends on the structure of the mandibles, and since the mandibles differ greatly according to the habits of the ants it will be advisable to consider these appendages somewhat more closely. The typical mandible has a three-cornered blade, with a straight or more or less convex, entire outer border and two straight inner borders, one basal and toothless, the other apical and armed with teeth. A great many different types of mandibles may be recognized among the Formicidæ, but I will reduce them to nine: first, *biting* mandibles, of moderate size, with subequal internal borders and a moderate number of sharp teeth on the apical border (figs. 7, 9, 12); second, *gnawing* mandibles, which are short and stout, with a few broad, strong teeth (fig. 12*a*); third, *crushing* mandibles, which are thick and stout, very convex externally, with few or no teeth (fig. 8a, 10a–d); fourth, *cutting* or scissor-like mandibles which are broad, flat and rather thin, with sharp, toothed apical border (fig. 11); fifth, *grappling* mandibles, which are very long, slender, with long apical border, armed with a few or numerous, often unequal teeth (fig. 13–15); sixth, *clipping* mandibles, which are long, linear, straight or slightly curved, with a few sharp, abruptly incurved teeth at the apex, and the inner borders toothless or finely serrate (figs. 16 and 17); seventh, *piercing* mandibles, which are slender, sickle-shaped and pointed, without teeth or with minute vestiges of them along the inner border (fig. 18*e–h*); eighth, *vestigial* mandibles which are reduced and apparently useless organs, occurring only in the male sex (figs. 10g and 17*b*); ninth, *aberrant* mandibles, including a number of singular forms of still unknown function (figs. 19 and 20). Of

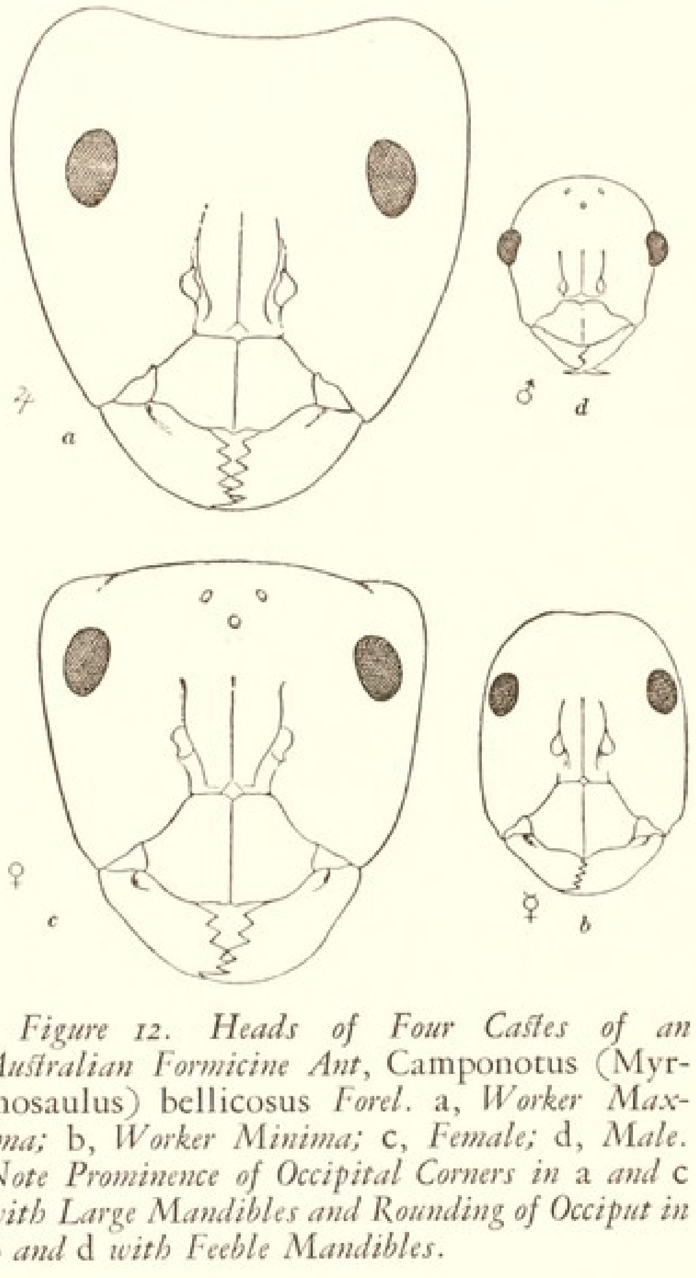

Figure 12. Heads of Four Castes of an Australian Formicine Ant, Camponotus (Myrmosaulus) bellicosus *Forel*. a, *Worker Maxima;* b, *Worker Minima;* c, *Female;* d, *Male. Note Prominence of Occipital Corners in* a *and* c *with Large Mandibles and Rounding of Occiput in* b *and* d *with Feeble Mandibles.*

these various types, the biting, gnawing, crushing and cutting mandibles are large and powerful; the grappling, piercing, clipping, vestigial and aberrant though sometimes of large size are rather weak and therefore furnished with less powerful flexor muscles.

We may now examine several examples which show very clearly the correlation between the size and development of the mandibles, their flexor musculature and the shape of the head, a correlation so intimate that an expert mathematician might be able to express it in definite formulæ. In figure 21 I have represented the various castes of the harvester, *Pheidole instabilis.* The large individual below (*g*) is the deälated fertile female, or queen; the small winged individual (*h*) is the male; the very large-headed individual (*a*) is the largest type of worker, or soldier, the very small individual (*f*) the worker proper. Between these two extremes we find in any flourishing colony of the species, a complete graded series of intermediates, some of which (*b* to *e*) are represented. The worker (*f*) forages and collects the seeds and stores them in the nest. The big-headed forms may be called the official nut-crackers of the colony because they crush the seeds with their mandibles. You will notice that the head decreases in size and length and in the convexity of its occipital lobes, as indicated by the gradual rounding of the posterior corners and decreasing concavity of the occipital border, till we reach the worker, which has a very small, rounded rectangular head, as broad as long. The crushing mandibles gradually become mandibles of the biting type as we pass from the soldier to the worker proper, and in my preparations the flexor muscles, which in all the forms fill out nearly the whole cranium, show a corresponding gradual decrease in volume.

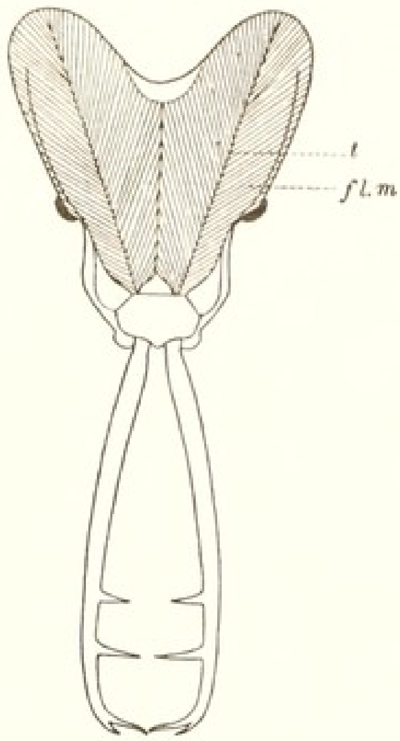

Figure 13. Head of Strumigenys *sp., Worker, Showing the Long Grappling Mandibles, with Their Flexor Muscle Fibres* (fl. m.), *and the Pinnate Attachment of the Latter to the Tendons* (t.)

The same phenomenon is exhibited in the Indomalayan harvester, *Pheidologeton diversus* (fig. 10), but in an even more exaggerated form. In this figure only the outlines of the heads of a series of soldier and worker individuals and of the queen and male are represented. In the soldier provision is made for the huge flexor muscles by such a great increase in the width as well as in the length of the head, that the difference between the two extremes of the worker series becomes enormous. The queen's head (*f*) resembles that of the soldier (*a*) but you will notice that the male (*g*), which has small mandibles, has a small, broad head, with very short and rounded occipital region.

Another instructive example is furnished by the large leaf-cutting and fungus-growing ants of the neotropical genus Atta (fig. 11). Among these the head of the biggest workers, or soldiers (*a*) is not only greatly enlarged but its front and occipital lobes are extremely convex. The leaves are cut by the intermediate worker castes (*b* to *e*) with the scissor-like mandibles, whereas the smallest workers (*f*) never leave the nest but live among the delicate hyphæ of the fungus-gardens, weeding out deleterious spores and alien mycelia. This caste, which therefore works only on soft materials, has small, weak mandibles and the head is accordingly very much smaller, narrower and less convex. The queen (*g*), which has to dig her nest in the soil and defend her young brood, has a head much like that of the larger workers. The male (*h*), unlike most male ants, has well-developed mandibles and therefore exhibits a much greater development of the head behind the eyes.

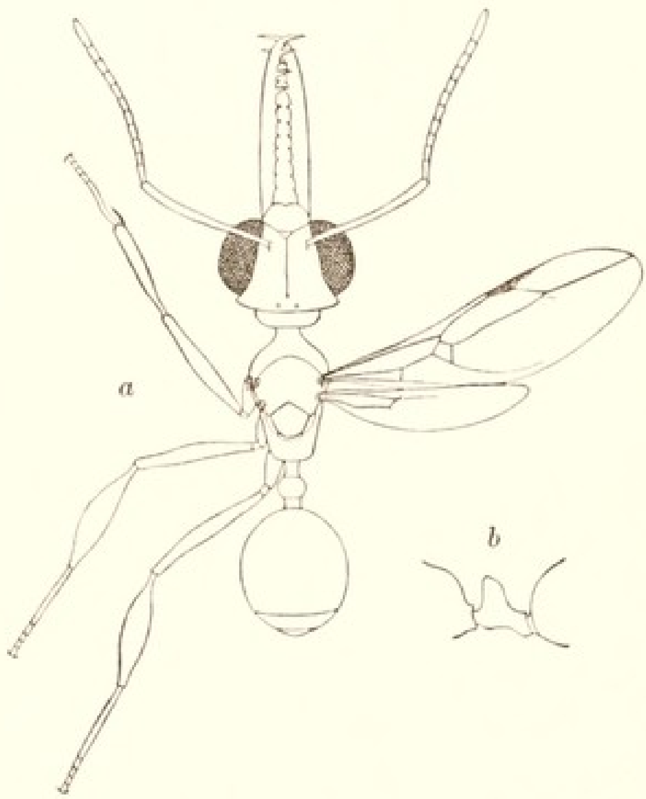

Figure 14. Myrmoteras donisthorpei *Wheeler, a Formicine Ant from Borneo;* a, *Female;* b, *Petiole. Note the Grappling Mandibles and Huge Eyes.*

The series of worker ants which I have used for illustration recalls the graded series of Harvard professors who have

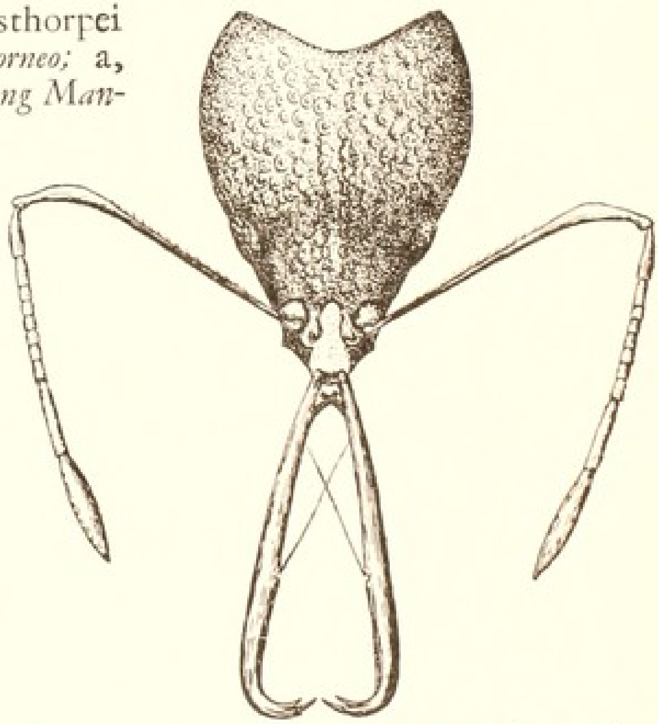

Figure 15. Head of Acanthognathus lentus *Mann from Central America. (After Mann.)*

been classified by some of the students as high high-brows, high-brows, low high-brows, high low-brows, low-brows and low low-brows. Some authors regard the soldiers, the highest high-brows of our ant series, as monstrous, or pathological forms on account of the excessive development of their crania. Certain facts might seem to lend support to such an opinion. If the soldier of *Ph. instabilis* be placed on its head on a perfectly smooth, hard, horizontal sur-

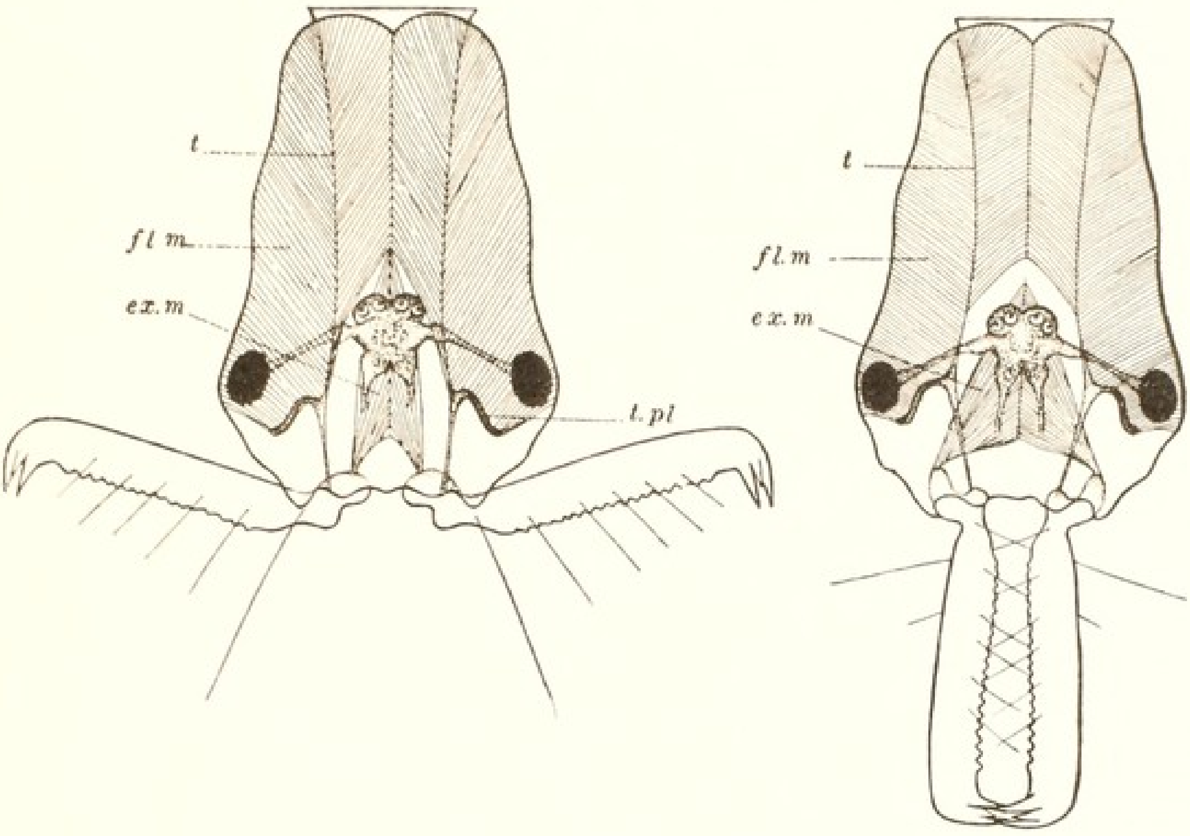

Figure 16. Head of Odontomachus hastatus *F. with Mandibles Open and Closed;* ex. m. *Extensor Muscles of Mandibles;* fl. m. *Flexor Muscles of Latter;* t. *Tendon;* t. pl., *Plate of Tendon.*

face, the insect may be quite unable to right itself and may even die standing on its head. But this is a typical laboratory experiment. In its natural environment the soldier never encounters such surfaces. Closer study shows that all these supposedly monstrous forms are really exquisitely specialized and adapted for the functions they have to perform in the life of their respective colonies. The soldiers of the harvesting Pheidoles and Pheidologetons are needed not only as seed-crushers, but those of the latter genus have another very different function. Several observers have seen groups of the minute Pheidologeton workers sitting quietly on the huge heads of the soldiers and riding to and from the nest. The soldiers of the insect-eating Pheidoles dismember the tough prey before or after it has been carried into the nest. Hingston (1922 p. 61 *et seq.*) has recently described in vivid language the extraordinary powers of communication exhibited by the diminutive *Pheidole indica* worker when notifying the soldiers to come out of the nest and oversee the transportation of the prey. As I have noticed a somewhat similar behavior in some of our American Pheidoles in the Southwestern States, I will quote part of his remarks:

As soon as a worker discovers a caterpillar or other suitable material for food, it proceeds to make a careful examination of its prey. It runs all over the caterpillar, exploring it with its

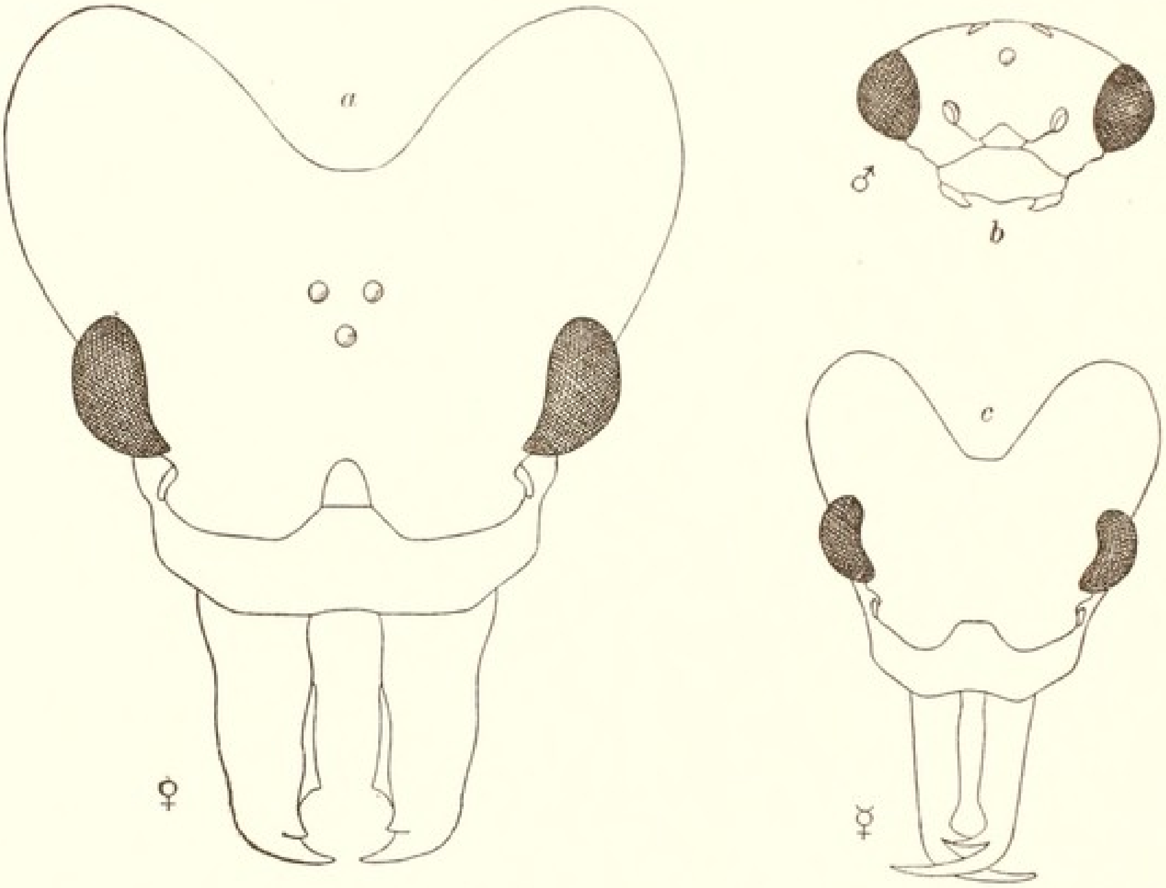

Figure 17. Heads of a South American Ant, Daceton armigerum *Perty, with Clipping Mandibles;* a, *Head of Female;* b, *of Male;* c, *of Worker. Note the Absence of Occipital Development Correlated with Vestigial Mandibles in the Male.*

sensitive antennæ, shaking it with its jaws and attempting to drag it to the nest. The worker, satisfying itself that the discovery is suitable for storage and finding the removal of it beyond its own weak efforts, hastens off to the nest in great excitement and by the shortest route. It meets another worker on its path; their antennæ meet; the second worker is imbued with the enthusiasm of the first, has received information of the discovery and hastens off to the insect. A third, a fourth, and possibly more workers are similarly informed on the route and all hurry away to lend their assistance. But the excited discoverer hastens on to the nest. Now it has reached the entrance. It enters and is lost to view. In a few seconds a swarm of rushing, bustling and excited ants come dashing headlong from the nest. From the way they are all lying in readiness just within the door and emerge at the same moment in one body as though they were awaiting a call for aid, I have no doubt but that these ants so divide their labor that certain workers are detailed for the duty of discovering food, and others, under the guidance of the soldiers, are under orders to remain in permanent readiness within the door of the nest to hurry out and render assistance when news arrives that a discovery has been made.

The news has come. Out they swarm in a dense throng preceded by the soldiers. Without the slightest hesitation they hurry over the ground, passing and repassing one another in their excited haste. . . . On all sides they besiege the larva, which tries in vain by violent contractions to throw off its enemies. The battle grows hot and fierce. The caterpillar in its struggles now gains the mastery, but ants hurrying on in increasing numbers gradually overpower it. Workers, at intervals, retire from the battle and hasten back to the nest at the greatest speed to call out more reinforcements and hurl them into the fight. The caterpillar weakens; it cannot face these repeated additions to the strength of its foes. It is overwhelmed by the force of numbers,

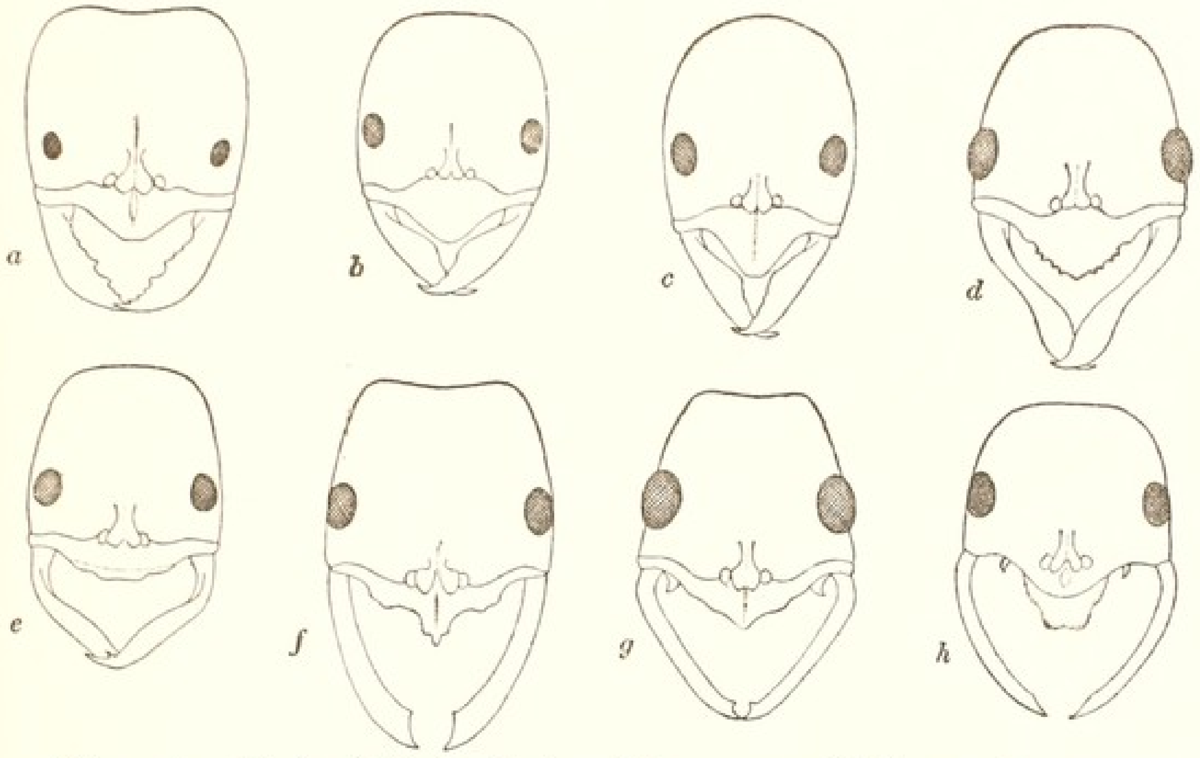

Figure 18. Heads of Eight Species of Leptogenys (*Subgenera* Leptogenys, Lobopelta, Odontopelta *and* Machærogenys), *Showing Correlation of Feeble Mandibular Development with Narrowing and Rounding of Occipital Region of Head.*

soon becomes exhausted, and then lies at the mercy of the ants which, clinging in a body round their powerless victim, drag it slowly to the nest.

Hingston also describes the peculiar behavior of the soldiers during migration to a new nest.

The main burden of toil falls on the smaller workers. It is they alone that transport the larvæ, and they often carry their companions from nest to nest. The soldiers carry nothing. They are not humble toilers, but are the directors of the transport. They are the aristocracy of ant life. They hurry out of the nest singly and at intervals with a throng of laden ants following in their rear, and as each powerful soldier hastens along the migrating line it looks like an officer leading and directing his company of men. Nor do the soldiers return again to the old nest. The smaller workers, once they have deposited their larvæ in the new nest, hasten back for a fresh burden, but a returning soldier is never seen. It, no doubt, busies itself with important duties within the new nest, but takes no further part in the migrating line.

It may be readily shown that the conditions sketched for the cranial physiognomy of ants obtain also in other groups of insects, and especially among the Coleoptera. Two examples must suffice. Among many Lucanidæ, or stag-beetles (fig. 22) we find series of forms closely analogous to those of Pheidole, Pheidologeton and Atta, but in the beetles it is the males that are polymorphic. They have been arranged according to the development of the mandibles in series beginning with large macrodont forms, passing through amphiodont, eopriodont and priodont forms and ending with individuals with small mandibles like the female (Griffini, 1905, Champy, 1924). In such a series the head gradually decreases in width *pari passu* with a reduction in the size of the mandibles. There is also a corresponding reduction in the volume of the prothorax and fore legs. This occurs also in the ant series and might be expected, because the muscles that raise, lower and rotate the head are situated in the prothorax. In the highest high-brows among the Lucanids we even find the posterior corners of the head provided with crests or protuberances which increase the surface for the insertion of the enormous mandibular flexors and are therefore analogous to the bony crests on the skulls of many mammals that have powerful jaws and temporal muscles.

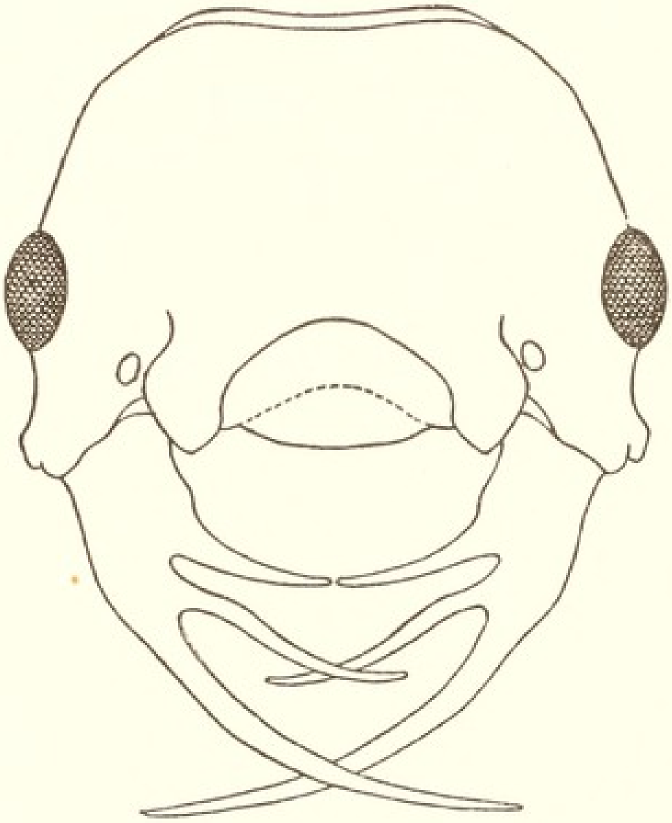

Figure 19. Head of Worker of the Neotropical Thaumatomyrmex ferox *Mann, with Weak, Aberrant, Three-toothed Mandibles and Underdeveloped Occipital Region.*

The correlation between the size and shape of the mandibles, head and prothorax is also clearly shown by a comparison of the male and female *Eupsalis minuta* (fig. 23). In the specimens figured, whose bodies behind the prothorax happen to be of the same size, you will observe that the prothorax is shorter and anteriorly narrowed in the female in correlation with the much smaller head and mandibles. The slender prolongation of the head in this sex is specially adapted for oviposition. The huge mandibles are used by the male Lucanids in their fierce sexual contests, which have been witnessed by many observers. The males of Eupsalis also fight with their mandibles, though according to Leconte and Horn (1876) their combats are bloodless and "seem, so far as the records go, to be actuated rather by chivalric sentiment, than by animal passion." According to Blatchley and Leng (1916, p. 21):

> Smith says that when the beaks of the females become wedged, as they sometimes do, the males use their forceps-like jaws to pull them out, but Riley states that the male helps in removing the beak by "stationing himself at a right angle with her body and pressing his heavy prosternum against the tip of her abdomen, her stout fore legs thus serving as a fulcrum and her long body as a lever."

After this digression I return to a consideration of some other types of heads and mandibles among the ants. Even in the smallest workers of the species hitherto described the mandibles are moderately strong and of the typical biting type, but in species that feed on soft substances and excavate their nests in soft soil or very rotten wood or merely occupy cavities made by other insects, the mandibles may be weak and narrow and the head not only elongate and rounded behind but drawn out into a distinct neck.

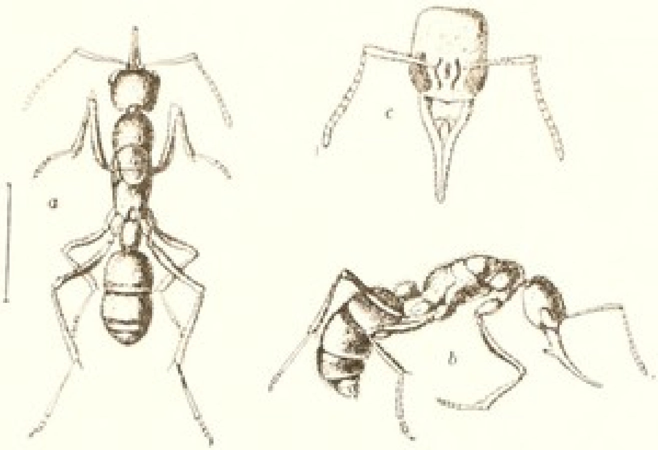

Figure 20. A Jumping Ponerine Ant, Harpegnathos venator *var.* rugosus, *with Aberrant Mandibles from Hongkong.* a, *Deälated Female, Dorsal View;* b, *Same, Lateral View;* c, *Head, from Above. (After G. Mayr.)*

Among the best examples of this condition is *Apterostigma pilosum*. This ant, though related to Atta, does not nest in coarse ground and cut leaves but lives in cavities under bark or stones and makes its fungus gardens of insect excrement. Similar types of head (fig. 24*c*, *d*, *h*) occur in other asthenic species belonging to very different genera (Aphænogaster, Dolichoderus, Leptogenys, Leptomyrmex) either as the only type among the workers or in the worker minima of species which have a large-headed soldier or worker maxima (Dinomyrmex, Pheidole, Ischnomyrmex).

The grappling and piercing mandibles are also comparatively weak organs. The former, which are well-developed in certain Ponerinæ like the "bull-dog" ants of Australia and the species of the peculiar genus Mystrium are adapted for holding on to the prey while the abdomen is being bent around and the powerful sting inserted. Large hook-like mandibles which seem to combine the functions of grappling and piercing organs are found in the soldiers of some of the army ants (Eciton *sens. str.*) (fig. 25*a*) although the next lower grade of worker (*b*) has curved, grappling mandibles and the smaller and far more abundant worker forms have cutting or biting man-

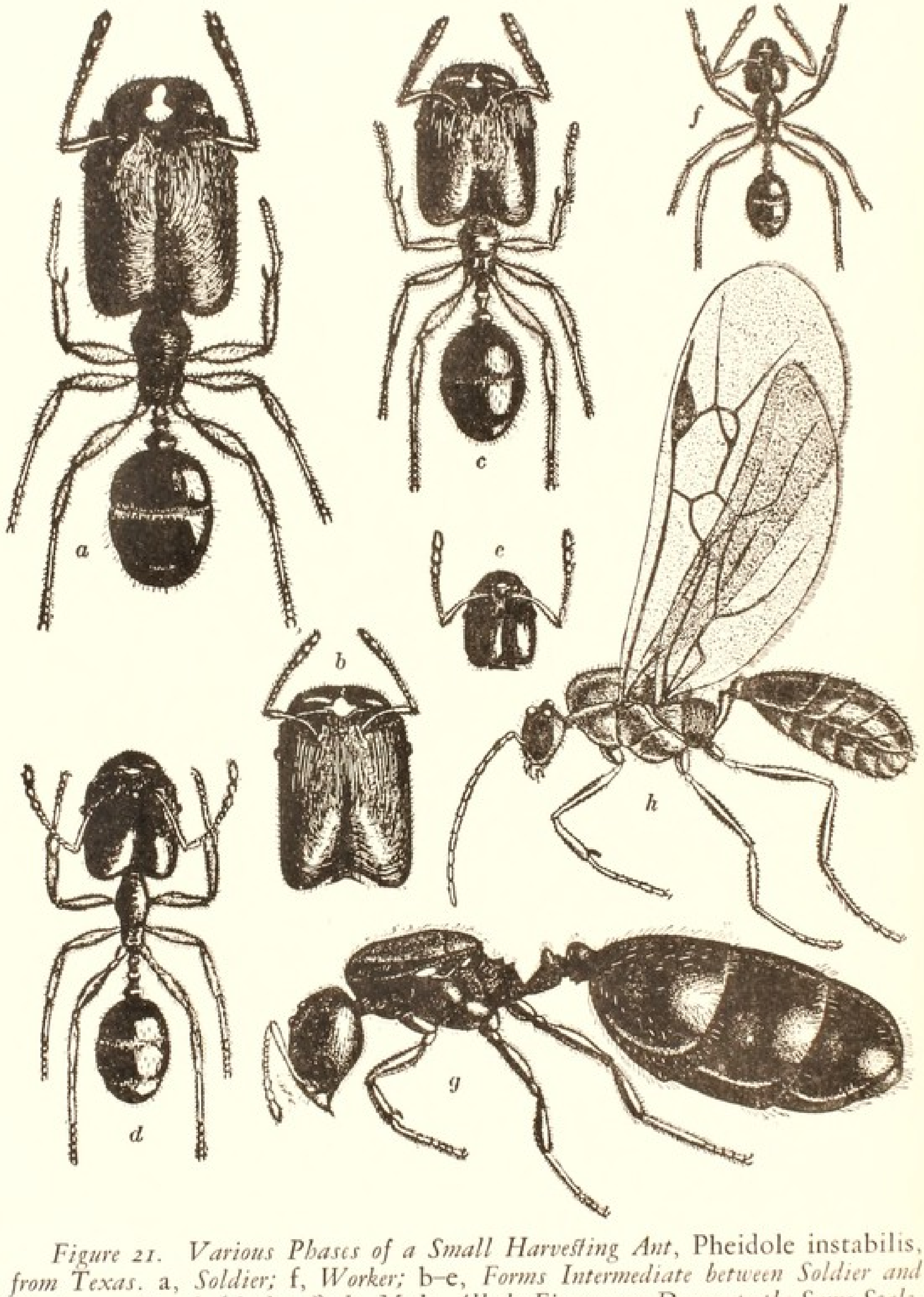

Figure 21. Various Phases of a Small Harvesting Ant, Pheidole instabilis, *from Texas*. a, *Soldier;* f, *Worker;* b–e, *Forms Intermediate between Soldier and Worker;* g, *Female (deälated);* h, *Male. All the Figures are Drawn to the Same Scale.*

dibles (*c*, *d*). Both in our slave-making "amazons" of the genus Polyergus and in certain other genera (Strongylognathus and Leptogenys) the mandibles are of the true piercing type. The amazons use them for perforating the heads of their enemies and the species of Leptogenys (fig. 18*d–h*) evidently kill the soft-bodied termites, on which they prey, in the same manner. It will be noticed that the posterior portion of the head is distinctly narrowed and rounder in these various forms.

A highly specialized condition obtains in the clipping mandibles which show some extraordinary convergent developments in genera belonging to three different subfamilies of ants (the Odontomachii (fig. 16) among the Ponerinæ, the Dacetonini among the Myrmicinæ (fig. 17) and the Myrmoterini among the Formicinæ (fig. 14)). Odontomachus may be selected for more detailed description (fig. 16). The numerous species, known as clicking ants ("fourmis tic") in the tropics, have singular, elongate-subhexagonal heads, with the eyes placed far forward on lateral eminences while the mandibles are inserted close together at the anterior end of the head and consist of long, parallel-sided blades, with a few powerful, abruptly inflected terminal teeth and on their inner border a series of serrate denticles and long sense-hairs. The insect has a curious method of employing these organs. When it is excited they are widely opened as in the figure, and as soon as the long hairs, which act as triggers, touch an object, the blades are closed with lightning rapidity and an audible click. If during the closure their tips happen to strike against a hard body the insect is thrown off its feet and backward through the air to a distance of several inches. On opening an Odontomachus nest on a hot day one may hear a series of sharp clicks and

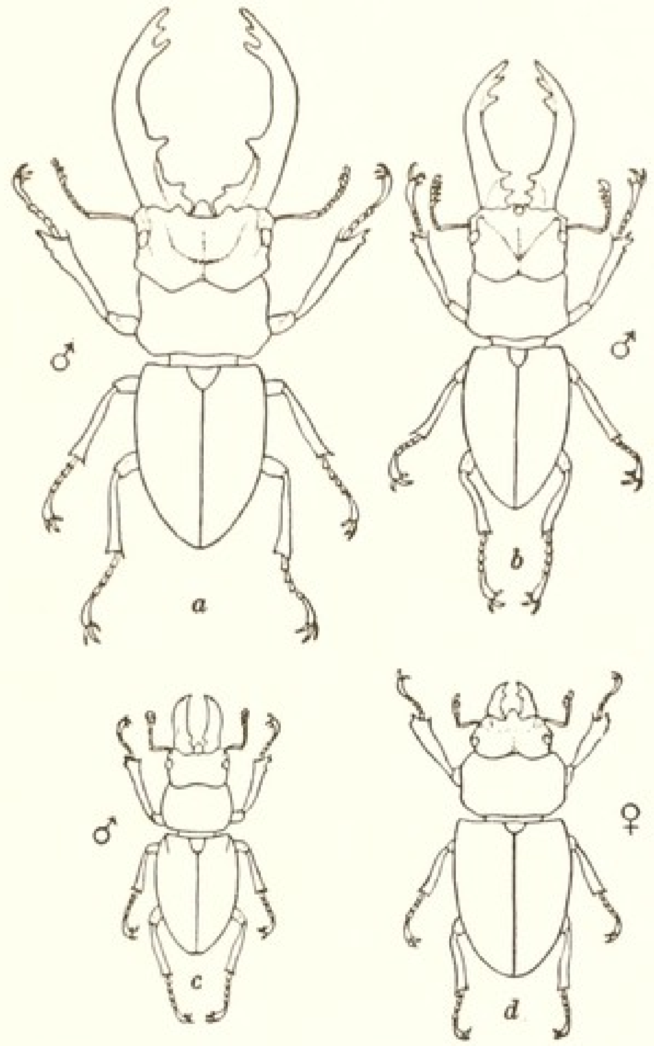

Figure 22. Forms of a Stag Beetle, Metapodontus umhangi *Fairm.* a, *"High";* b, *Intermediate;* c, *"Low" Male;* d, *Female. (After Planet.)*

find that the whole colony has suddenly evaporated into the surrounding vegetation. When the worker is hunting it cautiously approaches its insect prey with wide-open mandibles, suddenly darts forward, clips off an appendage and then retreats. It again advances and clips off another leg, antenna or wing and keeps repeating the performance till it has reduced its prey to a helpless, easily mastered torso. [For additional notes on the habits of Odontomachus see Wheeler (1900).]

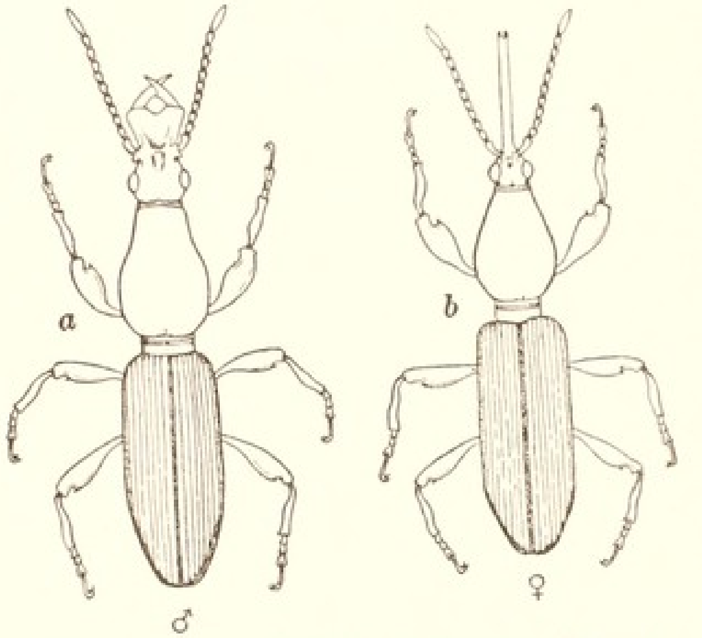

Figure 23. A North American Brenthid Beetle, Eupsalis minuta *Drury.* A, *Male;* b, *Female.*

In conformity with this unique behavior, the musculature of the mandibles is peculiarly modified. The flexor mandibulæ (*fl.m.*) is very long and fills out the whole elongated posterior portion of the cranium. The tendon (*t*), attached to the swollen internal mandibular hinge, is expanded behind near the eye into a twisted, somewhat crescentic, chitinous plate (*t.pl.*) from which two long slender tendons run back very nearly to the posterior border of the head. Only one of these tendons is shown in the figure, because the other, which runs mesially and ventrally is concealed. The muscle-fibres are numerous, very short and attached to the tendons like the barbs of a feather to its shaft, but in three dimensions of space. In the neighborhood of the eye fibres also run from the crescentic chitinous plate to the anterolateral walls of the cranium. Since short muscle-fibres can contract more quickly than long ones, the whole arrangement seems to be beautifully suited to closing the jaws with much greater velocity than in other ants. And the large size of the flexor muscle as a whole shows that closure is effected with considerable vigor.

The mandibles of Dacetonine ants show a bewildering variety of forms, often much like those of Odontomachus. Some of the species are also able to leap backward. The head, however, has a very different shape (figs. 13 and 15). It is usually more or less cordate in the worker and female, with very prominent occipital lobes and these are filled with the huge flexor mandibulæ muscles. Their fibres, in some of the species at least, are arranged along the sides of a long tendon (fig. 13). Unfortunately we possess no information in regard to the feeding habits of these ants. If we may judge from their faces they certainly do not spend their lives diffusing sweetness and light. The heads of the male Dacetonini are extraordinarily different, as will be seen from the figure of the South American *Daceton armigerum* (fig. 17). The two large drawings (*a* and *c*) represent the heads of the female and worker, the

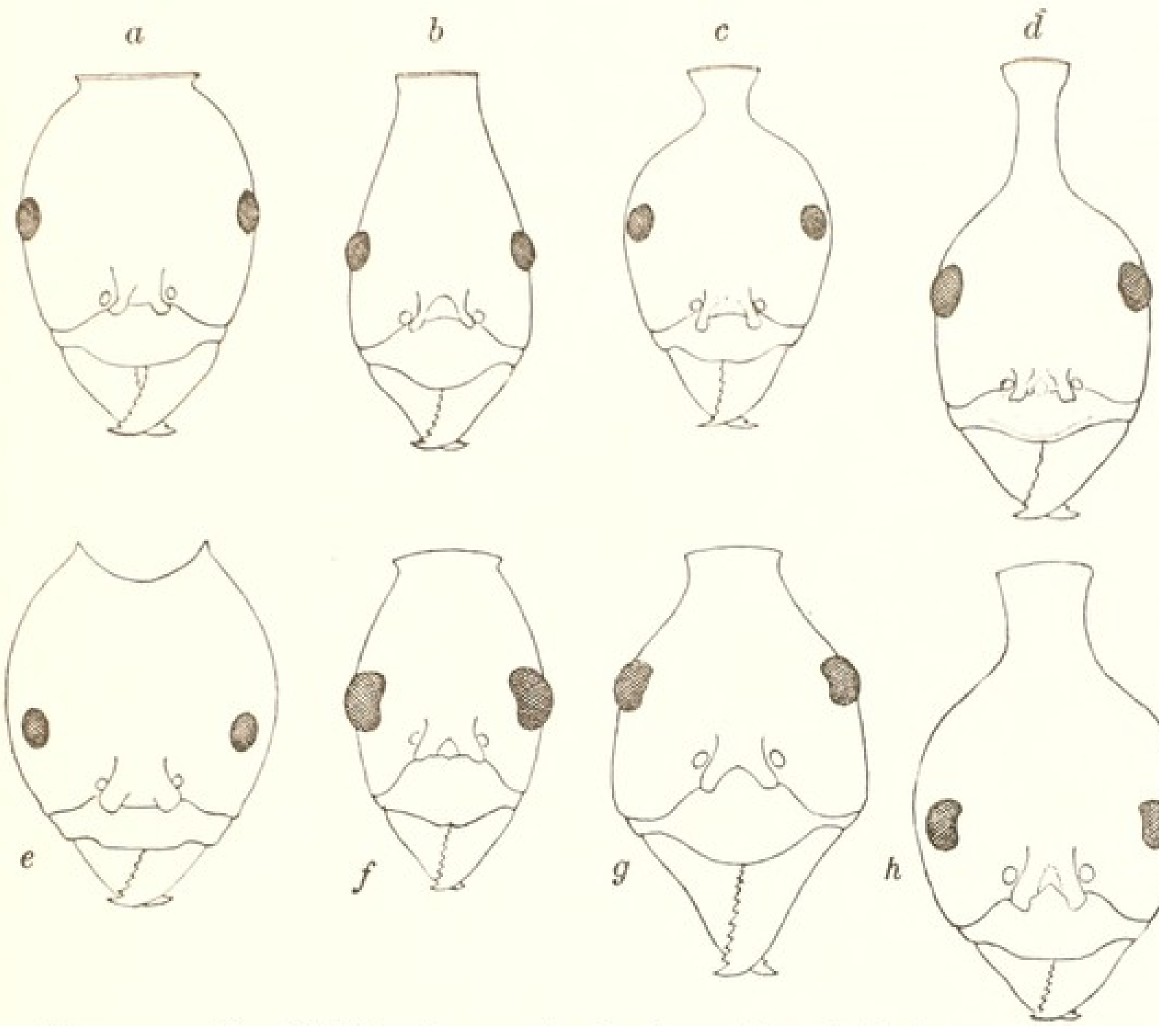

Figure 24. Parallel Development in the Contraction of the Occipital Region in Old World Species of Aphænogaster (a–d) *and Neotropical Species of* Dolichoderus (e–h). a, Aphænogaster (Nystalomyrma) longiceps *Sm. (Australia);* b, A. (Deromyrma) phillipsi *Wheeler and Mann (Palestine);* c, A. (Deromyrma) swammerdami *Forel (Madagascar);* d, A. (Planimyrma) loriai *Emery (New Guinea);* e, Dolichoderus decollatus *Sm.;* f, D. imitator *Emery;* g, D. rugosus *Sm.;* D. attelaboides *Fabr.*

small one the head of the male (*b*). Notice the vestigial condition of the mandibles, the shortness of the cranium and the complete suppression of the great lobes which in the other castes contain the flexor muscles of the mandibles. Owing to these deficiencies the countenance of the male wears a very meek and vacuous expression compared with the satanic countenances of the female phases.

Among the ants with aberrant types of mandibles I will select only two.

In one of them, Thaumatomyrmex (fig. 19), of which only a couple of tropical American species are known, each mandible is split into three long slender spines. The narrowing and rounding of the posterior portion of the head indicates that the flexor muscles must be very feeble. We know nothing of the habits of these insects, only a few, isolated specimens of which have ever been taken. Perhaps they feed on very soft-bodied larvæ or small snails, in which case the mandibles might be used for puncturing the integument of the prey in several places. The other type is that of Harpegnathos, an East Indian ant with extraordinary mandibles known to be employed in leaping (fig. 20). The insect apparently bends its head completely under the body, presses the tips of the mandibles against the ground and by suddenly raising its head, leaps forward to a distance of a yard or more. This habit, however, does not completely account for the unusual conformation of the mandibular blades, especially of their large basal teeth (Wheeler, 1922).

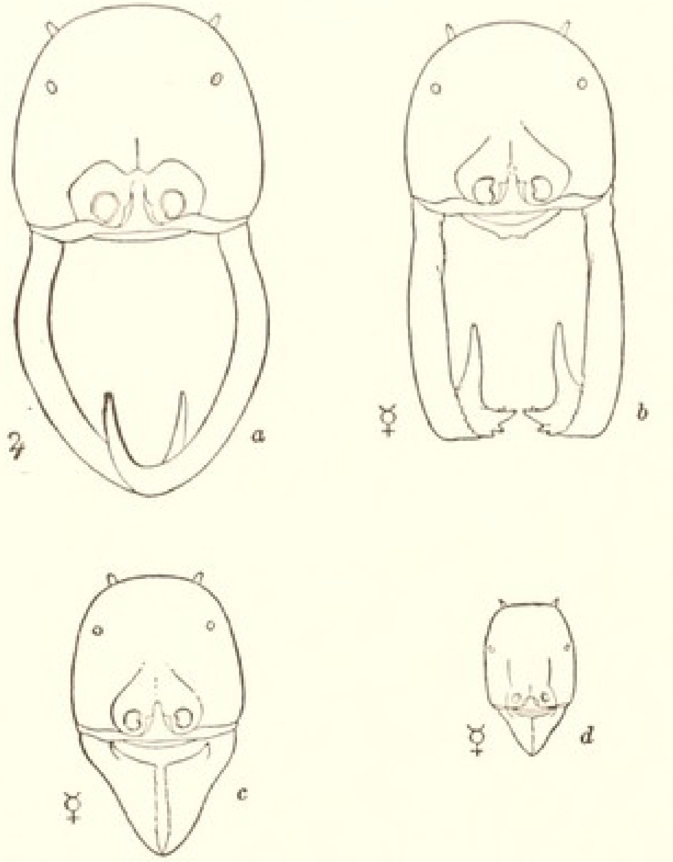

Figure 25. Heads of a Neotropical Army or Legionary Ant (Eciton burchelli *Westw.*) a, *Soldier;* b, *Form Intermediate between Soldier and Worker;* c, *Large;* d, *Small Worker.*

Much of what I have said about the mandibles of ants, their musculature and the shape of the head will, I believe, hold good of many other mandibulate insects. Professor C. T. Brues, however, calls my attention to two unrelated groups of Parasitic Hymenoptera, the Alysiidæ and Vanhorniidæ, in which the function of the mandibles and probably also the development of their musculature are reversed. In the accompanying outline figure of the head of *Alysia manducator* (fig. 26) it will be observed that the mandibles have the teeth on their external instead of their internal borders. Obviously in this case the extensor muscles have much more work to perform than the flexors and are therefore probably larger. This is indicated by the unusual width of the head and the distance between the eyes. Of course, such exodont mandibles cannot be used for biting or mastication, but might be employed by the insect in forcing its way through soft wood, mushroom-tissues, etc.

We unfortunately possess no observations on the habits of the Alysiidæ beyond the fact that their larvæ live in the larvæ of various Diptera, Coleoptera and Lepidoptera.

The heads of ants vary considerably in the convexity of their dorsal surface. As a rule, they are most convex in the region of the vertex and occiput, a condition which is, of course, correlated with the development of the flexores mandibulæ already described, but in a few genera and notably in Polyrhachis (fig. 27) the front is conspicuously convex or protuberant. Since the antennæ are always long and very mobile in such insects I believe that the frontal convexity must be due to the greater development of the flexor and extensor antennal muscles, which run from the articulations of the appendages downward, backward and outward and are inserted on the limbs of the tentorium. I advance this merely as a suggestion, because I have not yet had an opportunity to study the anatomy of Polyrhachis.

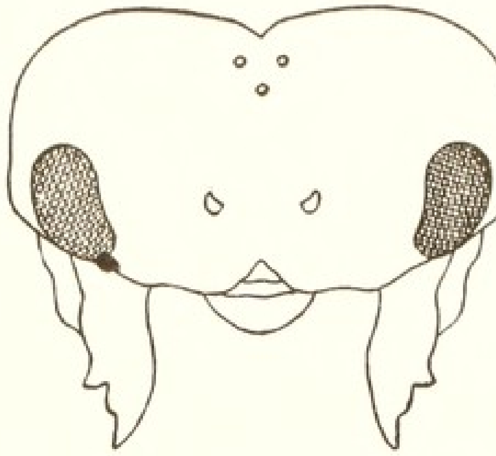

Figure 26. Head of Alysia manducator *Panz. of Europe. Note the great width of the Head, Presumably to Accommodate the* extensor *Muscles of the Mandibles, and the Teeth on the* external *Borders of the Latter.*

DEVELOPMENT OF GROOVES FOR ANTENNÆ

THE sides of the head in ants are sometimes peculiarly modified by the development of grooves, or scrobes for the partial or complete concealment of the antennæ. In their simplest form, *e.g.*, in many species of Pheidole, Harpagoxenus and Tetramorium, these scrobes are formed by a backward prolongation of the frontal carinæ and a longitudinal depression of the adiacent cranial surfaces. In certain other genera, however, the grooves become deeper. In Paraponera (fig. 28) we find a very peculiar scrobe with two limbs forming an angle around the eye. At first sight this structure would seem to be an adaptation for receiving both the scape and the flagellum of the antenna, but the scape and flagellum are really too long to form an angle that will fit into the scrobe. Hence the dorsal limb can accommodate only the basal portion of the scape when it is folded back and the ventral limb only the tip of the flagellum. In Paranomopone the scrobe is divided near the middle by a slender partition into two grooves one of which accommodates the scape, the other the flagellum. In still other genera the scrobe is simple but sufficiently deep to receive the whole folded antenna or at any rate the whole scape (fig. 29). In Cryptocerus (*a*) the scrobe lies in front of the eye, in Procryptocerus and Meranoplus (*b* and *c*) it runs backward over the eye, in Cataulacus (*d*) it descends below the eye. In all of these genera, and especially in Cryptocerus, the frontal carinæ may be greatly expanded laterally, so that the head becomes very broad and shield-shaped with plate-like lateral margins (fig. 30).

The scrobes suggest an interesting evolutionary problem. It would seem

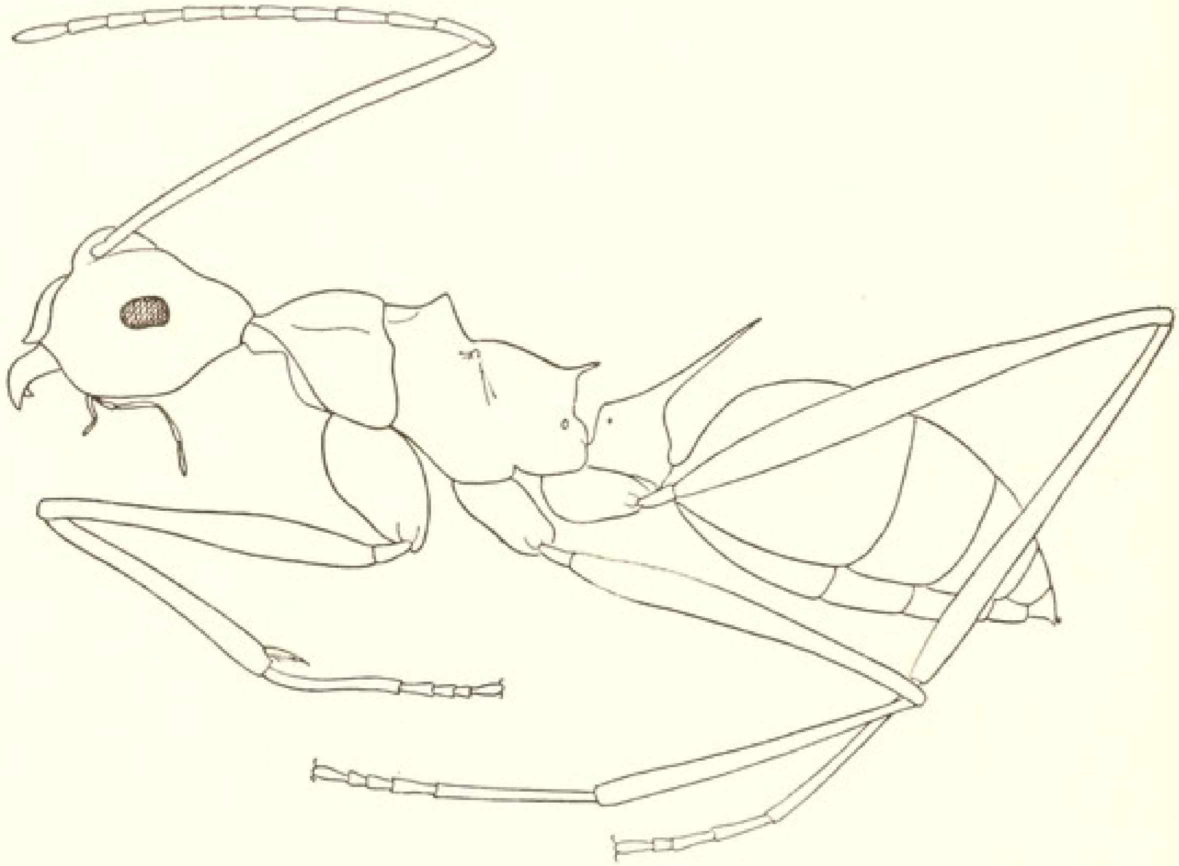

Figure 27. Polyrhachis (Myrmatopa) ulysses *Forel from the Solomon Islands; Worker in Profile, Showing Convexity of the Front.*

that they might be formed in the pupa by the pressure of the antennæ against the still soft and plastic cranial integument, but when we examine the young pupæ of the various genera I have mentioned we find that the antennæ are not folded up against the sides of the head but are drawn down over the ventral surface of the legs as in the pupæ of many other insects. The scrobes therefore develop independently during the ontogeny and we are compelled to conclude that these grooves, so beautifully adapted in the adult to the reception and protection of the very sensitive and important antennæ, must have arisen during the phylogeny of the various species in which they occur. The notion that they were produced by natural selection may be dismissed as improbable for the simple reason that they cannot have had survival value, because they are altogether lacking in most of the larger and more dominant genera (Monomorium, Crematogaster, Polyrhachis, Formica, most Camponotus, etc.). The only hypotheses, it seems to me, that might be advanced to account for the scrobes are those that have been discussed in con-

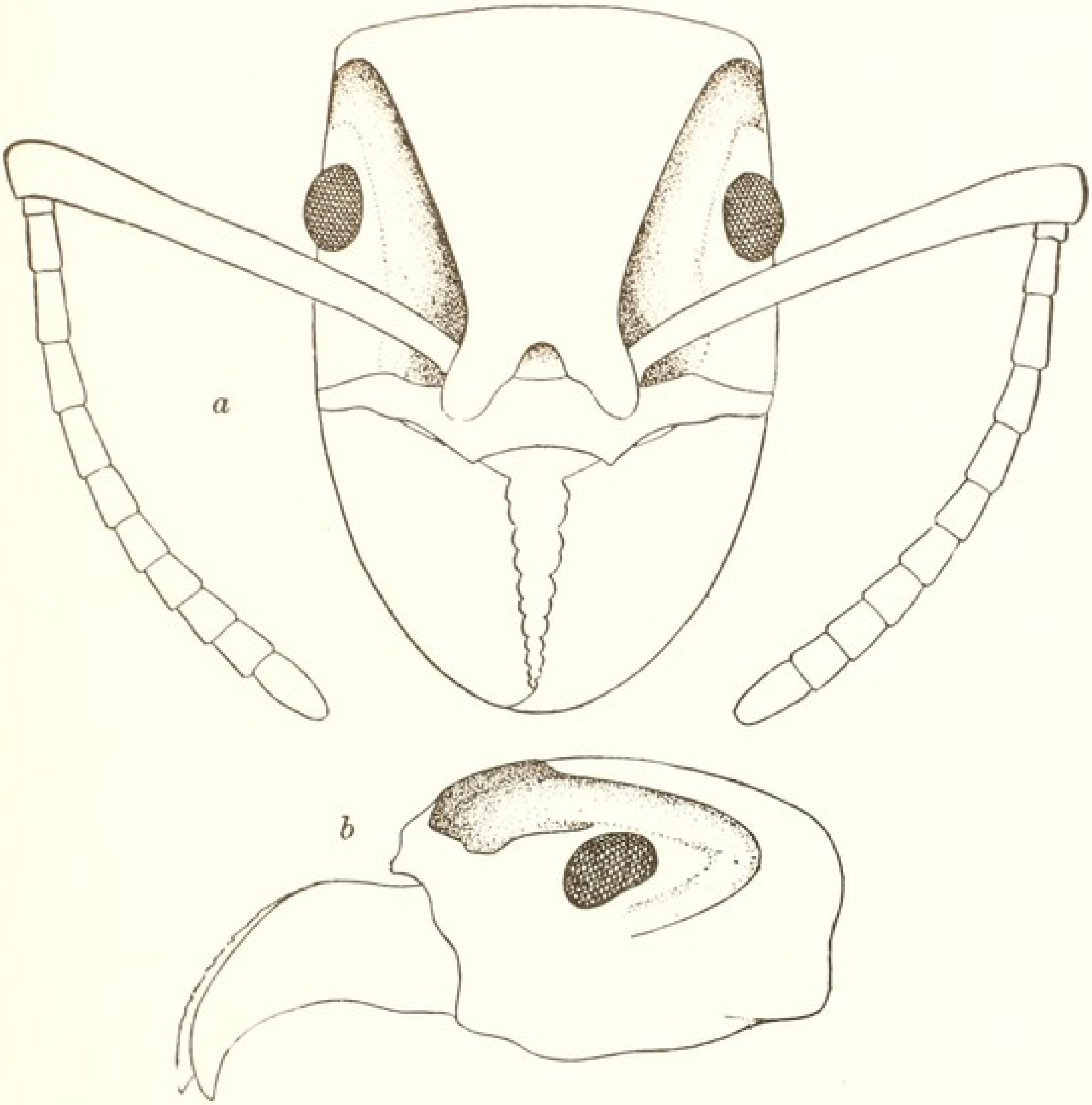

Figure 28. Head of the Formidable "Tucandeira" Ant, Paraponera clavata *Fabr., of Tropical America, Showing the Peculiar Angulate Scrobe;* a, *Seen from Above;* b, *in Profile.*

nection with many similar cases of functionally correlated structures, namely, first, the Lamarckian hypothesis that habitual pressure of the antennæ against the hard integument of the adult cranium has affected the germplasm in such a manner as to lead to the gradual development of scrobes in the pupal offspring of succeeding generations, and second, the mutation hypothesis of the chance, spontaneous origin of scrobe-producing genes in the germplasm. The latter hypothesis fails to account for the highly adaptive character of the scrobes and the former labors, of course, under the difficulty of explaining how the habitual pressure of the antennæ against the hard, unyielding cranial cuticula of the adult could translate itself into a definite formative, or morphogenic tendency in the individuals of succeeding generations.

PROBLEMS OF ADAPTATION

A NUMBER of exquisite structures similar to those here described have been discussed by Cuénot (1925) in his very interesting little book on adaptation under the head of "coaptations." These he defines as "reciprocal adjustments of two independent parts analogous to that formed by the blade fitting into the handle-groove of a pocket-knife, or a button into its button-hole." As examples he cites the fore legs of certain Phasmids which are curiously bent at the bases of the femora to fit around the head, a case originally described by Stockard (1909), the pressure-button (used on gloves and invented in France about 1886), shown in the two attachments of the mantle in cuttlefishes and the attachment of the hemielytra to the thorax in numerous aquatic Hemiptera, or Hydrocorisa (Ranatra, Belostoma, Notonecta, Naucoris, etc.), the devices in many insects for attaching or fitting the wings or elytra to one another, the coaptation of the blades of the ovipositor in Orthoptera, the stridulatory apparatus of Elaterids and other insects and the raptorial fore legs of numerous bugs, Mantids, Mantispids, scorpions and crustaceans. To this list we may add the Hymenopteran strigil which is formed by the spur of the tibia and basitarsus. After excluding the origin of such structures by mutation, and omitting all mention of the Lamarckian hypothesis, Cuénot says:

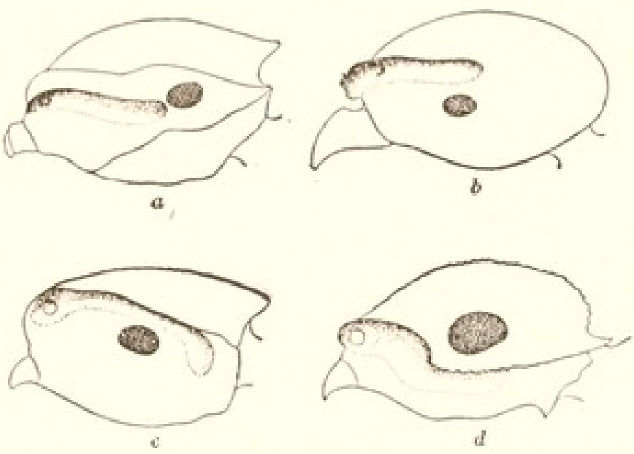

Figure 29. Profiles of Heads of Various Ants to Show Development of the Antennal Scrobe and Its Relation to the Eye; a, Cryptocerus multispinus *Sm.;* b, Meranoplus mars *Forel;* c, Procryptocerus belti *Forel;* d, Cataulacus erinaceus *Stitz.*

> Without a doubt, coaptation is the end-stage of a *directed* evolution. Sufficient indications of this evolution are known to permit its affirmation. There are Phasganourids with short ovipositors which have gutters that are rather imperfect though adequate for the movements of oviposition. There are, foreshadowing the saltatory apparatus of Elaterids, certain imperfect conformations of a similar type; the Corisas have an apparatus simpler and less compact than the pressure-button of other aquatic Hemiptera, many predatory insects have ambulatory legs

which serve equally well for seizing the prey though not of the highly differentiated type of the specialized raptorial legs in the Mantids and Naucorids. Now the only directing agency we know is Darwinian selection. This would have to play the rôle of a handicraftsman gradually correcting and perfecting his work, successively and tentatively, till it attained a complete and definitive functional specialization which could not be surpassed. Even admitting the omnipotence of natural selection, however, it could not create the coördinated details of the coaptations, and it is just the origin of these details we find so difficult to understand. And then how improbable it is that the elytral apparatus of a Lucanus, the spur of the raptorial legs of a Ranatra, the stridulatory rasp of a longicorn, can have had sufficient vital importance during their incipient stages to have brought about differential extinction! But after these negations, nothing remains. It would be pure metaphysical amusement to imagine within the species a meticulous and fanciful demon, a regulator and director of mutations, even if he were decorated, as he has been by some, with such pompous epithets as "internal perfective tendency," "élan vital," "entelechy," or some other term. Again we must resign ourselves to saying: *ignoramus!*[2]

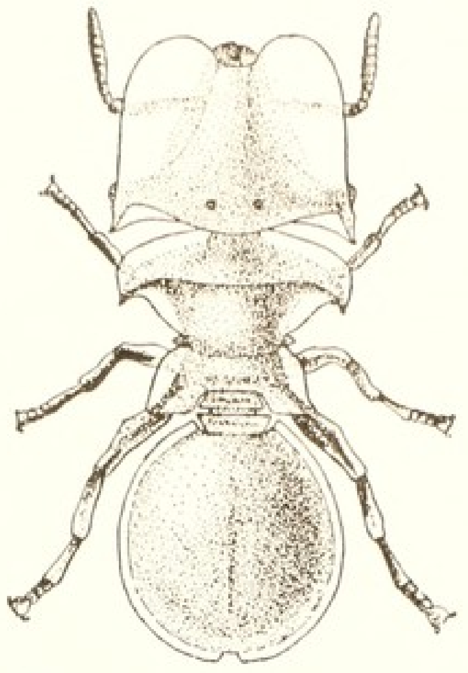

Figure 30. Cryptocerus (Zacryptocerus) clypeatus *F. Worker, with the Head Broadened and Flattened For Use in Phragmosis. (After C. Emery.)*

DEVELOPMENT OF EYES

Much might be said about the physiognomic significance of the eyes of ants and other insects, but the space allotted to this article and the reader's

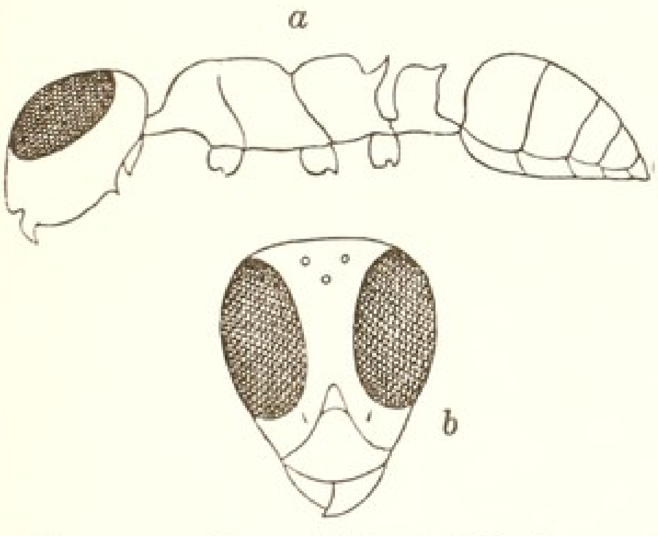

Figure 31. Santschiella kohli *Forel; a Huge-Eyed Formicine Ant from the Congo;* a, *Worker in Profile;* b, *Head of Same from Above. (After Forel.)*

[2] A number of coaptations in aquatic Hemiptera have been made the subject of an interesting study by R. Poisson (Contribution à l'Étude des Hémiptères Aquatiques. Bull. Biol. France Belg. 58, 1924, p. 49-305, 13 pls. 35 figs.). He shows that they are present in the embryonic or nymphal insect and abandons the problem of their explanation with Buffon's remark concerning the wood-pecker: "l'animal tient sa destinée des organes avec lesquels il est né." The problem will probably be found to be even more difficult of solution in the case of the copulatory organs of animals, both hermaphroditic and of separate sexes, since these coaptations are interindividual instead of being intraindividual.

patience are limited, and I must be brief. In nearly all male Formicidæ, of course, the eyes are very large, but this is true of the females and workers only in a few rather primitive and archaic genera. The facial expression of these macrophthalmic forms is very unlike that of other ants. Thus Santschiella (fig. 31), which is known only from a single worker specimen taken in the Belgian Congo, looks as if it were hopelessly flabbergasted by the problem of existence and therefore resigned to race-suicide, and the species of the Australian genus Opisthopsis (fig. 32) and the neotropical Gigantiops (fig. 33), which have the large eyes at the posterior corners of the head, wear the expression of pained astonishment which as children we have all seen on the face of some school-marm or elderly maiden relative. It is more difficult to characterize the expression of the East Indian Myrmoteras (fig. 14) with its unique combination of huge eyes and clipping mandibles. If there are Anthony Comstocks, movie censors and prohibition agents among the ants we might, perhaps, expect them to have just such faces.

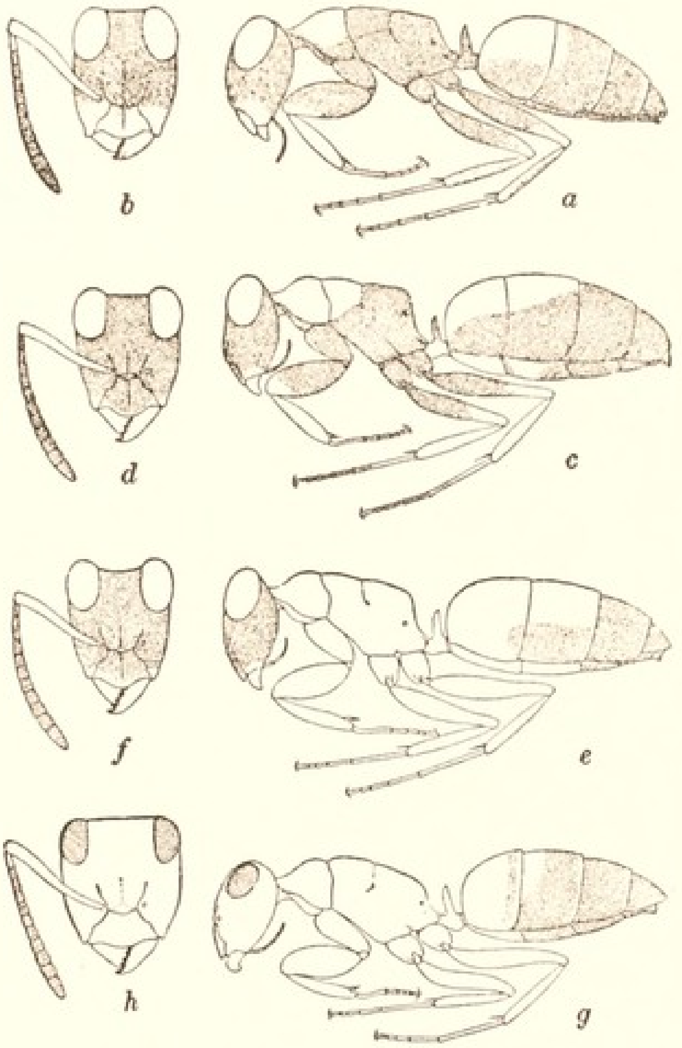

Figure 32. Workers of Four Species of the Large-Eyed Australian Genus Opisthopsis. a *and* b, O. respiciens *Sm.*, c *and* d P. pictus *Emery var.* lepidus *Wheeler;* e *and* f, O. rufithorax *Emery;* g *and* h, O. major *Forel.*

Large as are the eyes in these various ants they are not nearly as well-developed as those of many other insects, like the Diptera, Lepidoptera, Odonata, many Hemiptera, etc. In most of these orders, however, the mandibles are poorly developed or reduced to stylet-like appendages. In many male Diptera the eyes form nearly the whole head. An instructive case is furnished by Bibio (fig. 34) in which this condition is seen in the male, while the female has very small eyes and a very different head, narrowed and rounded behind like that of certain ants (Lobopelta) with poorly developed mandibles.

BEARDED ANTS

Of course, the physiognomy of ants is also determined to some extent by the character of the sculpture and pilosity. The sculpture, especially when it assumes the form of rugæ or reticulations is sometimes strangely suggestive of the wrinkles in the aged human countenance (Diacamma, some species of

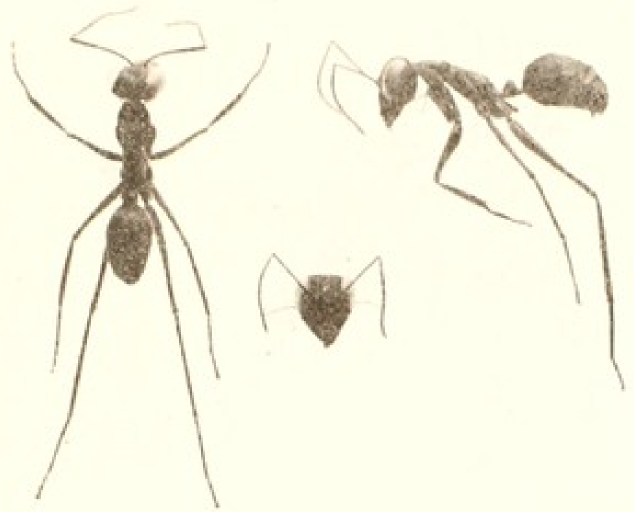

Figure 33. A Large-Eyed Leaping Ant, Gigantiops destructor *from British Guiana. Dorsal and Lateral View of Worker and Head Seen from Above.*

Pheidole, etc.). The various coiffures and styles of moustaches, whiskers and eyebrows are often extraordinary, but I will not dwell on them, because I might be tempted to depart too far from the arctic dignity so becoming to an entomologist. Nevertheless there is one type of beard to which I must call attention, because it has a very precise and practical function, unlike the human beard, which is supposed to have a great variety of functions—æsthetic, honorific, bacteriologic (or rather bacteriolegic), camouflagic, calorific, or merely problematic. And whereas in the human species it is the peculiar prerogative of the male to wear this form of

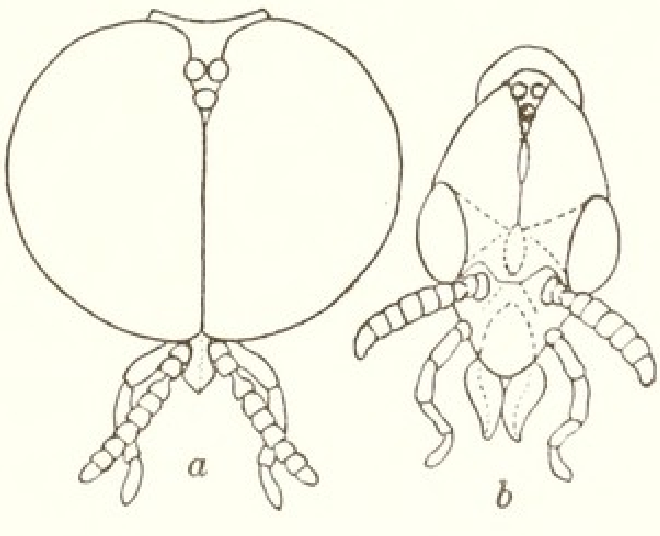

Figure 34. Bibio hortulanus *L., A European Dipteron;* a, *Head of Male;* b, *Head of Female. (After Berlese.)*

pilosity, among the ants it is—*horribile dictu*—the females, *i.e.*, the queens and workers that insist on cultivating it. But such improper customs prevail only among the species that live in deserts. Some years ago I discussed these ants in a tonsorial paper which might have attracted more attention had it been published in some barber's monthly instead of the Biological Bulletin (Wheeler, 1907).

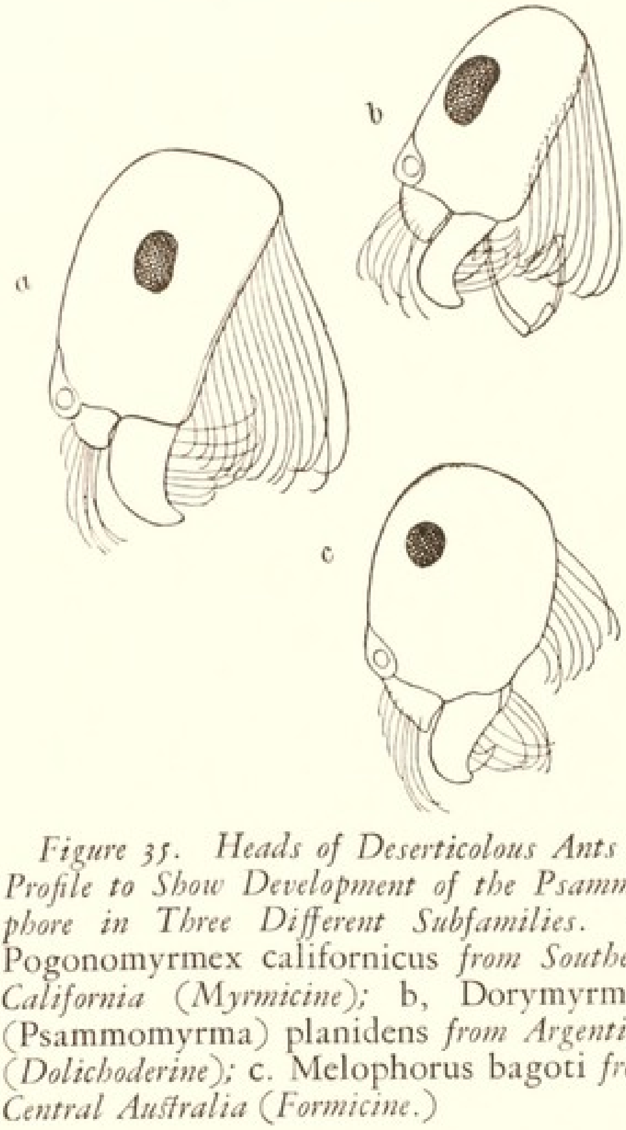

Figure 35. Heads of Deserticolous Ants in Profile to Show Development of the Psammophore in Three Different Subfamilies. a. Pogonomyrmex californicus *from Southern California (Myrmicinæ);* b, Dorymyrmex (Psammomyrma) planidens *from Argentina (Dolichoderinæ);* c. Melophorus bagoti *from Central Australia (Formicinæ.)*

Among the dominant ants of the arid, desert regions of the globe there are a number of species belonging to several genera and no less than three of the seven natural subfamilies (Myrmicinæ, Dolichoderinæ and Formicinæ) which have series of conspicuously long, curved hairs on the chin (gula), mandibles, and clypeus (fig. 35). The arrangement of these hairs which form a kind of crate is most typical and most like that of the old-fashioned Irishman's chin-whiskers in the large Western harvesting ants of the genera Pogonomyrmex (fig. 35*a*) and Veromessor, and of the genus Messor, which range over the dryer parts of Africa, southern Europe, and Central Asia. Similar hairs are also developed in the deserticolous species of Monomorium, Dorymyrmex (fig. 35*b*), Melophorus (fig. 35*c*), Cataglyphis, Myrmecocystus, and Camponotus. Santschi (1909) has shown that the gular crate, which he calls the "psammophore," is used as a basket in which to carry the sand and dust to the surface while the insects are excavating their burrows. Without such equipment the species nesting in dry sand or earth would probably find excavation extremely laborious and time-consuming, because the mandibles are not suited to the transportation of very finely-divided or powdery substances.

Besides the psammophore just described there are in certain ants other more important modifications of the head that may be interpreted as adaptations to the non-living environment. The most conspicuous of these have evidently developed in response to the habitual contacts of the insects with the walls of their burrows, especially when they are tubular and excavated in solid wood. Similar and even more striking cases are well-known among both larval and adult beetles, notably among the Ipidæ, Platypodidæ, Bostrichidæ, Ptindæ, Cerambycidæ, etc. The insect, especially if it rotates while boring through the wood, makes a perfectly tubular gallery, in adaptation to which the body takes on a more or less perfectly cylindrical

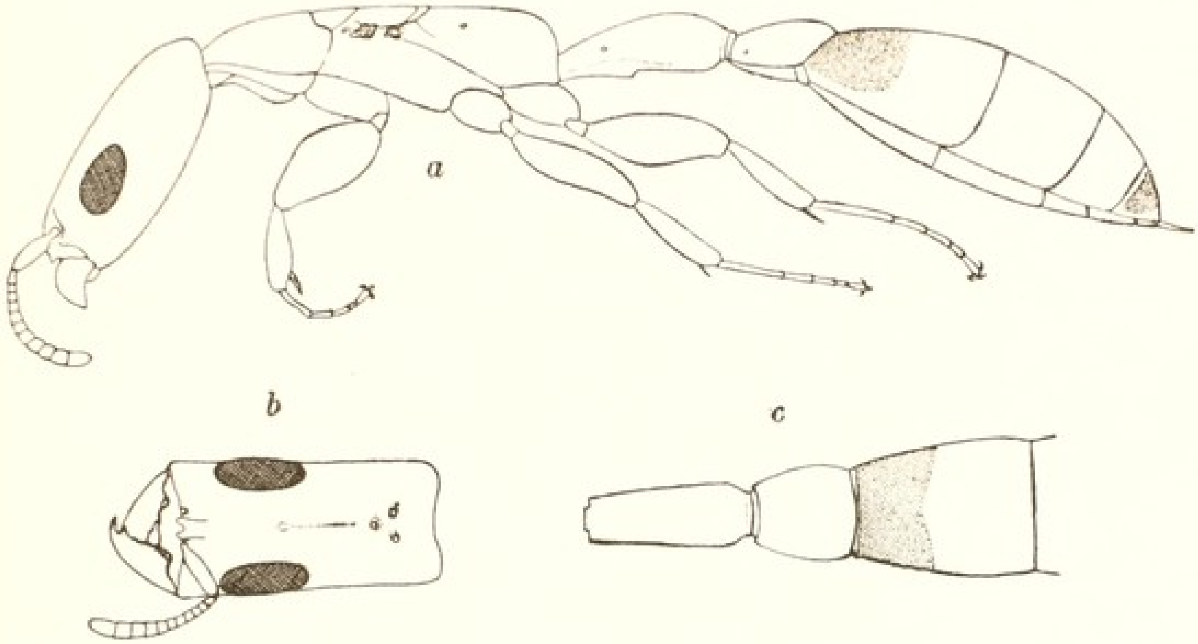

Figure 36. A Neotropical Pseudomyrmine Ant, Pseudomyrma filiformis *Fabr., Adapted to Living in Hollow Twigs;* a, *Female (Deälated) in Profile;* b, *Head of Same from Above;* c, *Pedicel and First Gastric Segment from Above.*

form. But since most ants, even many of the wood-boring species, have rather long, slender bodies, they need to acquire no special adaptive change in structure, though in some tropical species, and especially in the queens, the tenuity of the body may be greatly exaggerated. This is the case, *e.g.*, in the Myrmicine *Pseudomyrma filiformis* (fig. 36) which, according to my observations, regularly inhabits the very narrow pith-cavities of a particular neotropical shrub. And in *Camponotus (Myrmostenus) mirabilis* (fig. 37), which belongs to a different subfamily, the Formicinæ, we find a very similar elongation of the head and body. The latter species is known only from single female specimens taken at lights, but there can be little doubt that its nesting habits are much like those of *Ps. filiformis*.

PHRAGMOSIS

A MORE interesting adaptation to living in hard-walled, tubular cavities occurs in several genera, *.e.g*, Camponotus (subgenus Colobopsis), whose queens and soldiers have short, cylindrical and anteriorly sharply truncated heads, with the truncated surface circular, indurated and more strongly sculptured than the remainder of the body (fig. 38). These ants use the head, like the thick door of a safe, to close the entrance of the nest and keep out intruders. The nest which is excavated in hard wood, ligneous galls or the stems of rushes, has a perfectly circular entrance which is guarded by a soldier whose head exactly fits the orifice. When a worker desires to forage she strokes the soldier's abdomen with her antennæ and the animated door moves back and as soon as she has passed out of the nest returns at once to its previous position. On returning she knocks with her antennæ on the exposed truncated surface of the janitor's head and a similar response per-

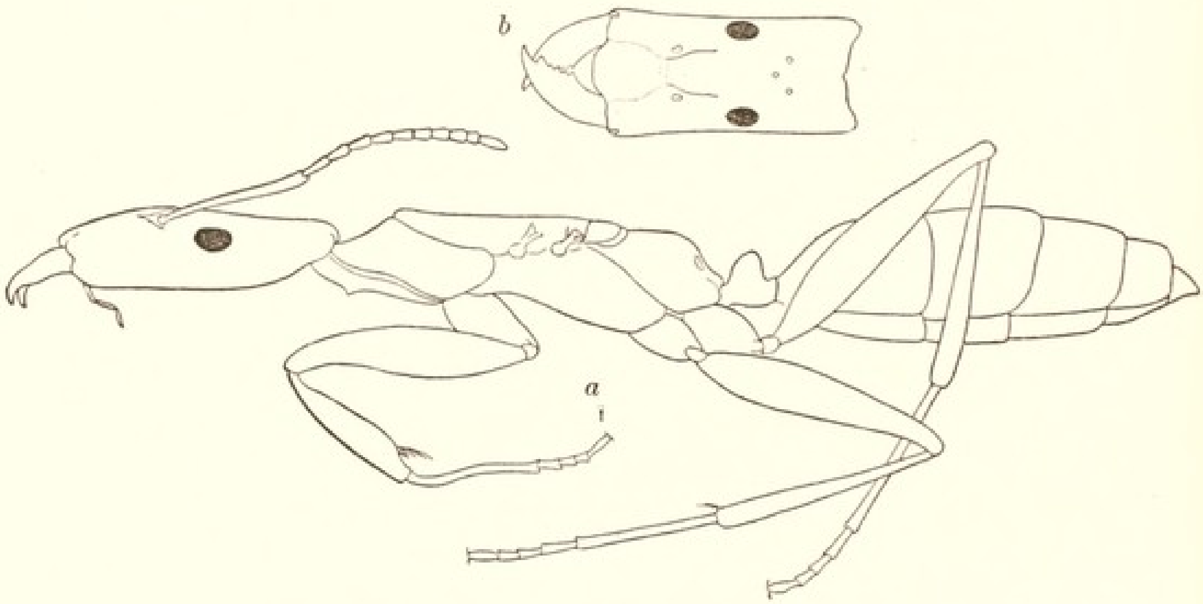

Figure 37. a, *Female (Deälated) of a Peruvian Formicine Ant,* Camponotus (Myrmostenus) mirabilis *Emery, Adapted to Life in Hollow Twigs;* b, *Head of Same from Above.*

mits her to enter. I find this same type of head in single exotic species of three other unrelated genera: Pheidole, Crematogaster (fig. 39), and Epopostruma (fig. 40), which, in all probability have much the same habits. There are also several lignicolous subgenera of Camponotus (Paracolobopsis, Pseudocolobopsis, Manniella, Neomyrmamblys) which exhibit similar modifications of the head in the queens and major workers. In some species of Cryptocerus, which also live in hard wood, the heads of the soldiers are broad and shield-shaped, and are also used for closing the nest-entrances (fig. 30).

The peculiar plug-like modification of the ant's head, like the scrobes, suggests an interesting problem which can be briefly discussed in this place. Very similar adaptations for closing the entrances to the burrows are found not only in a number of other Arthropods (*e.g.*, in the termites of the genus Cryptotermes) but also in animals belonging to other phyla. In some cases the head, in others the posterior end of the body is adaptively modified, but in both instances the truncation, its circular outline and the hardening of its integument are strangely similar. Sometimes, as in the larvæ of tiger-beetles (Cicindela) and the burrowing bees of the genus Halictus, the whole head is nearly circular and plug-shaped, in other forms, like the bark-beetles (Scolytidæ, Platypodidæ) and the caterpillars of *Cicinnus melsbaemeri* and *Perophora sanguinolenta* which inhabit tubular cases made of leaves, the posterior end of the body is sharply truncated and roughened or spinulate.

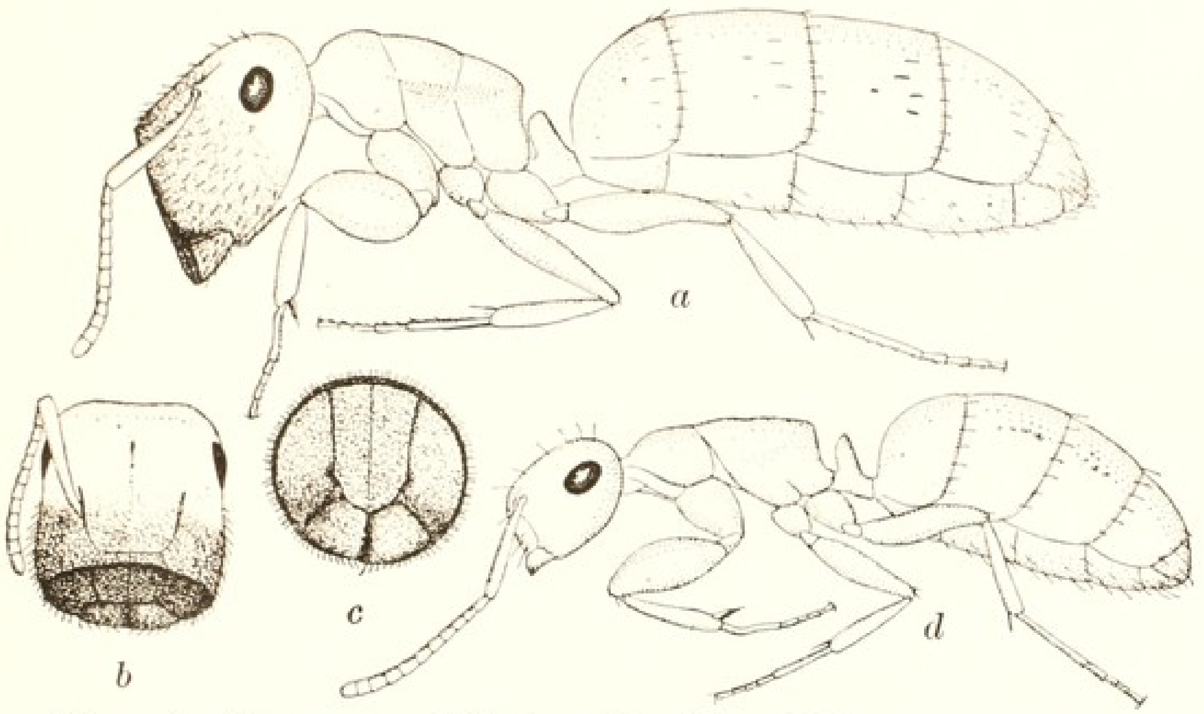

Figure 38. Camponotus (Colobopsis) etiolatus *Wheeler, A Common Phragmotic Ant in the Live Oak Galls of Texas.* a, *Soldier;* b, *Head of Soldier from Above;* c, *Same from Front;* d, *Worker.*

A figure and description of the habits of *C. melsbaemeri* is given in Harris (1862), while *P. sanguinolenta* is figured in Sharp (1899). I have observed the caterpillars of the latter or an allied species in British Guiana. In certain Annelids (Maldanidæ, Amphictenidæ) that live in tubular burrows, the head is hard and shelly. I reproduce Petrunkevitch's figure of a peculiar Theraphosid spider (*Chorizops loricatus*) (fig. 42) which, instead of making a trap-door like the allied species, uses the posterior end of its body for closing its burrow.[3]

[3] *C. loricatus* is a Mexican species. In our Southern States there is an allied spider, *Cyclosomia truncata* Hentz, which exhibits a similar modification and use of the posterior end of its abdomen. (See "The Arachnological Writings of N. M. Hentz," Boston Soc. Nat. Hist., 1875, p. 16 and Pl. I. Fig. 1.)

Barbour (1914, 1919, 1926) and Dunn (1926) have recently called attention to several interesting cases of the closure of burrows with modified heads and posterior ends in vertebrates. Barbour in his delightful book on reptiles and amphibians says: "It is well known that in many frogs the skin of the head becomes involved in the cranial ossification and becomes adherent, indurated, and rugose. This makes a hard bony head and should the frog back into a burrow he has but to tip his head down to close the entrance effectively. That this was ever regularly done on a large scale was never known until by chance, the author, after many long hunts for *Bufo*

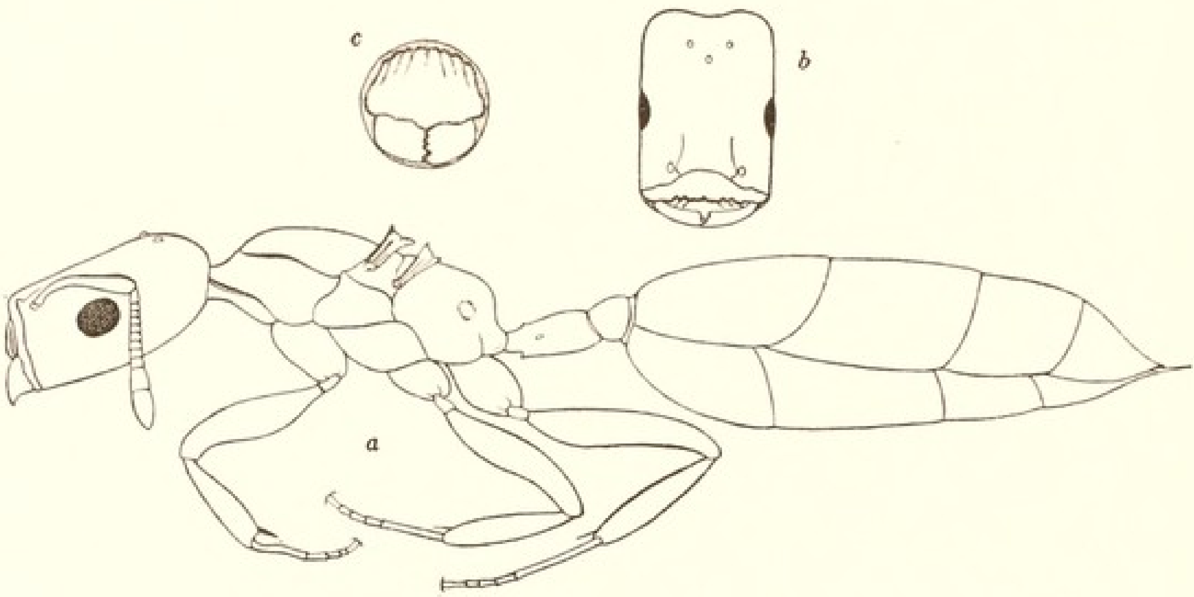

Figure 39. Crematogaster (Colobocrema) cylindriceps *Wheeler, A Phragmotic Twig-Inhabiting Ant from the Philippines;* a, *Female (Deälated) in Profile;* b, *Head from Above;* c, *Anterior View of Head.*

empusus in Cuba, chanced upon an open field over which were scattered many small burrows. These were evidently of two sorts, for the openings of some were carefully rimmed with smooth patted clay, while the others were rough and looked unfinished. Each of those with the rims contained one of the toads for which he had searched so long—the *sapo de concha* in Spanish—the shell-headed toad. These tube-like burrows were perfectly cylindrical, and perhaps seven to ten inches deep. The toad, which always looked larger than the burrow, when it was removed, was to be found near the bottom of the hole, the horn-like head forming a perfect operculum and perfectly fitting the caliber of the tube." With Dr. Barbour's permission I reproduce his figure of this toad (fig. 41). Both he and Dunn have shown that a very similar closure of the burrow occurs in a number of wood inhabiting tree-frogs (*e.g.* in *Hyla lichenata* of Jamaica). In this connection Barbour also calls attention to two other groups of vertebrates in which the posterior end of the body is similarly employed, namely the snakes of the family Uropeltidæ, "where the head is sharp and the tail knobbed and shielded or even sometimes roughened," and certain small armadillos, of which he

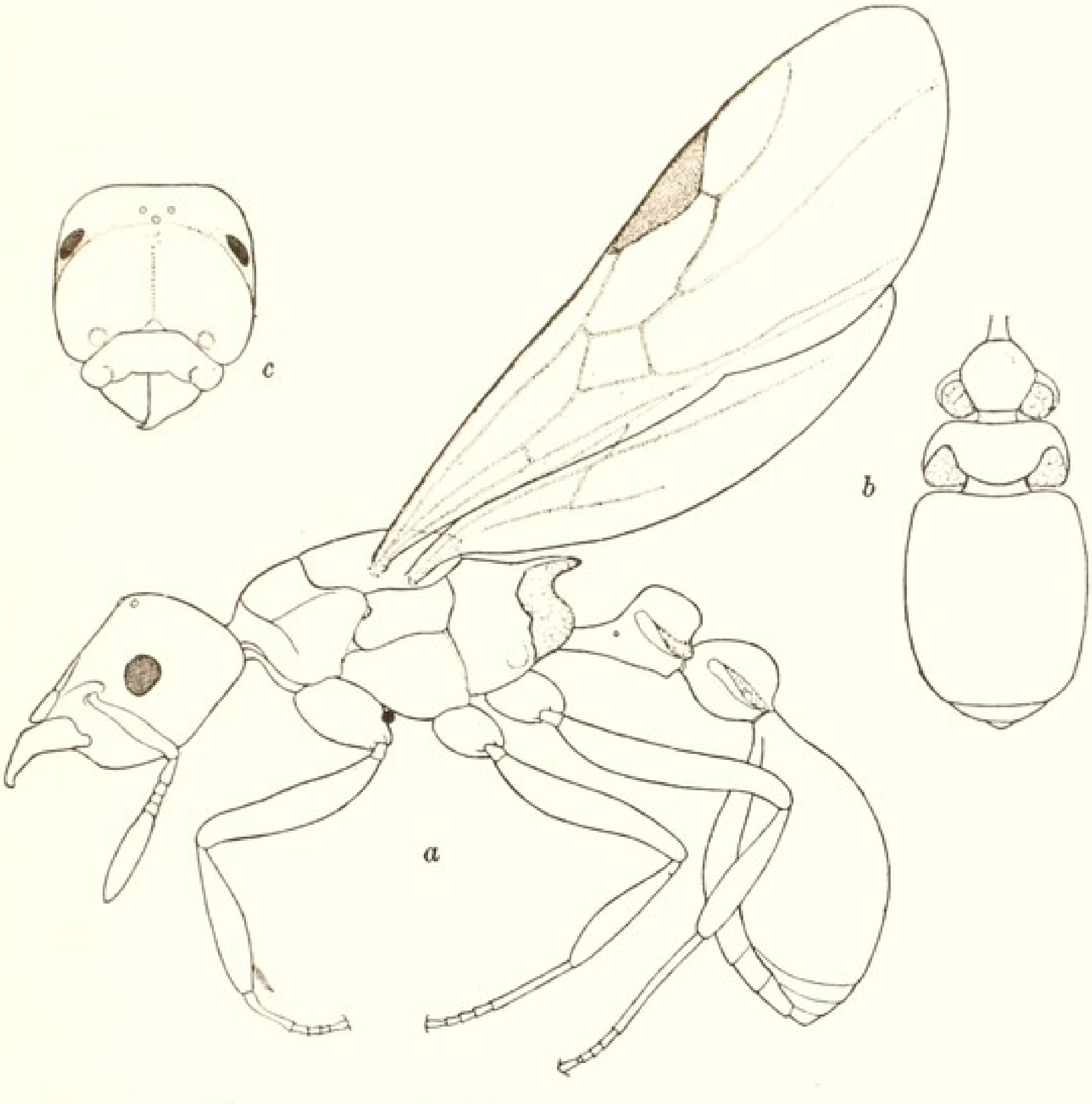

Figure 40. Epopostruma (Colobostruma) leæ *Wheeler, A Phragmotic Ant from Australia;* a, *Female in Profile;* b, *Pedicel and Gaster;* c, *Head from Above.*

says: "Perhaps the most marvelous example of all is to be seen among mammals, in the two species of Pichiciegos of Bolivia and northwestern Argentine. These little armadillos of the genus Chlamydophorus burrow and live underground. Their body is nearly cylindrical, the head sharp and pointed, and the great fore limbs are mole-like in the extreme, but the posterior end of the body is as if sharply chopped off and is covered by a bony shield. This closes the burrow perfectly and no prying snake following its underground path could possibly get its jaws about it."

As there is no general term to cover all the peculiar, sporadic but convergent modifications of the ends of the body for closing tubular burrows I suggest the word "phragmosis," from φραγμός, a fence or barricade. From evolutionary and behavioristic points of view the phenomenon, as one of the most striking and definite methods of protection and defence, would

Figure 41. A Toad, Bufo empusus, *from Cuba, which Closes Its Earthen Burrow with Its Hard, Shelly Head. (After T. Barbour.)*

seem to deserve more careful investigation than it has received. The phragmotic insect, instead of secreting or constructing a stopper, like the operculum or epiphragm of snails and the earthen or silken barricades or doors erected at the entrances of their burrows by many ants, wasps and trap-door spiders, actually employs for the purpose a specialized portion of its own body, thus affording a proof that no hard and fast line can be drawn between behavioristic activities on the one hand and physiological and morphogenic processes on the other. The phylogenetic development of phragmosis is obscure. The ants, at least, seem to indicate that it cannot have arisen as a sudden, saltatory variation, but must have developed gradually, since we have among the many species of lignicolous Camponoti continuous series of approximations to the perfected condition observed in Colobopsis (fig. 38).

DETERMINATION OF SHAPE OF THORAX AND ABDOMEN

IT WILL be seen from the foregoing discussion that the most important general factor in determining the shape and size of the head, at any rate in insects with biting mouthparts, is the flexor musculature of the mandibles. When

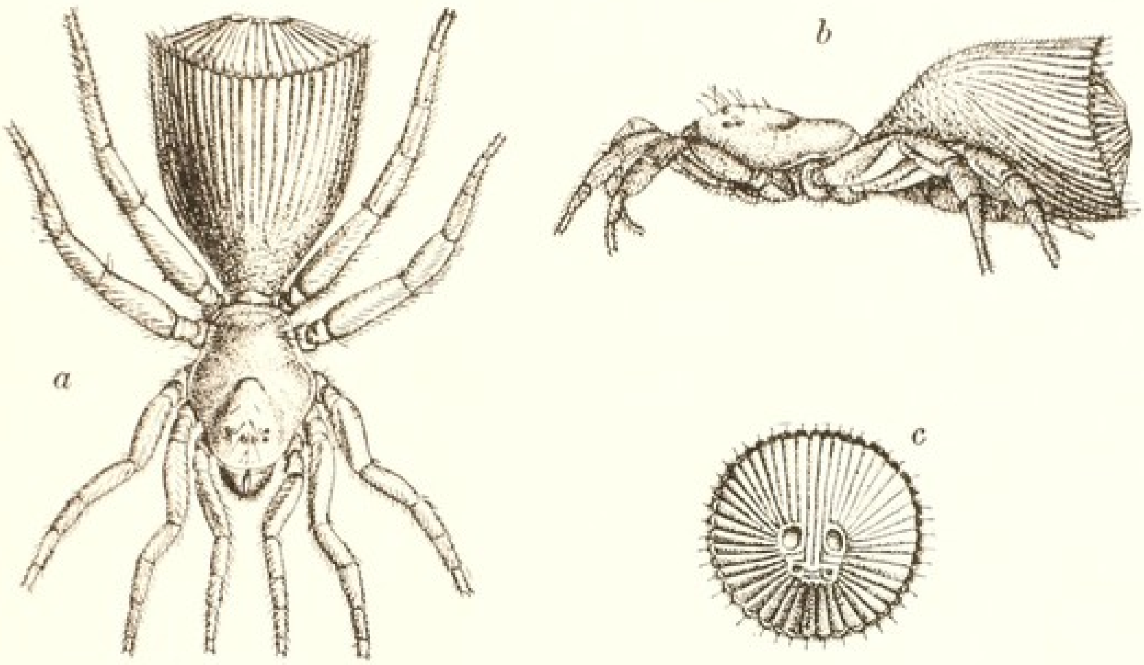

Figure 42. A Neotropical Spider, Chorizops loricatus, *which Closes Its Burrow with the Truncated Posterior End of Its Abdomen.* a, *Dorsal View;* b, *Lateral View:* c, *Truncated Surface of Abdomen. (After A. Petrunkevitch.)*

we turn to the great motor region of the insect body, the thorax, the dependence of the size and shape of the skeleton on the volume of the leg and especially of the wing musculature, becomes even more manifest. Attention has been so often directed to this matter, that little remains to be said about it. Such insects as the aphids show the correlation very clearly during their post-embryonic instars, but the various castes even of a single species of ant, furnish an even more impressive illustration. In worker ants, which never develop wings, save as rare, pathological vestiges, the thorax is greatly simplified in structure and diminished in size as compared with the thorax of the winged castes; and among the queens of certain species (*Leptothorax emersoni*) we discern a gradual reduction in its size and complexity as we pass from the macrothoracic, winged individuals, through steno- to microthoracic, apterous forms essentially like the workers. (See p.122, figs. 45 and 46.) That the development of the wing-muscles very largely determines the size and shape of the thorax is also revealed by a comparative study of insects like the Odonata, Hymenoptera, Diptera and Coleoptera, in which the relative volumes of the meso- and metathoracic segments are clearly correlated with the relative size and efficiency of their respective pairs of wings.

The physiognomy of the insect abdomen, however, is not determined so much by the development of the musculature of the various segments as by the volume of the viscera, i.e., the alimentary canal, reproductive organs and fat-body. The phenomenon of "physogastry," or hypertrophy of the abdomen is in some cases due to an enormous increase in the contents of the crop, as in the honey-ants, in others to enlargement of the ovaries or fat-body, as in the aged queens of termites (fig. 47) and certain ants (Dorylinæ, Anergates) and the various termitophiles of the more extreme type (Corotoca, Spirachtha, etc.). This physogastry is really of considerable physiological interest but its adequate consideration would unduly expand this article.

In conclusion we may revert briefly to some of the general types observed in man—the dysplastics, giants, dwarfs and acromegalics. Stockard has shown that very similar types may be clearly recognized among the various breeds of dogs, such as the St. Bernard (acromegalic), bull-dog (achondroplastic dwarf), black-and-tan (ateleotic dwarf), etc. Many cases of giantism and nanism might be cited among the insects, and among the dwarfs the soldiers of certain ants (Pheidole, Acanthomyrmex, etc.) are in many respects strangely analogous to the achondroplastics (fig. 21*a*), while the small workers (fig. 21*f*) are even more like the ateleotics. The development of these forms evidently depends on both genetic and endocrine factors, but the proportional intervention and interrelation of these factors have not been established. Owing to lack of knowledge of the precise functions of the various glands which in insects might be regarded as analogous to the endocrine glands of vertebrates, we are unable to frame any satisfactory physiological explanation of the Hexapod dwarfs. If certain ants have really learned to produce achondroplastics and ateleotics *ad libitum* and to turn over to them the main asexual activities of the colony, we should have another fine example of the extraordinary ability of insects to exploit to the utmost everything in their environment. As yet man has learned to employ his achondroplastics, ateleotics and other dysplastics only as court pets, court jesters and circus freaks.

LITERATURE

BARBOUR, T. 1914. Zoogeography of the West Indies, Mem. Mus. Comp. Zool., 44, pp. 242–243.

——. 1919. The Herpetology of Cuba. Ibid., 47, p. 100, Pl. 1, Fig. 3.

——. 1926. Reptiles and Amphibians, their Habits and Adaptations. Houghton Mifflin Co.

BAUER, J. 1924. Die Konstitutionelle Disposition zu inneren Krankheiten. 3. Aufl. Berlin, J. Springer.

BLATCHLEY, W. S., and LENG, C. W. 1916. Rhynchophora or Weevils of North Eastern America. Indianapolis.

BONNER, H. 1913. The Christian Hell from the First to the Twentieth Century, London, Watts & Co.

CHAMPY, CH. 1924. Les Caractères Sexuels considérés comme Phénomènes du Développement et dans leurs Rapports avec l'Hormone Sexuelle. Paris, G. Doin.

CUÉNOT, L. 1925. L'Adaptation, Paris, G. Doin & Co.

DUNN, E. R. 1926. The Frogs of Jamaica. Proc. Boston Soc. Nat. Hist. 38, pp. 111–130, 2 pls.

GRIFFINI, A. 1905. Studi sui Lucanidi. Torino, P. Gerbone.

HARRIS, T. W. 1862. Treatise on Some of the Insects Injurious to Vegetation, p. 416, Fig. 206.

HINGSTON, R. W. G. 1922. A Naturalist in Himalaya, Boston, Small, Maynard & Co.

KRETSCHMER, E. 1922. Körperbau und Charakter. 2. Aufl. Berlin, Julius Springer. Engl. transl. "Physique and Character" by W. J. H. Sprott. N. Y., Harcourt Brace & Co. 1925.

LECONTE, J. L., and HORN, G. H. 1876. The Rhynchophora of America North of Mexico. Proc. Amer. Phil. Soc. 15, p. 327.

MACAULIFFE, L. 1925. Les Mécanismes intimes de la vie. Paris, A. Le Grand.

SANTSCHI, F. 1909. Sur la Signification de la Barbe des Fourmis Arénicoles. Rev. Suisse Zool. 17, pp. 449–458, 9 figs.

SHARP, D. 1899. Insects. Part II, p. 379.

STOCKARD, C. R. 1909. Inheritance in the Walking-Stick, *Aplopus mayeri*. Biol. Bull. 16, p. 239.

——. 1923. Human Types and Growth Reactions. Amer. Journ. Anat. 31, p. 261–288, 3 figs.

WHEELER, W. M. 1900. A Study of Some Texan Ponerinæ. Biol. Bull. 2, pp. 1–31, 10 figs.

——. 1907. On Certain Modified Hairs Peculiar to the Ants of Arid Regions. Biol. Bull. 13, pp. 185–202. 14 figs.

——. 1922. Observations on *Gigantiops destructor* Fabricius and Other Leaping Ants. Biol. Bull. 42, pp. 185–201, 3 figs.

INSECT PARASITISM AND ITS PECULIARITIES

LECTURE DELIVERED AT THE MARINE BIOLOGICAL LABORATORY, WOODS HOLE, MASS., AUGUST 8, 1911, AND PUBLISHED IN THE *Popular Science Monthly*, NOVEMBER 1911

Whoever looks at the insect world, at flies, aphids, gnats and innumerable parasites, and even at the infant mammals, must have remarked the extreme content they take in suction, which constitutes the main business of their life. If we go into a library or news-room, we see the same function on a higher plane, performed with like ardor, with equal impatience of interruption, indicating the sweetness of the act.

EMERSON

Qu'est-ce donc que le parasitisme, s'il faut le chercher entre animaux de race différente? La vie, dans sa généralité, n'est qu'un immense brigandage. La nature se dévore elle-même; la matière se maintient animée en passant d'un estomac a l'autre. Au banquet des existences, chacun est tour à tour convive et mets servi; aujourd'hui mangeur, demain mangé; hodie tibi, cras mihi. *Tout vit de ce qui vit ou a vécu; tout est parasitisme. L'homme est le grand parasite, l'accapareur effréné de tout ce qui est mangeable.*

J. H. FABRE,
"SOUVENIRS ENTOMOLOGIQUES," III

It is universally admitted that economic entomology, like such other branches of applied biology as medicine and sanitary science, is to a very considerable extent the strategics of our warfare with a host of parasites, which are forever endeavoring to destroy our bodies, our domestic animals, our food supply, our clothing and the very materials with which we construct our dwellings and on which we write or print our interpretations of the wonderful world in which we live. In other words, economic entomology is, to nearly all intents and purposes, merely that portion of applied parasitology which deals with insects. Naturally, therefore, the destruction of the insect parasites of man and of the plants and animals on which his very existence depends, must always constitute the basic interest of this science.

A vague notion of putting certain of the parasites themselves to some use in the struggle to which I have referred, seems to have been apprehended even in pre-scientific times and among primitive peoples. We have read of savage tribes, which, like monkeys, eat their Hexapod ectoparasites. The Aztecs invented another use for these creatures, as we learn from a quaint work published many years ago by Cowan.[1] He cites the following story from Torquemada "respecting the revenue of Montecusuma which consisted of the natural products of the country, and what was produced by the industry of his subjects. During the abode of Montecusuma among the Spaniards, in the palace of his father, Alonzo de Ojeda one day espied in a certain apartment of the building a number of small bags tied up. He imagined at first that they were filled with gold dust, but on opening one of them, what was his astonishment to find it quite full of lice! Ojeda, greatly surprised at the discovery he had made, immediately communicated what he had seen to Cortes, who then asked Marina and Aguilar for some explanation. They informed him that the Mexicans had such a sense of their duty to pay tribute to their monarch that the poorest and meanest of the inhabitants if they possessed nothing better to present to their king, daily cleaned their persons, and saved all the lice they caught, and that when they had a good store of these, they laid them in bags at the feet of their mon-

[1] "Curious Facts in the History of Insects," J. B. Lippincott & Co., Philadelphia, 1865.

arch." A more scholarly, not to say more spiritual, use of parasites, seems to have been invented by no less a personage than the founder of the Dominican order of monks, since it is related in the same work "that the Devil, teasing St. Domingo in the shape of a flea, skipped upon his book, when the saint fixed him as a mark where he left off, and continued to use him so through the volume."

Although we may infer from such personal and therefore very trivial uses of fleas and lice as food, book-marks and taxes, that both saints and savages have occasionally endeavored to make their parasites subserve a useful purpose, it is only within very recent times that what may be properly called an *economic* use has been suggested for certain parasitic and predatory insects; namely, that of controlling the insects injurious to our crops, forests, domestic animals, stored foods and fabrics. The notion of using predatory beetles in destroying garden pests seems first to have occurred to Boigiraud de Poitiers in France in 1843 and in the following year to Antonio Villa in Italy.[2] The latter country also produced the two entomologists Rondani and Ghiliani, who, during the fifties and sixties of the past century, first suggested the use of parasitic insects for similar purposes. Since 1870 this suggestion has taken firmer hold of entomologists, especially in France, Italy and the United States, largely owing to the remarkable results achieved by Riley, Howard and their collaborators in our federal Bureau of Entomology. To mention only a single example, it has been found that the fluted scale (*Icerya purchasi*), so destructive to the orange, can be controlled by an Australian ladybird (*Novius cardinalis*), and this control has been successful in California, New Zealand, Cape Colony, Hawaii, Florida, Portugal, Italy, Syria and Egypt. The scale was accidentally introduced into all of these countries and in all of them the beetle, when in turn introduced, showed itself capable of preventing the pest from spreading and destroying the orange trees. This and many similar, though perhaps less striking, cases, have led entomologists to ransack remote regions of the globe for parasites to rear and turn loose on the noxious insects, which, after accidental introduction into our country, increase so alarmingly and do so much damage, owing, in great measure at least, to the absence of the parasites and other enemies that keep them in check in their native environment. The most elaborate experiment of this nature and one which is being followed with keen interest by all economic entomologists, is now being carried on at the Parasitological Laboratory at North Melrose, near Boston. Here for several years past great numbers of parasites have been received from Europe and northern Asia, carefully reared and studied, and, when found to be suffi-

[2] For a fuller account of the work of these and other early promulgators of the use of predators and parasites in combating noxious insects, see Trotter, "Due precursori nell' applicazione degli insetti carnevori a difesa delle piante coltivate," *Redia*, V., 1907, pp. 126–132.

ciently promising, liberated in the hope that they will multiply and eventually control the gypsy and brown-tail moths.[3]

The fact that such economic uses have been suggested for insect and not for any other parasites seems to imply that the former must be peculiar in certain important particulars. This I believe to be true and has led to the following considerations. That I have chosen to read them to you, who are primarily interested in the problems of zoology in its broadest sense, is due to a conviction on my part that many of the accounts of parasitism, even in the best of our zoological hand-books, are more or less one-sided and anthropomorphic, probably as a result of the stepmotherly treatment necessarily bestowed upon the insects in such treatises. Before I say more about the insects, however, I wish to make a few remarks on animal parasitism in general.

Parasitism is, of course, a form of "behavior," and may be described as one of several complex types of the reactions of organisms to the most important source of their energy, their food supply. Other reactions to this element of the environment are predatism, commensalism, scavengerism and mutualism. There is in the main sufficient consensus of opinion concerning the distinctions between these different phenomena. Predatory animals kill other animals and devour them wholly or in part. Parasites put other organisms in the position of "hosts" by living *directly* on their tissues in such a manner as not to cause their immediate death. The parasite thus draws *indirectly* on the food supply of another organism by permitting or compelling it to do the hard work of procuring the food and of converting it into much more accessible and much more easily assimilable compounds. The parasite may be said, therefore, to use its host as an instrument not only for procuring, but for predigesting, its food. The commensal also uses another animal as an instrument, but merely in gaining access to a foo supply which the latter has procured but has not yet assimilated. Th scavenger, like the saprophyte among plants, may be described as a parasite of the dead, deriving its sustenance from decomposing animals or plants or from the excretions of the former. The mutualist, finally, as the name implies, lives in a condition of balanced energetic or nutritional cooperation with another organism.

[3] Excellent general accounts of the subject here touched upon are contained in the following papers: Marchal, "Utilization des Insectes Auxiliaires Entomophages dans la Lutte contre les Insectes Nuisibles à l'Agriculture," *Ann. de l'Inst. Nat. Agronom.* (2), VI., 2, 1907, 74 pp., 26 figs.; translation in part in *Pop. Sci. Monthly*, LXXII, 1908, pp. 352–370, 406–419; Silvestri, "Sguardo allo Stato Attuale dell' Entomologia Agraria negli Stati-Uniti del Nord America, etc.," *Boll. Soc. Agric. Ital.*, XIV, No. 8, 1909, 65 pp.; Howard and Fiske, "The Importation into the United States of the Parasites of the Gypsy Moth and the Brown-tail Moth," Bull. No. 91, Bur. of Ent., Dep. Agric., 1911, 312 pp., 73 figs., 25 pls.

Of all these types of reactions to the food supply, parasitism is far and away the most prevalent; so prevalent, in fact, that it may be doubted whether there is any animal that does not resort to it, at least during a brief portion of its life, even if this be only during the period when, as an egg, it is drawing its supply of food-yolk from its parent. That parasitism has been most frequently developed from predatism is certain, that it may occasionally have its origin in commensalism, mutualism or scavengerism is highly probable, that it can, especially when it affects a considerable portion of the life-cycle of an organism, develop into anything but a more extreme form of parasitism, is very doubtful.

It would be easy to show by the citation of many examples that parasitism is an extremely protean phenomenon, one which escapes through the meshes of any net of scholastic definitions in which we may endeavor to confine it. Nor is this surprising when we stop to consider its great prevalence and the fact that during the course of time the organic world, *pari passu* with its increasing differentiation, has become ever more and more heavily weighted with parasitism and mutualism. That this nutritive dependence of organisms on one another has been steadily growing during paleontological time is clearly seen in the comparatively recent development of viviparity in mammals and many other animals, in the development of the alternating generations of plants into a condition in which the gametophyte is parasitic on the sporophyte (gymnosperms and angiosperms) or the sporophyte on the gametophyte (ferns and mosses), in the increasing mutualistic relations between insects and flowering plants, in the enormous development of parasitism among the highest orders of insects, the Diptera, Hymenoptera, Coleoptera, Lepidoptera and Homoptera, which are not known to have existed before Jurassic and Triassic times, and even in many apparently more primitive parasites like the true lice, bird lice, bat lice, fleas and many tape-worms, flukes and round-worms, which could not have developed till after their mammalian and avian hosts had made their appearance. Social life, too, which is hardly more than a mixture of parasitism and mutualism, shows a similarly recent development. Man himself, with whom we do not commonly associate the idea of parasitism, although the term is derived from a certain type of man well known to the ancient Greeks, not infrequently displays an extraordinary variety of parasitic activities. As an embryo he is always entoparasitic, using his allantois in a manner that vividly suggests the root-system of a Sacculina attached to a crab. At birth he becomes a kind of ectoparasite on his mother or nurse, and throughout his childhood and youth he is commonly what might be called a family parasite, depending for his sustenance on his parents, brothers and sisters or remoter relations. At maturity, in addition to the possibility of becoming parasitic on his wife, he has a choice of many kinds of social parasitism. As a member of a trust, political party or legislative body, not to mention many other organizations and institutions, he may graft successfully on the community at large or on some particularly lucrative portion of it, and should he fail through these activities to store up a sufficient *corpus adiposum* in the form of a bank-account, he may parasitize, with advancing years and till the end of his days, on his own offspring.[4]

But the roots of parasitism may be traced even deeper within the very fabric of the organism itself. The theories of Roux and Weismann have made us familiar with the struggle among the parts of the individual organism, *i. e.*, among its organs, tissues, cells and the components of its cells, a struggle in which these elements often grow and develop at the expense of other elements in a manner that can only be regarded as parasitic. The more modern theories of mutation and Mendelism, with their insistence on unit-characters and "factors," obviously admit of an interpretation in similar terms. We can even shift this interpretation to the psychic plane, where we find the fixed ideas, obsessions and monomanias behaving as so many processes which draw their sustenance from other psychic processes to such an extent that they may in the end not only dominate but destroy the whole personality.

Some of you will be shocked at this account of what we are in the habit of describing in very different language, for the same emotional reason that we all admire the tiger and the tiger-beetle and loathe the tape-worm and the louse, namely, because our instinctive horror of the parasites to which our species is so constantly exposed, prevents us even as twentieth-century zoologists from appreciating the extent to which all life, ourselves included, is saturated with parasitic proclivities. I fear, however, that this attempt to justify my shocking language will fail to convince some others among you, who will accuse me of being myself a host of one of the obsessions to which I have just alluded—of the parasitic obsession, namely, of the idea of parasitism. You will say that in thus subtilizing or volatilizing what has always seemed to be a concrete biological phenomenon, and in thus diffusing the concept of parasitism over the whole organic world, I have not only distorted it beyond recognition, but have deprived it of any usefulness which it may have had. To such accusations I can only reply that I gladly

[4] Certain general aspects of social parasitism in man are admirably presented by Massart and Vandervelde in their work entitled "Parasitisme Organique et Parasitisme Social," *Bull. Sci. de France et de la Belg.*, XXV, 1893, 68 pp., and by Ross in Chapter XXVIII of his "Social Control," Macmillan Co., New York, 1910. The conception of viviparity as a form of parasitism has been developed by Giard ("Sur la signification générale du parasitisme placentaire," *C. R. Soc. Biolog.*, 1897), Houssay ("La Forme et la Vie. Essai de la Méthode Mécanique en Zoologie," Paris, 1900) and Faussek ("Viviparity and Parasitism," in Russian, *Russkoje Bogatswo*, 1893).

concede that it is admissible for practical purposes to circumscribe parasitism by arbitrary names and definitions in special fields of biological, sociological and psychological study, but I must insist, nevertheless, that it is a very fundamental and far-reaching phenomenon, which, for theoretic and heuristic purposes, may properly be said to include any complex of vital processes, which maintain themselves at the expense of other vital processes, in the same or in other organisms, without reacting on these processes in an equivalently sustentative manner. But let us return to the more conventional conception of the subject.

When an organism becomes parasitic it, of course, undergoes structural and physiological changes. These express themselves in the loss or modification of previously existing characters and in the acquisition of new characters. The amount of this loss, modification and acquisition depends, first, on the intimacy of relationship of the parasite to the host; second, on the nature of this relationship; third, on the time in the parasite's ontogeny when this relationship is established, and fourth, on the portion of the ontogeny which it covers. Ectoparasites, as we all know, are, as a rule, less modified than entoparasites, but each of these categories includes very different degrees of modification, according as the parasite is confined to a particular organ of the host or is capable of moving more freely over its surface or through its tissues. The habitus of a parasite is most profoundly influenced and characterized by the moment in its ontogeny when it joins its host, and especially by the length of the period during which this association is maintained. According as the association is coextensive with the parasite's life or merely for a briefer period, we may distinguish *permanent* and *temporary* parasites. The latter, again, may be divided into those that are free from their hosts only during larval or early life and those that are free as adults. To these three types practically all animal parasites can be referred. They are best represented by such forms as certain tape-worms and flukes, by such crustaceans as Sacculina, and by such insects as the Ichneumonidæ and Chalcididæ among Hymenoptera and the Tachinidæ among Diptera. Permit me to describe very briefly the salient peculiarities of a typical example of each of these groups.

The tape-worm is an excellent example of a permanent parasite. It produces an enormous number of very minute eggs, and either these or the singular embryos, known as onchospheres, which they contain, are passively swallowed by the host. The onchosphere passes from the alimentary tract into the tissues of the host and there becomes a bladder-worm. This, in order to become a sexually mature tape-worm, must enter the alimentary tract of a second host. The transfer is effected passively by the second, or definitive, devouring the first, or intermediate host. Both stages of the parasite exhibit extreme modification of structure, the second being characterized by an enormous development of the hermaphroditic gonads and of the alimentary surface, which is merely the integument, and is therefore in immediate contact with the food supply. To this type of parasitism we may also refer the Dicyemids, and many of the flukes and round-worms. In many of these cases the association with the host may be effected without any effort on the part of the parasite, and the small size, the enormous number and the method of distribution of its eggs are properly interpreted as so many direct and necessary adaptations to chance.

The Rhizocephalous crustacean Sacculina, which may serve as a paradigm of the second type, or that of temporary parasitism with free early ontogenetic stages, also produces an enormous number of minute eggs. These, however, develop into free-swimming Nauplii, which in turn become Cypris larvæ and as such seek out their Decapod or Isopod hosts. Owing to the activity and comparatively high organization of these larvæ, the element of chance in bringing about the host association, though still considerable, is not as great as it is in the tape-worm. When it has joined its host, the Cypris larva, through one of the most remarkable methods of development known to exist among animals, proceeds to undergo structural modifications so extreme that, without a knowledge of the earlier stages, the crustacean affinities of the organism would never be suspected. "In the adult state the body consists of two portions: a soft bag-like structure, external to the host, carrying the reproductive, nervous and muscular organs and attached to some part of the host's abdomen by means of a chitinous ring; and a system of branching roots inside the host's body, which spring from the ring of attachment and supply the external body with nutriment."[5] In Sacculina, as in the tape-worm, the gonads are hermaphroditic and reproduction takes place by a continual round of self-fertilization. To this type of temporary parasitism with free larval stage we may also refer the Myzostomes and other parasitic Annelids and the parasitic mollusks. In all these cases metamorphosis supervenes while the animal is still very small and hence *precedes* growth and the incidence of the modifications produced by the parasitic habit.

As an example of the third type or that of temporary parasitism with free adult stage, we may select the Ichneumonid Hymenopteron. The eggs are few in number and rather large and are deposited by the mother directly in or on the host, which is the larva of some other insect. The sluggish, bag-shaped parasitic larva, on hatching from the egg, feeds for some time on the blood-tissues and fat-body of the host, but is careful not to prevent the latter from moving about, procuring its food and growing to maturity. When it has reached this stage, however, the parasite quickly destroys it by consuming its vital tissues. It then completes its own growth, pupates and

[5] Geoffrey Smith in the Cambridge Natural History, Vol. IV, p. 95.

eventually emerges as a very active, highly organized and beautifully colored fly, provided with a splendid nervous system, exquisite sense-organs and powerful locomotor organs in the shape of legs and wings. It is either a male or a female and, if of the latter sex, soon proceeds to place its offspring in immediate contact with the host. Although the larval Ichneumon exhibits modifications of structure almost as extreme as those of the adult Sacculina, these produce no effect on the organization of the adult insect. The association of the larva with its host is the work of the mother insect, a creature gifted with complex instincts that enable her to ferret out the host even in the most intricate concealment. The large size and small number of her eggs and her highly specialized method of oviposition indicate very clearly that chance, which plays such a rôle in the life-cycle of the tape-worm and Sacculina, has given way to an almost inevitable association of the parasite with its host.

Of course, the Ichneumon represents only one of many forms of parasitism among insects. I have chosen it because it is the most characteristic and most highly specialized. There are insects like the Strepsiptera and the Rhipiphorid and Meloid beetles which seem to combine the Sacculina with the Ichneumon type in that they produce many small eggs that hatch as very active triungulin larvæ and only later develop into legless, bag-like larvæ of the Ichneumon type. It is interesting to note that in the Strepsiptera the adult female prolongs the parasitic habit of the larva, while the adult Meloidæ, or oil-beetles are rather sluggish and seem to show other after-effects of their larval life. There are also many insects, like the true lice and bird lice which are, to all intents and purposes, permanent parasites comparable with the ectoparasitic flukes, though they never exhibit such extreme modifications. And, finally, there are other animals besides insects that have parasitic larval and free adult stages, *e.g.*, the fresh-water mussels.[6]

Zoologists have naturally been deeply impressed by such wonderful parasites as the tape-worms, flukes and Sacculina and have regarded them as fine examples of degeneration or degradation. Many, indeed, have dwelt on these words in a manner which leaves no doubt that they are used in a purely anthropomorphic sense as implying deterioration or "an impairment of natural or proper qualities" in the parasites, notwithstanding Ray Lankester's assertion that "degeneration may be defined as a gradual change of the structure in which the organism becomes adapted to less varied and less complex conditions of life."[7] It is easy to trace the source of this anthropomorphism to the atrophy of the parasite's neuro-muscular system, a

---

[6] *Cf.* Lefevre and Curtis, "Reproduction and Parasitism in the Unionidæ," *Journ. Exper. Zool.*, IX, No. 1, 1910, pp. 79–115, 5 pls.

[7] "Degeneration," p. 32.

system by which we as intellectual beings necessarily set great store, and the hypertrophy of the alimentary and reproductive organs, which, notwithstanding their immense biological significance, have nevertheless been assigned a very inferior place in our scheme of ethical values. But parasites may properly be regarded as more advanced organisms than the predators, for they have not only had a more eventful phylogenetic career, but, during their long history, have learned to use other organisms in a very economical manner as instruments of nutrition. From a consistent biological point of view, therefore, and from one embracing insect as well as vermian and crustacean parasites, it is evident that the peculiar convergent complexions of these organisms should be attributed to *specialization*. "Degeneration" is properly a pathological term, and parasites, however pathogenic they may be, are, of course, no more pathological, or diseased than predatory animals. There is some evidence to show that the Myzostomes have persisted in their modern form since Silurian times, with a conservatism equalled only by that of their Crinoid hosts. If all the generations of these peculiar Annelids have been pathological for millions of years, they should long since have disappeared from the waters of the globe, but we find that though many or all of the original species have doubtless become extinct, this was probably due simply to the extinction of their hosts, for nearly every extant species of Crinoid supports at least one species of Myzostoma. Moreover, if we regard parasitic modifications as an expression of degeneration, we must suppose that such forms as the adult Ichneumon are produced by a post-larval regeneration. Apart from adding an unusual meaning to the word "regeneration," this fails to express the actual conditions correctly. The whole ontogeny of such insects is in reality very highly specialized, the adult representing in many particulars as great a departure from the primitive insect type as the larva, albeit in a very different direction. In discussions of this subject I would therefore substitute the words "parasitic specialization" for such terms as "degeneration" and "degradation." Together with these, another term, "retrogression," should be avoided, for the reason that the parasitic modifications of structure to which it is often applied can be more properly attributed to "arrest of development."

It will be seen from the foregoing discussion that the leading peculiarity of insect parasitism, at least in such groups as the Hymenoptera and Diptera, which are almost the only ones of value in controlling noxious insects, is *the restriction of the parasitic habit to the sluggish larva and the specialization of the free adult for the purpose of disseminating the species and of placing the coming generation in intimate contact with the host.* No one who observes one of our large, graceful Ichneumonids, such as *Megarhyssa lunator*, alighting on a tree-trunk and then conveying its greatly attenuated eggs by means of its long hair-like ovipositor through some three inches of hard wood into the burrow of a Tremex larva, the presence of which it has been able to detect by means of its marvelously acute sense-organs, can fail to appreciate the advantages of such a method of bringing a parasite to its host, rather than by the tape-worm's shot-gun method of scattering minute eggs about promiscuously, or by the Sacculina's almost equally haphazard method of employing minute, feeble, aquatic larvæ.

Another peculiarity of economic importance in the parasitism of Hymenopterous and Dipterous insects is its *highly predatory character*, for the voracious larvæ of these orders almost invariably kill their hosts.[8] Other forms, like the Strepsiptera, which permit their hosts to reach the adult stage, nevertheless destroy their gonads and thus decrease the reproductivity of the host species. In some cases, indeed, it is impossible to decide whether we are dealing with parasitism or predatism. The Sphex, that lays her eggs on caterpillars which she has carefully paralyzed, is commonly regarded as a predatory insect, but she is from another point of view, an even more specialized parasite than the Ichneumon. Her sting immobilizes but does not kill the active full-grown or nearly full-grown caterpillars, and her larvæ are careful to feed in such a manner as to spare as long as possible the life of their victims. We have here merely a farther extension of the maternal instincts primarily devoted exclusively to bringing about the union of the parasite with the host, to a unique and effective preparation of the host's body for easier exploitation by the parasite.

A third peculiarity of economic importance in the Hymenopterous and Dipterous insects is their *pronounced tendency to confine their attacks to species of large, recently developed and eminently noxious groups*, such as the Lepidoptera, Coleoptera, Homoptera and other plant-destroying insects.

There are also a number of peculiarities some of which are of less practical but of no less theoretical interest. These, which I must consider very briefly in the limited space at my disposal, are the following:

1. The occurrence of *hypermetamorphosis* which is frequently exhibited by parasitic insects often of the most remote taxonomic affinities, such as the Proctotrypids, and certain Chalcidids (Orasema and Perilampus) among the Hymenoptera, Mantispa among the Neuroptera, the whole order of Strepsiptera, and the Meloidæ and Rhipiphoridæ among Coleoptera. The complication of development arises in all of these cases from an inability of the mother insect to find the host or at any rate to reach it during the proper

---

[8] It would seem that the death of the insect host is necessitated either by the relatively very large size of its insect parasite at maturity, when acting alone, or (in cases of polyembryony and simultaneous infestation by several individuals of the same species) to the equally considerable bulk of a number of small parasites acting together. The comparatively slight difference in stature between host and parasite is certainly one of the most remarkable peculiarities of insect parasitism.

ontogenetic stage, and hence from the need of an active and inquisitive first larval stage to supply this defect.

2. The prevalence of *hyperparasitism*. We may distinguish primary, secondary, tertiary, quaternary and even quinary parasites among insects, according to the principle of the "little fleas *ad infinitum*." The numerical appellations in this series have been restricted to insects parasitic on other insects, although the primary parasites are really secondaries when they attack insects like caterpillars, since these are, of course, plant-parasites.[9]

3. The absence in parasitic insects of *hermaphroditism*, a phenomenon so prevalent among vermian, crustacean and annelidan parasites. Only one small group of insects is known to be hermaphroditic, namely, the Termitoxeniidæ, comprising a few genera of extraordinary flies that live in termite nests.[10]

4. The rare occurrence of *heteræcism*, or change of host, a phenomenon very prevalent among tape-worms and flukes. It has been developed, however, within apparently very recent times in such groups as the plant-lice and in certain myrmecophilous beetles of the genera Atemeles in Eurasia and Xenodusa in North America.

5. The increasing development of *viviparity* as seen in such a series of parasites as Hemimerus, which, according to Hansen and Heymons, develops within the ovary of its mother,[11] the larviparous Tachinidæ and Sarcophagidæ, the nymphiparous Hippoboscidæ, Nycteribidæ and plant-lice.

6. The development of *polyembryony* among the Chalcidid and Proctotrypid Hymenoptera. Owing to the greatly increased reproductivity of these parasites through the formation of dozens or even hundreds of adults from a single original egg by a process not unlike that employed in the egg-shaking experiments of our laboratories, this phenomenon, though restricted to comparatively few species, is nevertheless of considerable economic importance.[12]

---

[9] Fiske ("Superparasitism: An Important Factor in the Natural Control of Insects," *Journ. Econ. Ent.*, III, 1910, pp. 88-97) and Pierce ("On Some Phases of Parasitism Displayed by Insect Enemies of Weevils," *ibid.*, III, 1910, pp. 451-458) have distinguished between "hyperparasitism" and "superparasitism." The former term is defined by Pierce as "the normal attack of a parasite species upon another parasite species," whereas superparasitism "occurs when a normally primary parasite attacks a host already parasitized, and the result is that the latest comer generally attacks its predecessor." The distinction is important, but for the sake of brevity I have not introduced it into the text.

[10] It has been shown recently that these insects are not hermaphroditic.

[11] *Cf.* Hansen, "On the Structure and Habits of *Hemimerus talpoides* Walk.," *Entom. Tijdskr. Arg.*, XV, 1894, and Heymons, "Eine Plazenta bei einem Insekt (*Hemimerus*)," *Verh. deutsch. zool. Gesellsch.*, 1909, pp. 97-107, 3 figs.

[12] The occurrence of polyembryony was first clearly recognized and thoroughly investigated by Marchal in *Encyrtus fuscicollis* ("Recherches sur la Biologie et le Développement des

7. The development of *social life* among insects. This, as I have shown on former occasions, has its origin both ontogenetically and phylogenetically in the parasitism of the offspring on the parent.[13]

Paleontology seems to show very clearly the conditions that have favored the enormous development of parasitism among insects especially within comparatively recent times. Some of these conditions are:

1. The *diminution in insect stature* which occurred in the late Carboniferous and during the Permian and seems to have been originally in great part an adaptation to increased reproduction and dispersal. Other things equal, a small animal will, for very obvious reasons, become a parasite more easily than a large one.

2. The *development of metamorphosis*. This was already clearly established in the earliest known insects, the Palæodictyoptera, which were predatory and amphibiotic like the may-flies of the present-day, living in the water during their apterous larval stages and spending their winged imaginal stage in the air. They show plainly the great peculiarity of insect development, *i.e.*, metamorphosis *succeeding* growth and not *preceding* it as in the crustaceans, mollusks and Annelids. Dimly foreshadowed in this method of development are the more complete modern types of insect metamorphosis, which have their morphological origin, as we now know, in a doubling of most of the rudiments of the organs in the embryo. On hatching, one set of these rudiments develops immediately into the larval body, while the other set remains in abeyance in the form of minute germinal centres, or histoblasts, from which the body of the adult will be fashioned during the quiescent pupal stage. The higher insects are therefore beautiful examples

---

Hyménopteres Parasites. I. La Polyembryonie Spécifique ou Germinogonie," *Arch. Zool. Expér. Gén.* (4), II, 1904, pp. 257-335, 5 pls., and an earlier paper: "La dissociation de l'oeuf en un grand nombre d'individus distincts chez l'*Encyrtus fuscicollis*," *C. R. Acad. Sci. Paris*, CXXVI 1898, pp. 662-664), although Bugnion ("Recherches sur le développement postembryonnaire, l'anatomie et les mœurs de l'*Encyrtus fuscicollis*," *Rec. Zool. Suisse*, V., 1891, pp. 435-534, 6 pls.) had previously studied the same insect. Silvestri has published several valuable papers on polyembryony, the most important being "Contribuzioni alla Conscenza Biologica degli Imenotteri Parassiti. I. Biologia del *Litomastix truncatellus* (Dalm.)," *Ann. R. Scuola Sup. d'Agric. Portici*, VI, 1906, pp. 1–51, 5 pls. More recently important contributions to our knowledge of polyembryony have been made by Patterson, Leiby and others.

[13] Wheeler, "Ants, their Structure, Development and Behavior," Columbia Univ. Press, 1910. Holmgren ("Termitenstudien, I. Anatomische Untersuchungen," *R. Svensk. Vetensk. Handl.*, XLIV, No. 3, 1909, 216 pp., 3 pls., 76 text-figs.) and Escherich ("Termitenleben auf Ceylon," Gustav Fischer, Jena, 1911, 262 pp., 3 pls., 68 text-figs.) have accumulated much evidence to support the conclusion that the mutual attraction among the individuals and the development of the castes of the termite colony are due to the habit of these insects of feeding on the fatty exudates of one another's bodies and on that of their queens. This may also be true of ants and other colonial insects. A very similar method of feeding on the surface secretions of their host-ants is adopted by certain myrmecophiles (Oxysoma, Attaphila and Myrmecophila) and certain parasitic ants (*Leptothorax emersoni*) (see p. 87).

of double personality, much more perfect examples of this phenomenon, in fact, than any that has been discovered in man. The larval insect is, if I may be permitted to lapse for a moment into anthropomorphism, a sluggish, greedy, self-centred creature, while the adult is industrious, abstemious and highly altruistic, concentrating its activities on reproduction and the dissemination of the species. Unlike ourselves, who are Mr. Hydes and Dr. Jekylls in varying degrees, for brief alternating periods in our lives, or even simultaneously, the youthful insect sows its wild oats with a vengeance as a glutton or even as an assassin and then experiences a change of heart and reforms for good and all.

Parasitism must have been very easily grafted on to such a sharply dichotomic method of development as that of the holometabolous insects, for the larvæ of the predators are already much inclined to sloth and gluttony when the food supply is abundant, and comparatively little modification would be required to convert them into parasites. But the same peculiarities of metamorphosis have also made the holometabolic insects ideal hosts. We have already seen that insects, as a rule, are themselves not only parasitic during larval life, but also prefer larvæ as hosts. It is not improbable that this is the primitive, and that parasitism on the egg, pupa or adult is a secondary, or derivative condition. The real secret of both host and parasite being larvæ lies in the peculiar significance of anabolism in this stage. The host accumulates great quantities of fats and proteins as a so-called "fat-body," which is of little or no immediate use to the organism itself, but is stored up to be utilized during metamorphosis. This fat body may, therefore, be devoured by the parasite and converted into its own fat-body without seriously injuring the host. Furthermore, the fact that the parasite, too, stores up its food in the form of a fat-body instead of at once turning it over to its gonads and becoming reproductive, accounts for the striking differences between the insect parasite, on the one hand, and the tape-worm and Sacculina, on the other. The few exceptions among insects, such as the female Strepsiptera, in which the food taken by the larval parasite from its host is soon turned over to the gonads and used for reproduction, leads to a permanent parasitism resembling that of the tape-worms or the adult Sacculina. The larva is at once arrested in its development and begins to reproduce by pædogenesis. We may conclude, therefore, that the existence of parasites of the Ichneumon type, with free, active and highly developed adults is rendered possible by an inhibition of gonadic growth during larval life; whereas parasites which begin to reproduce while still living with their hosts are thereby prevented from either leaving them or undergoing further morphological differentiation.[11]

---

[11] This singular ability of the insect to inhibit the development and growth of its gonads

3. A third primitive peculiarity of holometabolic insects, which seems greatly to have favored parasitism is the astonishing *rapidity of their larval metabolism and growth* and the equally remarkable *quiescence of their pupal stages*. These have, of course, converted insects into the most wonderful opportunists, through enabling them to take advantage not only of the changing seasons and the very diverse physical conditions of our planet, but also of the most evanescent supplies of food, both living and in process of decomposition.

4. *Parthenogenesis* may also be cited as a widely prevalent phenomenon, which has been put to good use by parasitic insects. Like polyembryony, it has an economic significance, because it enables such noxious parasites as the plant-lice to multiply enormously under conditions that would preclude reproduction in non-parthenogenetic species, and for the same reason greatly assists many Hymenopterous parasites in checking the undue multiplication of these and other plant-destroying insects.

Although I may have had little difficulty in convincing you that parasitism is a very specialized kind of behavior, you will probably still be of opinion that there is something inherently and radically wrong with animals that resort to it rather than to predatism, mutualism or some other means of maintaining their vital activities. It must, of course, be admitted that in becoming satellites of their hosts, parasites have renounced the primitive, wasteful and erratic freedom of the predator and are compelled to mould their activities on those of the host. This necessarily puts them in a condition of such abject dependence that their very existence as individuals and species is imperilled whenever they overstep that margin of vitality which the host, like every other healthy organism, can afford to sacrifice to the accidents of its environment.[15]

The parasite not only tends to restrict itself to the use of a particular

---

till adult life is not only significant in connection with the development of parasitism within the group, but is also of fundamental importance in the development of colonial life among all the social insects. In the worker castes of these organisms the inhibition of the gonads, except under unusual conditions, is simply prolonged into and throughout adult life. Perhaps in last analysis this inhibition is merely a special manifestation of the extraordinary independence of the insect soma and germ-plasm, as has been so beautifully shown in the castration and transplantation experiments of Oudemans, Meisenheimer, Regen and Kopeč. For a discussion of this subject see my paper, "The Effects of Parasitic and Other Kinds of Castration in Insects," *Journ. Exp. Zool.*, VIII, No. 4, 1910, pp. 377–438, 7 figs.

[15] Within this "margin of vitality" must also be included the reproductivity of the host species. Thus certain ants, like *Formica fusca*, throughout the north temperate zone, are able to survive the inroads of a number of parasitic ants (*Polyergus rufescens*, *Formica sanguinea*, *F. rufa*, *F. exsecta*, and many allied species), largely on account of their great reproductive powers, coupled with an ability to live in the most diverse physiographic conditions.

host as a food-procuring instrument, but is also compelled to exercise the most exquisite care in the use of this instrument. From the very nature of the situation, therefore, parasitism is an extremely precarious type of behavior. But this is true also of all highly specialized behavior, that of biologists included, and points the way to, but does not constitute, the real difficulty with parasitism. This, I take it, is the suppression of the voluntary movements, which necessarily results from the intimate host relations, especially when these are confined, as is so often the case, to some one particular organ or tissue. It is not, therefore, the parasite's habit of taking something for nothing from another organism, that is so fatal, for all creatures, in matters relating to nutrition, find it more blessed to receive than to give, but the acceptance of the most important supply of its energy under conditions that preclude an exercise of the muscular and hence also of the sensory and nervous activities and restrict its vital activities to a round of assimilation, metabolism and reproduction. This unbalancing of functions is probably hastened by a kind of intraorganismal parasitism or "Kampf der Theile" in Roux's sense, the alimentary and reproductive tissues drawing their nutriment not only from the host but also from the more inactive tissues of the parasite's own body. That this torpor, or inactivity of the neuromuscular system is at the bottom of the peculiar disability of parasites is shown by many non-parasitic organisms, which have easy access to an abundant food supply consisting of dead or inorganic substances. Most plants and many invertebrates, such as the barnacles, and especially the scavengers among insects, exhibit essentially the same modifications as parasites. In fact, the larval stages of many insects that feed on carrion or decomposing animal and vegetable matter, are quite indistinguishable from parasitic larvæ. This and the further fact that plant-eating species are not generally regarded as parasites by entomologists have led to considerable confusion in certain accounts of insect parasitism.

While most parasites among the lower invertebrates have never succeeded in freeing themselves from the tyranny of the host relation and the fatal torpor to which it inevitably leads, this is, as we have seen, by no means true of the typical insect parasites. To the ontogeny of these organisms the dictum "once a parasite, always a parasite" most certainly does not apply. That it is inapplicable to their phylogeny I am not prepared to say, although I am unable to think of any non-parasitic insects that show evidence of descent from parasitic species. There can be no doubt, however, that parasites are still able to give rise to new specific forms. This capacity is without doubt very feeble or languishing in the permanent parasites of the tape-worm and Sacculina types as compared with that of the insects. Indeed, there is much evidence to show that in insects, parasitism, far from interfering with the process of species formation, may actually have a tendency to favor or accelerate it. Sharp estimates the number of species of parasitic Hymenoptera on our globe at 200,000, and of this vast number probably 80,000 belong to a single family, the Chalcididæ, of which only some 6,000 species have been described. Another parasitic family, the Tachinidæ, belonging to the great order Diptera, seems to be in such an active stage of species formation that the most diligent and thoughtful students of the group flounder about in it with a dazed and almost ludicrous helplessness. And not only is practically the whole enormous group of moths and butterflies to be regarded as parasitic, but the same is true also of untold legions of plant-lice, scale-insects and beetles. Hyperparasitism, which may be regarded as a kind of permutation of parasitism, must also be mentioned in this connection, because it gives us a glimpse of the virgin fields which the holometabolic insects, owing to their peculiar method of development, are beginning to invade.

I believe that the foregoing discussion of the peculiarities of insect parasites adequately supports the view that these organisms are eminently fitted to function in controlling the depredations of injurious insects. That they can not be regarded as instruments of extermination is obvious from the fact that under natural conditions the complete extinction of the host species involves the destruction of the parasitic species, unless the latter is able to live on more than one host. Although it is not improbable that during geological time such joint extermination of host and parasite has repeatedly occurred, we are unable to cite any case that has fallen under the observation of the entomologist. Purely local extermination of injurious hosts by their parasites has, however, been observed.

Before bringing my lecture to a conclusion two matters must be briefly discussed. One of these, which is mainly of theoretical interest, relates to the development of the parasite's association with its host, the other, of more practical significance, to the methods of greatest promise in the study of insect parasitism. We need not stop to consider cases of the tape-worm type which reach their hosts by chance. In the two other types which I have distinguished, we have the association with the host established through the initiative of the larval parasite itself (Sacculina type) or through the parasite's mother (insect type). While the former type does not seem to call for any special explanation, there seems, at first sight, to be something mysterious in the insect parasite, for when we see an adult organism, such as an Ichneumon, coming from a distance—out of the blue, so to speak—and seeking out a concealed larva in which to deposit its egg, we are tempted to turn to some teleological explanation, such as is implied in the common conception of "instinct," or perhaps to something in the nature of a "divinatory sympathy" between parasite and host. Although such conceptions are necessarily anthropomorphic, I would not deny them a certain, albeit provisional, value. As biologists, however, we are fortunately in a position to suggest a simpler explanation. The intimate practical knowledge (*sit venia verbo*) which the mother Ichneumon possesses of the host, loses much of its mystery when we stop to consider, that she has during her own larval life, devoured just such an insect, for the same reason that we may be said to have an excellent practical knowledge of an orange after we have eaten it. The Ichneumon is therefore familiar with the situation, feeling, odor and taste of the creature in which she will lay her eggs, if we make the not improbable assumption that the results of her own larval experience persist as mnemic factors, notwithstanding the profound morphological and physiological changes which she has undergone during metamorphosis. There would then be nothing surprising in her tropism-like reactions to the mechanical and chemical stimuli represented by the host larva and its immediate environment.

As the time at my disposal is nearly exhausted, I must bring my discussion to a close. Having made the pilgrimage to the American Mecca of experimental zoologists, I could hardly hope for salvation if I departed without at least saluting the Kaaba. This I can do most effectively, perhaps, by calling attention to the great need of experimental work in animal and especially in insect parasitology. Biologists, during the romantic period of Darwinism, made much of the parasites. These organisms, in fact, supplied them with no end of ammunition in defence of natural selection, the influence of the environment and the biogenetic law. Then came the period of morphological minutiæ with its tacit assumption that particles of a dead organism are vastly more interesting and illuminating than the whole of a living one. During this period the parasites were, of course, sectioned and studied in the same manner as other organisms, but, since it is impossible to explain a living whole by pulling it to pieces and sticking the inert fragments together again, parasitism, which is a process and not a thing, retained its ethological interest mainly for biologists who were engaged in the practical applications of their science.[16]

Now that we have reached the third period, or that of emphasis on experiment with the living organism as the best means of elucidating the life-processes, those of us who had the misfortune to live and exhaust our

---

[16] In support of this statement the reader may be referred to the following general articles on insect parasitism, written by well-known economic entomologists in our own country during the period characterized by a very exclusive occupation with morphology in our universities: Riley, "Parasitism in Insects," *Proceed. Ent. Soc. Wash.*, II, No. 4, 1893, 35 pp.; Webster, "Insect Parasites," 15 pp. (reprint without date); Osborn, "Insects Affecting Domestic Animals," Bull. No. 5, U. S. Dept. Agric., 1896, 302 pp., 170 figs.; Howard, "A Study in Insect Parasitism," Tech. Ser. No. 5, U. S. Dept. Agric., 1897.

greatest enthusiasm during the romantic and morphological periods, can, I suppose, do nothing better with the meager remnant of our vitality than pray for breadth of sympathetic vision on the part of our younger, more numerous and more vigorous contemporaries. The splendid achievements of the investigators who assemble here every summer certainly whet one's desire to see experimental work of the same character accomplished in parasitology. A certain amount of simple experimental work on social parasitism in ants has been inaugurated by Wasmann and myself and continued with interesting results by Santschi, Emery, Viehmeyer, Donisthorpe and others, but more important work, having for its object the artificial production of individual parasites and such studies on the behavior of their descendants as those recently made by Kammerer on the offspring of Amphibia, whose breeding habits had been artificially modified, have not yet been undertaken. Here again, as in so many other cases, the botanists are blazing the trail for the zoologists. The familiarity of the former with grafting, which is merely an artificially induced parasitism, has led them to undertake interesting experiments, like those recently published by Pierce[17] and MacDougal and Cannon.[18] And although these experiments yielded less striking results than might, perhaps, have been expected, they nevertheless emphasize an important fact, which all biologists, except systematists and paleontologists, are too apt to overlook, namely, the extraordinary stability of specialized characters.

Experimental zoologists, including the students of animal behavior, are most keenly interested in the modifiability of the organism, and their experiments are usually devised for the special purpose of determining the amplitude and peculiarities of this modifiability. The entomologist, however, who is attempting to use parasitic insects as tools or implements in controlling the depredations of other insects, is primarily interested in the stability of structure and constancy of behavior. This follows from the very nature of his work. As the essential excellence of a tool consists in its remaining the same as it was when it left the hands of the manufacturer, so a parasitic species can be used as an efficient tool only if it behaves generation after generation with uniform constancy. Hence in combating pests, only those parasitic insects can be utilized to advantage that are not only prolific and will endure the climatic conditions into which they have been artificially introduced, but will maintain very definite relations only with individuals of a single or of a very few host species and destroy them in their earliest

---

17 "Das Eindringen von Wurzeln in lebendige Gewebe," *Botan. Zeitg.*, III, 1894, pp. 169–176; "Artificial Parasitism," *Botan. Gazette*, XXXVIII, 1904, pp. 214–217.

18 "The Conditions of Parasitism in Plants," Carnegie Inst. Publ., Washington, 1910, 60 pp., 10 pls., 2 text-figs.

possible ontogenetic stage before they can do extensive damage.[19] Such constancy is especially necessary in primary and tertiary parasites, since whenever these show a tendency to become secondaries and quaternaries, as is sometimes the case, they become harmful instead of beneficial.[20]

It is clear that the determination of the constancy or invariability of parasitic reactions as a basis for practical applications requires, if anything, an even greater insistence on the experimental method than does the determination of the range and character of modifiability for purely theoretical purposes. Ever since the days of Redi both theoretical and practical entomologists have resorted to the experimental method and therefore have no reason to regard themselves as behind the times in appreciation of what some zoologists have been heralding as a recent dispensation. In other respects, however, the students of insect life are "old fashioned" and resemble the botanists more closely than the zoologists, in that they are constrained by the extraordinary intricacy of their science to maintain the closest and most sympathetic cooperation with the taxonomists, morphologists, and students of geographical distribution. Without this cooperation their studies of insect parasitism would resolve themselves into a weltering chaos.

---

[19] Howard and Fiske (*loc. cit.*, p. 204) express a similar opinion when they say that "it is probably true also that among those parasites which are the most closely restricted in their host relationships are to be found those which are the most effective in bringing about the control of their respective hosts. This is primarily due to the fact that a correlation usually exists between the life and seasonal history of such a parasite and some one or more hosts which it is particularly fitted to attack. The existence of a correlation between parasite and host of such intimate character makes possible the continued existence of the parasite independently of alternate hosts, and it is thus enabled to keep pace with the one species upon which it is peculiarly fitted to prey when other circumstances are favorable to its increase. Some of the most interesting examples of correlation of this sort which have yet come to attention are to be found among the tachinid parasites of the gypsy moth or the brown-tail moth, and on this account as well as on a purely empirical basis they are now considered much more likely to become important enemies of these hosts than before their characteristics were so well understood."

[20] A very instructive case of such instability in hyperparasitism, or rather superparasitism, is seen in *Pteromalus egregius*, which was introduced into Massachusetts as a primary parasite of the brown-tail caterpillar. This European parasite, as Fiske has recently shown (Howard and Fiske, *loc. cit.*, p. 267 *et seq.*) has not only spread over a great area in eastern New England, since it was first liberated in 1906 and 1907, but besides acting as a primary parasite, it may also behave as a secondary, tertiary or quaternary superparasite.

A SOLITARY WASP (*APHILANTHOPS FRIGIDUS* F. SMITH) THAT PROVISIONS ITS NEST WITH QUEEN ANTS

FROM THE *Journal of Animal Behavior*, SEPTEMBER–OCTOBER, III, 1913

Chaque hyménoptère giboyeur est cantonné dans un genre de venaison, habituellement très limité. Il a son gibier attiré, hors duquel tout lui est suspect, odieux. Les embûches de l'expérimenteur qui lui soutire sa proie pour lui en jeter une autre en échange, les émotions du propriétaire détroussé et retrouvant aussi-tôt son bien, mais sous une autre forme, ne peuvent lui donner le change. Obstinément il refuse ce qui est étranger à son lot, à l'instant il accepte ce qui en fait partie. D'où provient cette répugnance invincible pour des vivres non usités dans la famille?

J. H. FABRE,
"SOUVENIRS ENTOMOLOGIQUES," III

SEVERAL years ago a correspondent sent me a few specimens of a beautiful black and yellow wasp, *Aphilanthops frigidus* F. Smith, each mounted on a pin with a winged queen of the typical *Formica fusca* L. These specimens were collected August 21, 1903, at Silver Creek, Baraga County, in northern Michigan, by Mr. Morgan Hebard. Although it seemed very probable that the ants had been taken as the prey of the wasps, I was not sure of this fact till the past summer (1913) when I was able to study the habits of these insects in the neighborhood of Boston. During this season, in fact, they seem to have been so abundant as to have attracted the attention of other entomologists in New England and Canada.

The nearctic genus Aphilanthops was first separated from the closely related Philanthus by Patton in 1880 and based on *Ph. frigidus* F. Smith as the type. Since that time Fox (1894), Baker (1895), Cockerell (1895, 1896) and Dunning (1896, 1898) have described a number of additional species. Eleven of these all together are enumerated by Dunning in his monograph of the genus (1898), all confined to the western states, except the type *A. frigidus*. This was originally described from Nova Scotia, but is now known to range over Ontario and New England, as far west as Illinois and as far south as New Jersey. Two other species from Mexico have been referred to the genus Aphilanthops by Cameron, but Cockerell believes that they really belong to the genus Eucerceris.

Concerning the habits of Aphilanthops nothing has been published, except the following observations by Ainslee (1909) on *A. taurulus* Ckll.: "Early in August, 1908, while marooned at Albuquerque, New Mexico, waiting for delayed mail, I noticed one day beside a concrete walk that bordered a vacant lot in that city a throng of large red ants which resembled *Pogonomyrmex occidentalis*. The bunch was seething with excitement, and stragglers were continually coming and going. As I watched I noticed a small quadrate-headed wasp drop from the upper air to the hard-trodden soil, alighting without previous reconnoitering. She stood perfectly motionless, not even dressing herself after the manner of her kind when idle. Presently an ant hurried by, busy about nothing, as usual, when instantly the wasp gave chase. The ant dodged and doubled as it fled, but the wasp overtook and seized it after a very brief and intensely active resistance, for a Pogonomyrmex is by no means a helpless infant in a skirmish. The wasp and its riotous victim rose heavily into the air and ascended at a sharp angle of flight, until they were lost in the blue of the sky. During the next few minutes I saw the same performance repeated again and again, with variations, until dozens of the ants had disappeared heavenward with the predatory wasps.

"So intent were the wasps on this work that they seemed not in the least disturbed by my presence, and I managed to secure a number of both wasps and ants by taking quick advantage of the struggle always incident to the moment of capture.

"Occasionally an ant, when pursued, would dodge around a blade of grass or rush beneath some welcome shelter and elude its hunter, but this happened in only a few cases. So swift and certain were the motions of the wasps that even with a vantage of six inches or more an ant once followed was almost certainly doomed. The wasps never, so far as I observed, assisted themselves with their wings to gain speed, but played fair with their victims and ran them down. The struggle generally lasted a second or two on the ground, and, as I have said, appeared to be continued fiercely in the air, judging from the frenzied actions of the two as they rose aloft." Ainslee mentions another, possibly undescribed species of Aphilanthops which he took at the same time preying on the same ants. Specimens of these, sent me for identification, proved to belong to the large, coarsely sculptured form of agricultural ant, *Pogonomyrmex barbatus* F. Smith subsp. *rugosus* Emery, which makes extensive clearings in the deserts of New Mexico and Arizona. Although not expressly stated, it is clear from Ainslee's vivid description, that *A. taurulus* preys on the workers of the Pogonomyrmex. As will be seen from the following account, our eastern *A. frigidus*, though it also provisions its nests with ants, selects only the fertile females, or queens.

My observations on *frigidus* were made in the Blue Hills, near Boston, during July and August. The wasps were found to be at the height of their activities from July 26 to August 16. By the end of the latter month all the wasps had disappeared and the nests had been effaced by recent heavy showers. Like the species of Bembex, *frigidus* nests in colonies. Several of these were located, but observations were confined to three, which happened to be within easy reach from Boston. They were situated in the ravine that separates Great Blue Hill from the adjacent portion of the range, two of them being in the stony and sandy trail passing through Wild Cat Notch, the other on Administration Road. Each colony covered several square yards of territory and comprised from about 30 to 60 nests, the entrances of which were often within an inch or two of one another. In two of the colonies the nests were interspersed with the burrows of large Crabronid wasps and of Cicindelid larvæ. The wasps prefer to make their burrows on slightly sloping surfaces. The opening, a little more than a quarter of an inch in diameter, is semi-circular and lies in front of a little pile of earth that has been thrown out by the burrowing insect. The wasp spends much time, especially during the morning hours or on cloudy days, sitting in her burrow and looking out with her conspicuous black face, marked with three vertical yellow bands like exclamation points. As the heat of the day increases, however, she becomes more active and either does more or less excavating in the nest, kicking the earth out backwards from the entrance to a distance of a few inches, or goes off foraging for her prey. In all of this behavior she exhibits a striking resemblance to Bembex.

The burrow descends obliquely and abruptly to a depth of only six to eight inches, where it terminates in a small cell. There are also two or three other cells, but it was found impossible to determine their precise relations to the other portions of the nest, owing to the very dry and crumbling condition of the soil and to the fact that each cell is closed off from the main burrow. A slender twig or grass culm carefully introduced into the opening of the nest as a probe was invariably stopped a few inches below the surface by an earthen plug or partition which has to be removed by the wasp whenever she enters the deeper portions of the nest.

The prey of *A. frigidus* consists exclusively of winged queen ants belonging to the genus Formica. Specimens wrested from the wasps while being brought in and also dug from the nests, belonged to the following four forms:

Formica fusca L. var. *subsericea* Say.

F. fusca L. (typical).

F. (*Neoformica*) *pallidefulva* Latr. subsp. *nitidiventris* Emery.

F. (*Proformica*) *neogagates* Emery.

Most of the specimens belonged to *subsericea*, very few to *neogagates*, while the true *fusca* was more abundantly represented than *nitidiventris*. The nature of the prey, however, depends on the situation of the Aphilanthops colony. Thus the prey in the Administration Road colony, which was situated very near the northern side of Great Blue Hill, consisted almost exclusively of the typical *fusca*, which is the only form of the species on this more boreal slope, whereas the more xerothermic *subsericea* and *nitidiventris* were the only forms found in the colony situated on the southern slope. As these two colonies were less than a mile apart, it is clear that the wasps do not range very far in search of their prey. The same wasp may collect queens of two or even three of the four Formicas enumerated above. The pronounced preference for the queens of *fusca* and its variety *subsericea* is shown also in other portions of the geographical range of *A. frigidus*. I have already stated that the specimens of this wasp taken by Hebard in northern Michigan had been preying on *fusca*. Recently while I was visiting my friend Dr. C. Gordon Hewitt at Ottawa, Ontario, the noted melittologist, Mr. F. W. L. Sladen, showed me a specimen of the wasp taken August 12, 1913, with a winged queen of the typical *fusca*. He pointed out to me the site of the colony where he had seen this and other specimens of the wasps carrying in their prey, in the midst of a cultivated plot on the Central Experimental Farm, but all traces of the nests had disappeared at the time of my visit (September 2). During August, Mr. C. W. Johnson brought me a specimen of *frigidus* mounted on a pin with a winged female of *subsericea*, which he had taken July 31 at Westport Factory, Mass., where he had found a large colony of the wasps nesting in a pebbly woodroad. They were bringing in the *subsericea* queens in great numbers and, curiously enough, were themselves being captured and destroyed by large robber-flies (*Deromyia umbrina*).

The queens of the four Formicas enumerated above differ considerably from one another, those of *subsericea* being much larger than any of the others and those of *nitidiventris* differing greatly in color, as they have the head and thorax red instead of black. The queens of the true *fusca* and *neogagates* are much alike in size and in being very smooth and shining, but the latter species is readily distinguished by the red color of the legs and the erect hairs on the lower surface of the head. It is significant that all these queens belong to species noted for their cowardly disposition, and as the normal hosts of the slave-making ants (*Polyergus lucidus* Mayr and the various subspecies of *Formica sanguinea* Latr.) and of a long series of temporary social parasites (the various subspecies of *F. rufa* L., *truncicola* Nyl., *exsectoides* Forel, etc.). Although nearly all of these predatory and parasitic ants are abundant in the Blue Hills, none of their queens is captured by the Aphilanthops. We must assume, therefore, that this wasp has learned to discriminate between different species of Formica and to avoid the more vigorous and aggressive queens of the *sanguinea*, *rufa* and *exsecta* groups. The queens of the *microgyna* group, represented in the Blue Hills by *F. difficilis* Emery, are in all probability avoided on account of their diminutive stature.

That the wasps capture the Formica queens while they are celebrating their nuptial flight and do not take them from their nests, was clear from observations made July 26, for on that day flights of *subsericea* and *sanguinea* subsp. *rubicunda* Emery were observed in the Blue Hills and the wasps were seen bringing in numbers of the queens of the former variety. Still I did not see the wasps in the act of capturing their prey till August 15, when there was a great flight from all the colonies of *subsericea* in Forest Hills and Jamaica Plain, Boston. While walking along the street I saw an Aphilanthops suddenly swoop down upon a queen that had just settled on the ground. Before I could reach the spot the ant had been stung and the wasp was dragging her along by the antennæ and trying to rise with her into the air.

The queen ants attract the attention of the wasps only during the few hours that intervene between the nuptial flight and the loss of their wings. On several occasions I saw deälated queens crossing the roads near the wasp colonies or even running near their nest entrances without being noticed by the wasps that were flying about. And on one occasion when I confined a deälated *subsericea* queen in a bottle with an Aphilanthops, the ant was still uninjured more than 24 hours later. It is probable, therefore, that the wasp responds only to the visual stimulus of the winged queen, which is, of course, very different from that of the same insect with her wings removed.

The ants are merely stung and paralyzed. The wasp does not mutilate or malaxate her victims, which still move their palpi, legs and antennæ either spontaneously or when touched, for several hours or even for a few days after they have been captured and placed in the nest. In the course of a few days and often sooner, however, all signs of movement have ceased, although the insects still have a fresh appearance, with flexible limbs and without any indications of the drying up of the tissues.

The wasp carries the ant under her body, supporting it by means of her middle and hind legs, while she holds its antennæ in her mandibles. Sometimes when she happens to settle for a moment on a slanting leaf-blade and is therefore obliged to stand on her legs, one may see the ant dangle for a moment from her jaws. On reaching the nest she may begin to enlarge the entrance by digging, still holding the ant by its antennæ and kicking the earth backward around it with her hind legs. Sometimes she may go directly into the nest without any preliminary digging and without dropping her prey. Occasionally, however, she may be seen to drop it just at the entrance, then go into the burrow, turn around and pull the ant in after her by one of its antennæ. This method of getting the ant into the nest is sometimes very awkwardly executed. Once I saw a wasp seize her ant by the petiole and with much effort pull it in doubled on itself. While the wasp is taking the ant into the burrow, she may be closely watched by two parasites, a beautiful metallic green Chrysis, or cuckoo-wasp, and a small gray Tachinid fly. I have not seen either of these insects oviposit on the wasp's prey, nor have I found their larvæ in the nests. The wasp usually introduces her prey into the burrow so expeditiously and then buries it so completely that these parasites must encounter great difficulties in gaining access to it.

After the ant has been dragged a few inches down the burrow, the wasp proceeds to cut off its wings. Usually she does this very neatly, although the stubs she leaves attached to the body are a little longer than they are in queen ants that have deälated themselves. More rarely the wasp simply gnaws off the tips or apical halves of the wings. That this deälation is accomplished before the ant is carried to the lower portion of the nest is shown by the fact that while excavating the nest one always finds the detached wings only a few inches below the surface and some distance from the bodies of the stored ants.

Although I excavated a considerable number of nests with the aid of

Messrs. W. M. Mann and F. X. Williams, I have had some difficulty in ascertaining the precise method employed by the Aphilanthops in rearing its young. By piecing together the observations made on different nests I have reached the conviction that the wasp secures several queen ants, usually five to seven, often belonging to more than one species, and stores them in two or three cells. Sometimes only a single ant is deposited in a cell, more frequently two, rarely three. No eggs were to be found on such stored individuals, but in each of two nests a young larva was found in a small cell devouring a single ant, which had been cut in two at the petiole. The mother Aphilanthops was sitting in the burrow in each of these nests and in one of them there was a paralyzed ant in a chamber separated from the one in which the larva was feeding. Several older nests were excavated in which there was a single adult larva spinning its cocoon and surrounded by fragments of three or four queen ants. These conditions seem to me to prove that the Aphilanthops feeds her single larva from a store of several ants deposited in several cells. The egg is evidently laid on an isolated ant which the mother wasp cuts in two in order that the larva may gain access to the nutritious contents of the thorax and gaster. Then the other ants are taken from storage and brought to the larva one by one as they are required, till all are consumed and the larva is ready to pupate. As the wasps were found in the nests even after the larvæ had pupated and in nests containing old and empty cocoons and freshly stored ants but no larvæ, we may infer that after one larva has been reared in the manner described above the mother sets about providing for another in the same nest but in a fresh chamber. Pupæ nearly ready to hatch were found August 5 and freshly pupated young August 16; young larvæ were found on the latter date and on August 8. The larva and cocoon closely resemble those of *Cerceris rybiensis* as figured by Marchal (1887).

If my interpretation of the feeding of the larva is correct, we have in Aphilanthops a very interesting condition intermediate between that of the great majority of solitary wasps, which first collect provisions and then lay an egg upon them and that of Bembex, which lays its egg on a single fly and feeds the hatching larva from day to day with fresh flies. If Fabre is right in supposing that Bembex does not always give all the captured prey to its young but keeps a portion of it temporarily out of the larva's reach in the burrow, we should have an approach to Aphilanthops, which brings in its store before beginning to feed its larva. This temporary storing of ants and the fact that they are not killed outright as in Bembex, but merely paralyzed, calls for an explanation. This, I believe, must be sought in the peculiarity of the prey, which is quite unlike that of other solitary wasps in that it can be obtained only at considerable and irregular intervals of time, namely, during the marriage flights of the various species of Formica. These flights may, to be sure, occur any time between the middle of July and the first of

September, but nearly all the colonies in a given locality celebrate their flight on the same date and often during only a few hours, so that many days may elapse before there is another flight. And although the wasps draw their supply of prey from several different species of Formica, this does not very greatly improve matters. In any event, the wasps have to make hay while the sun shines and carry in as many ants as they can secure before beginning to rear the larvæ. The need of thus temporarily storing the prey also explains why it is paralyzed and not killed outright as in the case of Bembex, nor mutilated before it is really fed to the young. Of course, it is not impossible that the Bembecine method may also be employed by Aphilanthops if nuptial flights of the ants occur in quick succession so that there is no need to store the prey before feeding it to the young, but whether this is the case or not can be determined only by future observations.

The behavior of Aphilanthops stands out in an interesting light by comparison with that of the other genera of Philanthidæ, Philanthus and Cerceris, which, unlike Aphilanthops, are represented by several species in Europe as well as in North America. Fabre (1891) has given us a fascinating account of *Philanthus apivorus* (=*triangulum*), which preys on the honey bee. He shows how this wasp kills the bee outright and then gorges itself with the honey which it presses out of the body of its victim. This extraordinary behavior he explains as a necessary adaptation to the diet of the larva, as he found by experiment that the insect in this stage thrives on nitrogenous food but is poisoned if it eats honey. The great depth of the nest of *Ph. apivorus* is given as one metre. The egg is laid on a dead bee and recently killed bees are fed to the growing larva from time to time after the manner of Bembex. Fabre also made some observations on *Ph. coronatus* Fabr. and *venustus* Rossi (=*raptor* Lep.) and found that the former provisions its nest with larger, the latter with smaller bees of the genus Halictus. He believes that in these cases also the honey is expressed from the bodies of the victims, but this opinion has not been confirmed. Ferton (1905) has also studied *Ph. venustus* and enumerates 14 different species of Halictus and one of Andrena which he found in the nests. He calls attention to the depth of the burrows but says nothing about the method of feeding the larvæ.

The only American Philanthus whose habits have been described is *Ph. punctatus* Say. According to the Peckhams (1898) this wasp nests in very small colonies and preys on bees of the genus Halictus, which it kills outright, but it does not malaxate them, nor express the honey from their bodies. The main burrow of the nest reaches a length of 22 inches. The following quotation shows that the method of rearing the young is very different from that described by Fabre for *Ph. apivorus:* "We did not find distinct pockets, as the soil was very crumbly and fell in as we worked, but we came upon clumps of bees an inch or so to one side of the gallery and about three inches apart, with larvæ in different stages of development. In one nest we found 26 bees in two clumps, some of them half-eaten and some of them fresh, but all quite dead. We have no doubt that *punctatus* completely provisions one pocket and closes the opening from it into the gallery, before she starts another, making a series of six or eight independent cells. The provision for one larva is probably 12 or 14 bees, the capture of which, in good weather, would be a fair day's work." Melander and Brues (1903) have seen this same species of Philanthus nesting in the midst of colonies of *Halictus pruinosus* Roberts and ruthlessly preying on the bees.

We are also in possession of a number of published observations on various species of Cerceris. Fabre (1894) describes the habits of several of these. One of them (*C. bupresticida* Duf.) provisions its nest with Buprestid beetles, five others (*C. arenaria*, *ferreri*, *truncatella* (=4-*cincta*), *labiata* and *julii*) prey on weevils and another (*C. rybiensis* = *ornata*) preys on bees of the genera Halictus and Andrena. Marchal (1887) shows, in a beautiful study of this last species, that the wasp not only stings the bee but also crushes, or malaxates the back of its neck and laps up the exuding juices and honey. As a result of this treatment the bee dies in the course of a few hours. Adlerz (1900, 1903) lists *C.* 5-*fasciata*, *arenaria* and *truncatella* as provisioning their nests with weevils, *C. hortivaga* as preying on bees of the genus Hylæus and *C. labiata* as collecting both Chrysomelid and Curculionid beetles. Ferton (1901, 1905) cites *C. specularis*, *truncatella* and *ferreri* as preying on weevils, *C. emarginata* on bees of the genera Halictus, Prosopis and Andrena, and *C. magnifica* on Halictus and Andrena. This last species laps the honey from the body of its victim through a hole made in the back of its neck, as described by Marchal in the case of *C. rybiensis*.

The Peckhams (1898, 1900) find that the American *C. clypeata* Dahlb., *deserta* Say and *nigrescens* F. Smith all prey on weevils, like the majority of European Cerceris, but that *C. fumipennis* Say preys on a Buprestid beetle, *Chrysobothris 4-impressa*, which it kills outright. In all the species of Cerceris observed up to the present time the cell is first provisioned with numerous specimens of the prey, the egg is then laid and the cell closed as in the great majority of solitary wasps.

It would seem, therefore, that the method of rearing the young in Aphilanthops is intermediate between that of Cerceris and *Philanthus punctatus* on the one hand and of *Ph. apivorus* on the other. The question then presents itself: Do *Ph. apivorus* and *A. frigidus* represent an advance on Cerceris or are the conditions in this genus derived from those of *Ph. apivorus*? In other words, is the Bembecine a primitive or a secondary method of caring for the young among the solitary wasps? Undoubtedly most observers would be inclined to regard Bembex as representing a later phylogenetic stage and one leading to the conditions in the social wasps, but the Peckhams take a different view. "It may be possible, then," they say, "that all wasps originally fed their larvæ from day to day as Bembex now does, and that while the instinct of paralyzing the prey and of storing the whole supply of food once for all was working itself out among the solitary wasps, the instincts connected with life in a true society, and of joining together in the work of feeding the larvæ, have, on the other hand, developed into those of our wasp communities."

It is difficult to decide between the evolutionary alternatives here indicated, but analogy with the phylogenetic history of the bees, in which two precisely similar methods of rearing the young occur, certainly points to the Bembecine method as secondary. This view is also sustained by the sporadic and independent occurrence in several highly specialized groups of wasps of this method as the one best adapted to certain peculiar conditions. Such cases are *Aphilanthops frigidus* and *Philanthus apivorus*. Two others are cited by the Peckhams, one in the genus Sphex (Ammophila), where they found "an instance which looks like a connecting link between the habits of Bembex and those of the solitary species. *A. urnaria* stores one caterpillar, lays an egg on it, catches another and stores it as soon as she can and then closes the nest. As a usual thing, no doubt, the nest is finally closed before the egg is hatched, so that she never sees her larva. In one of our instances, however, the capture of the second caterpillar was so much delayed that when it was brought in the mother wasp found a larva of a day old feasting on the one already provided." The other case is that of *Lyroda subita* Say, which these authors found to resemble Bembex in feeding its larva from day to day on small crickets. Most instructive in this connection, however, is the Aphilanthops, because its method of collecting a supply of queen ants before feeding them one by one to the growing larva, indicates very clearly that this wasp originally had the storing habits of the allied genus Cerceris and of *Philanthus punctatus* and has secondarily acquired the Bembecine method of feeding its young. I am, therefore, inclined to regard the Bembecine method as derivative, or secondary, and find further confirmation of this view in the fact that in all cases, except Lyroda, the prey of those solitary wasps which feed their larvæ from day to day, belongs to highly specialized groups of insects of comparatively recent phylogenetic origin—ants in the case of Aphilanthops, honey bees in the case of *Philanthus apivorus* and higher Diptera in the case of Bembex.

The species of Aphilanthops are not the only solitary wasps that prey on ants, for some four small Mediterranean Crabronids, belonging to two genera, are known to provision their nests with these insects. Ferton (1890) describes the habits of *Fertonius luteicollis* Lep. in Algiers, where it digs its nest in sandy soil, making burrows only about 4 cm. deep, but also nests in the crevices of walls. It preys exclusively on workers of *Tapinoma erraticum*

Latr., storing in each cell 40 to 50 of these strong-smelling ants, which are merely paralyzed and far from motionless at first. There are three generations of the wasps in the course of the year. Later (1895) Ferton described from Corsica a second species of the same genus (*F. formicarius* Fert.) which also preys on *Tapinoma erraticum* workers and closely resembles *F. luteicollis* in its other habits. In 1893 Emery described the habits of *Brachymerus curvitarsis* H. Sch., a Crabronid that preys on the workers of *Liometopum microcephalum* Panz. in Italy. He saw it pounce on the ants as they were moving along in files. The nest was found in a fig-tree, in the abandoned burrows of a longicorn beetle. The ants were stored in numbers (about 40) in each cell and were "imparfaitement paralysés, quelques uns capables même de se traîner sur leurs pattes." More recently (1901) Ferton has figured a second species of the same genus (*B. 5-notatus* Jur.) which, like the species of Fertonius, preys on workers of *Tapinoma erraticum*.

It is interesting to note that all of these Crabronids prey on strong-smelling ants of the subfamily Dolichoderinæ and that they select only the workers. Ainslee's observations show that the latter statement is also true of *Aphilanthops taurulus* but that in this case Myrmicine ants are selected. *A. frigidus*, as I have shown, confines its depredations to Formicine ants of the genus Formica and selects only the queens, which are, of course, the largest and most nutritious caste. This specialization in diet, while highly advantageous to the wasps, is very destructive to the ants, since each fecundated queen is really a potential colony. Still the prey preferred by *frigidus*, namely *F. fusca* and its var. *subsericea*, notwithstanding the depredations of the wasps and of our numerous slave-making and temporarily parasitic species of Formica, maintain their status as far and away the most abundant ants of their genus in the northeastern states and Canada. They are able to support this greedy host of prædators and parasites because they are extremely prolific, hardy, or eurythermic, and of a very industrious and peaceable disposition.

NOTE

The preceding article is republished mainly for the sake of the following note. When my observations on Aphilanthops frigidus *were written I believed them to be quite new, but some years later I came upon the Peckhams' book, "Wasps Social and Solitary" (1905), which I had never read because I supposed it to be a more popular presentation of their wasp studies of 1898 and 1900, and was astonished to find that it contained an account of the provisioning behavior of Aphilanthops. I was even more astonished to find that after advancing the hypothesis that the wasp might enter the ant-nests to secure the winged queens, the authors concluded with the following remarks:*

"We went on with these meditations for several days while lingering, with

gradually diminishing hopefulness, over one ant-hill after another. The wasps were carrying in winged queens by the score, but they did not come our way to find them; and although we ranged about widely, we failed to see the capture. Occasionally we met a frigidus hunting, running about on the ground and poking her head, not only into ant holes, but into holes of all sorts, and as we sometimes saw young queens (wingless however) starting to dig their nests, we thought these might be the object of the search. The weather was cold and windy, most unpropitious for swarming, and yet frigidus was working as briskly as ever; so that we began to feel sure that she could not depend upon meeting the queens outside the nest, but must enter to get them. Just at this point we received a letter from Mr. William M. Wheeler, well known as an authority on ants, saying that he felt sure that the wasp could not extract the queens from the nest, but must find them running on the ground, just after the nuptial flight, before they dug their holes and started their colonies. Respecting this opinion, but still feeling unconvinced, we caught a wasp in a glass, and carrying it to an ant-hill, inverted it so that she was confined just over the entrance. After buzzing up and down for a moment, she alighted and walked calmly into the hole; but a fraction of a second later she came running madly out again, pursued by the most furious lot of ants that ever defended the home city against invasion. Down tumbled our air castles about courage and duty, for however frigidus gets her queens, it is not in this way. We have not yet seen the meeting and the capture, but hope that sometime we may be lucky enough to be on the right spot at the right time."

I must have known, therefore, of the Peckhams' observations as early as 1904 or 1905! Certainly, if any of my fellow entomologists had compared the Peckhams' with my account of the wasp, the statement at the beginning of the third paragraph of my paper must have seemed extraordinary, to say the least. And to those who knew of my almost filial affection for the Peckhams and my habit of citing too much literature on any subject that happens to interest me, my procedure must have seemed inexplicable. Of course, the Freudians might explain it as an unconscious repression due to a "father complex" or an autistic craving for priority, but I am sure that only a lapse of memory and preoccupation with my observations were involved. Such lapses may be more frequent than we are apt to suppose. Recently one of my colleagues, who had been spending several months in the Orient, devoted the time of his voyage from Japan to San Francisco to an elaborate plan of a paper on certain biological experiments which he had performed the year before. On reaching his laboratory in Cambridge he found that he had already published the paper and that his off-prints were awaiting him on his desk!

LITERATURE

ADLERZ, G. 1900. Biologiska Meddelanden om Rofsteklar. Ent. Tidskr., pp. 161–200.

——. 1903. Lefnadsförhållanden och Instinkter inom Familjerna Pompilidæ och Sphegidæ. Kgl. Svensk. Vetenskaps. Akad. Handl., XXXVIII, No. 5, pp. 1–181.

AINSLEE, C. N. 1909. A Note on the Habits of Aphilanthops. Canad. Ent., XLI, pp. 99–100.

BAKER, C. F. 1895. Notes on Aphilanthops. Canad. Ent., XXVII, pp. 335–336.

COCKERELL, T. D. A. 1895. Descriptions of New Hymenoptera. Trans. Amer. Ent. Soc., XXII, pp. 289–297.

——. 1896. Still Another Aphilanthops. Canad. Ent., XXVIII, pp. 221–222.

CRESSON, E. T. 1865. Monograph of the Philanthidæ of North America. Proc. Ent. Soc. Phila., V, pp. 85–132, 4 figs.

DUNNING, S. N. 1896. Notes on Aphilanthops and Description of a New Species. Canad. Ent., XXVIII, pp. 203–206.

——. 1898. Monograph of the Species of Aphilanthops Inhabiting Boreal America. Trans. Amer. Ent. Soc., XXV, pp. 19–26.

EMERY, C. 1893. Sur un Crabronide Chasseur de Fourmis. Bull. Soc. Ent. France, pp. LXIII–LXIV.

FABRE, J. H. 1891. Souvenirs Entomologiques. 4e Sér., pp. 191–218.

——. 1894. Souvenirs Entomologiques. 1e Sér., 3e Ed., pp. 39–66.

FERTON, C. 1890. Un Hyménoptère ravisseur de Fourmis. Act. Soc. Linn. Bordeaux, 5e Sér., IV, pp. 341–346.

——. 1895. Nouveaux Hyménoptères Fouisseurs et Observations sur l'Instinct de quelques Espèces. Act. Soc. Linn. Bordeaux, 5e Sér., VIII, pp. 261–272.

——. 1901. Notes Détachées sur l'Instinct des Hyménoptères mellifères et ravisseurs avec la description de quelques espèces. Ann. Soc. Ent. France, LXX, pp. 83–148, 2 pls.

——. 1905. Notes Détachées, etc. 3e Sér., Ann. Soc. Ent. France, LXXIV, pp. 56–104, 2 pls.

MARCHAL, PAUL. 1887. Etudes sur l'Instinct du *Cerceris ornata*. Arch. Zool. Expér. Gén. 2e Sér., V, pp. 27–60, 6 figs.

MELANDER, A. L. and BRUES, C. T. 1903. Guests and Parasites of the Burrowing Bee, Halictus. Biol. Bull., V, pp. 1–27, 7 figs.

PATTON, W. H. 1880. Notes on the Philanthinæ. Proc. Bost. Soc. Nat. Hist., XX, pp. 397–405.

PECKHAM, G. W. and ELIZABETH G. 1898. On the Instincts and Habits of the Solitary Wasps. Wis. Geol. and Nat. Hist. Survey, Bull. No. 2, 245 pp., 14 pls.

——. 1900. Additional Observations on the Instincts and Habits of the Solitary Wasps. Bull. Wis. Nat. Hist. Soc. I, pp. 85–93.

——. 1905. Wasps Social and Solitary. Boston and New York, Houghton Mifflin & Co.

SMITH, F. 1856. British Museum Catalogue. Hymenoptera, IV, p. 475.

A STUDY OF THE GUEST ANT *LEPTOTHORAX EMERSONI*

It is certain that there may be extraordinary mental activity with an extremely small absolute mass of nervous matter: thus the wonderfully diversified instincts, mental powers, and affections of ants are notorious, yet their cerebral ganglia are not so large as the quarter of a small pin's head. Under this point of view, the brain of an ant is one of the most marvellous atoms of matter in the world, perhaps more so than the brain of man.

DARWIN, "DESCENT OF MAN,"
2ND EDIT., P. 54

Leptothorax emersoni[1] is of unusual interest as an ant that has assumed the role of a symphile, or true guest in the colonies of another ant, *Myrmica brevinodis*. The latter species belongs exclusively to the Canadian and Hudsonian faunal zones, ranging over the higher slopes of the Rocky Mountains northward to Alaska and eastward through Canada to the Maritime Provinces and the mountains of New England. In this great area it has developed a number of local varieties. The typical *brevinodis* occurs in Colorado; the varieties *frigida*, *subalpina*, *sulcinodoides*, *brevispinosa* and *alaskensis* are confined to Western North America, and only the var. *canadensis* occurs in the North Atlantic region, where it lives in moist, sunny bogs or meadows, as the host of the typical *L. emersoni*. In 1907 I described a subspecies, *glacialis*, living with the var. *subalpina* of *M. brevinodis* in Colorado, and in 1915 I found a second subspecies, *hirtipilis*, in the nests of the same host ant on Tunnel Mountain, near Banff, Alberta. Within recent years I have taken the typical *emersoni* with *canadensis* in numerous localities in the Berkshire Hills of Western Massachusetts and the Litchfield Hills of Northwestern Connecticut, at South Harpswell on the coast of Maine and at Hull, Quebec. Some years ago Mrs. Slosson captured a queen *emersoni* on the summit of Mount Washington. I am convinced that the specimen does not indicate that colonies are formed at such high altitudes, but merely that they occur at lower elevations in the bogs and meadows of New Hampshire. In its boreal distribution *L. emersoni* therefore resembles the great majority of parasitic ants, such as Polyergus, the Formicas of the *sanguinea*, *rufa*, *microgyna* and *exsecta* groups, *Lasius umbratus* and *fuliginosus*, Strongylognathus, Harpagoxenus, Myrmoxenus, Formicoxenus, Symmyrmica, Anergates, Epœcus, Sympheidole and Epipheidole, all of which seem to have developed their

[1] My study of ant-larvæ and trophallaxis, or mutual feeding among the social insects (1918), has led me to reconsider a singular little guest-ant, *Leptothorax* (*Mychothorax*) *emersoni*, the habits of which I described in three papers published in 1900, 1902 and 1907. Since the first of these contained an incomplete account of the insect's behavior, and since the second and third were published in a German journal devoted to psychology and neurology and a rather inaccessible bulletin of a local natural history society, it seems advisable to republish the articles in amended form, together with a few data I have been able to gather since 1907.

peculiar habits since the Glacial Epoch as adaptations to the limited food-supply available during the short summers of high latitudes and altitudes.

OBSERVATIONS ON LEPTOTHORAX EMERSONI DURING 1900

DURING the late afternoon of August 1, 1900, while walking over one of the Litchfield Hills near Colebrook, Connecticut, I found a number of nests of the common red-brown Myrmica (*M. brevinodis* Emery var. *canadensis* Wheeler) under some small stones that were rather deeply imbedded in the moss bordering the exposed glaciated rock of the hilltop. In four of these nests which were rather close together and not very populous I detected among the Myrmica workers a few decidedly smaller and more yellowish ants of a different species running about on the up-turned lower surface of the stones. As my stay in Colebrook was at that time limited to a few days, I carefully replaced the stones in the moss. The small ants proved to belong to an undescribed species of Leptothorax, which I called *L. emersoni* (1900, 1903). Later in August I returned and at once revisited the Myrmica-Leptothorax nests. Two of them had disappeared and the third contained only a few Leptothorax workers. The fourth nest was in good condition and was dug up completely and carried home in a canvas bag. On the morning of August 25 the ants were transferred to an extemporized Lubbock nest consisting of a board surrounded by water, and a little fine, moist earth placed on the board and covered with a pane of glass. A census of the two species of ants gave the following:

Myrmica: 6 deälated queens; 7 males; about 200 workers; a few eggs; 23 larvæ, both young and old (but apparently no queen larvæ); 8 worker and male pupæ. The latter hatched in the course of a few days.

Leptothorax: 1 deälated queen; 4 recently hatched males; 14 workers; 2 adult larvæ, which soon became male pupæ.

The earth with its occupants was dumped from the bag onto the pane of the Lubbock nest, and the ants, after the first flurry of excitement, began to seek refuge under the glass. As usual, the larvæ and pupæ were at once conveyed to a place of safety. While the operation was going on, it was noticed that some of the Myrmica workers carried the Leptothorax larvæ, and the Leptothorax workers reciprocated by occasionally carrying some of the Myrmica larvæ. This action on the part of both species was evidently the result of haste and excitement, as I never saw it repeated subsequently except once, when a Leptothorax carried a Myrmica larva a short distance and then dropped it.

As soon as the excitement had subsided the Myrmicas proceeded to dig galleries in the soft earth between the glass pane and the board, and the Leptothorax at once migrated into them. A few hours later the earth that had been dumped on the pane was carefully removed and replaced by a piece of opaque cardboard which was only lifted from the glass when the ants were under observation. A small dish containing a syrup of sugar and water was placed near the nest. It was soon found by two of the Myrmica workers which at once gorged themselves with the liquid and returned to the nest, where they proceeded to dole out the store of food to their hungry sisters. It was then that I was able to make my first observation on the mutual relations of the two species of ants. A Leptothorax worker was seen to follow up and to climb on to the thorax of one of the food-distributing Myrmicas soon after it had entered the nest. In this position the little ant proceeded to lick the back of the head and clypeus of the Myrmica with signs of agitation as indicated by the hastening of the tremulous beat of its antennæ and the throwing of its gaster and postpetiole into stridulatory oscillation. The Myrmica paused as if spellbound by this shampooing and occasionally folded its antennæ as if in sensuous enjoyment. The Leptothorax, after licking the Myrmica's pate, moved its head around to the side and began to lick the cheeks, mandibles, and labium of the Myrmica. Such ardent osculation was not bestowed in vain, for a minute drop of liquid—evidently some of the recently imbibed sugar-water—appeared on the Myrmica's lower lip and was promptly lapped up by the Leptothorax. The latter then dismounted, ran to another Myrmica, climbed onto its back and repeated the very same performance. Again it took toll and passed on to still another Myrmica. On looking about in the nest I observed that nearly all the Leptothorax workers were similarly engaged. In one corner of the nest a number of Myrmica workers had formed a circle about a few of their samll larvæ which they were cleansing and feeding. A Leptothorax soon found its way to this cluster and stepped from the back of one ant to that of another, lavishing a shampoo on each in turn and apparently filling its crop with the liquid contributions thus solicited.

These and numerous very similar observations, which could be made at any time on removing the cover of the nest, prove conclusively that the Leptothorax workers demand and obtain their food from the Myrmica workers. The method of soliciting food, however, differs from that of most myrmecoxenous insects which usually request food by tapping the ant with their antennæ (many myrmecophilous beetles), or stroking its face with their fore feet (Atemeles), but few of these guests are so unconventional as to mount the backs and scratch the heads of their hosts for the purpose of inducing them to regurgitate. Even the slave-holding Polyergus and the social parasite Anergates demand and receive food after the manner of other ants. The Leptothorax workers were so persistent in their peculiar attentions to the Myrmicas that I began to doubt whether the little guest ants ever really feed themselves. Once only was a Leptothorax seen to approach the dish of syrup, lap up a very little of it hastily, and then return to the nest. This happened before the ants had definitely settled under the pane of glass. After that only the Myrmica workers visited the manger, and the Leptothorax usually waylaid them as soon as they had entered the nest. During my first visit to the four natural Myrmica-Leptothorax nests I found the latter species loitering in the outer galleries just under the stone. I am convinced that they prefer this situation in order to be on hand the very moment a food-laden Myrmica enters the nest. The Leptothorax workers often walked on the lower surface of the roof-pane, although they had to turn over to mount the passing Myrmicas. They must do this also in the natural nests, for the specimens taken August 1 were, as above stated, crawling on the lower surface of the stones.

Although the feeding of the guest ants commonly proceeds as described, I have noticed that the Leptothorax after mounting a Myrmica sometimes turns about and, like Myrmecophila (Wheeler, 1900b), licks the metathorax or even the abdomen of its host, as if finding the surface covered with some agreeable secretion. It is perhaps unnecessary to add that the Myrmica does not always pay for the shampooing it has received. But the Leptothorax is not discouraged; it merely dismounts and runs about in the galleries till it falls in with another Myrmica.

On the evening of the day on which the ants moved into the Lubbock nest and during a portion of the following day, August 26, the queen Leptothorax wandered about outside the nest as if seeking a more favorable retreat. By 4 p.m., however, she had entered the nest and, with eight of her workers and her two mature larvæ gathered about her, was found occupying a small earthen chamber under the very middle of the roof-pane. This chamber, dug by the Leptothorax, was surrounded on all sides by the large galleries of their host. Seen from above, the Leptothorax nest had the appearance of Fig. 43A. The queen, workers and larvæ nearly filled the cavity, *a*, which communicated with a wide Myrmica gallery, *c*, by means of a passage, *o*, too small to admit a Myrmica. Through this narrow passage a few Leptothorax workers entered or passed out from time to time, but several always remained in the nest with their queen. Usually from one to six workers were to be seen soliciting food among the Myrmicas.

The Leptothorax in their small central nest passed their time in fondling and feeding one another or in lying motionless as if asleep, covering the two larvæ which had been placed in the bottom of the nest. The queen was assiduously fed by the workers and was never seen to leave the nest after once taking possession of it. On several occasions she was observed to throw one of the workers down on its back and to hug and kiss it in the most animated manner.

During the remainder of the day (August 26) the Leptothorax nest remained in the condition represented in Fig. 43A. By 8 o'clock the following morning, however, the bottom of the nest had been dug somewhat deeper, its narrow entrance had been closed up and a new one, equally tenuous, had been opened in a different position (Fig. 43B *r*). The two larvæ had become male pupæ. By noon the queen had laid three elliptical white eggs of rather large size. At 1 p.m. the Myrmica workers discovered the hiding place of

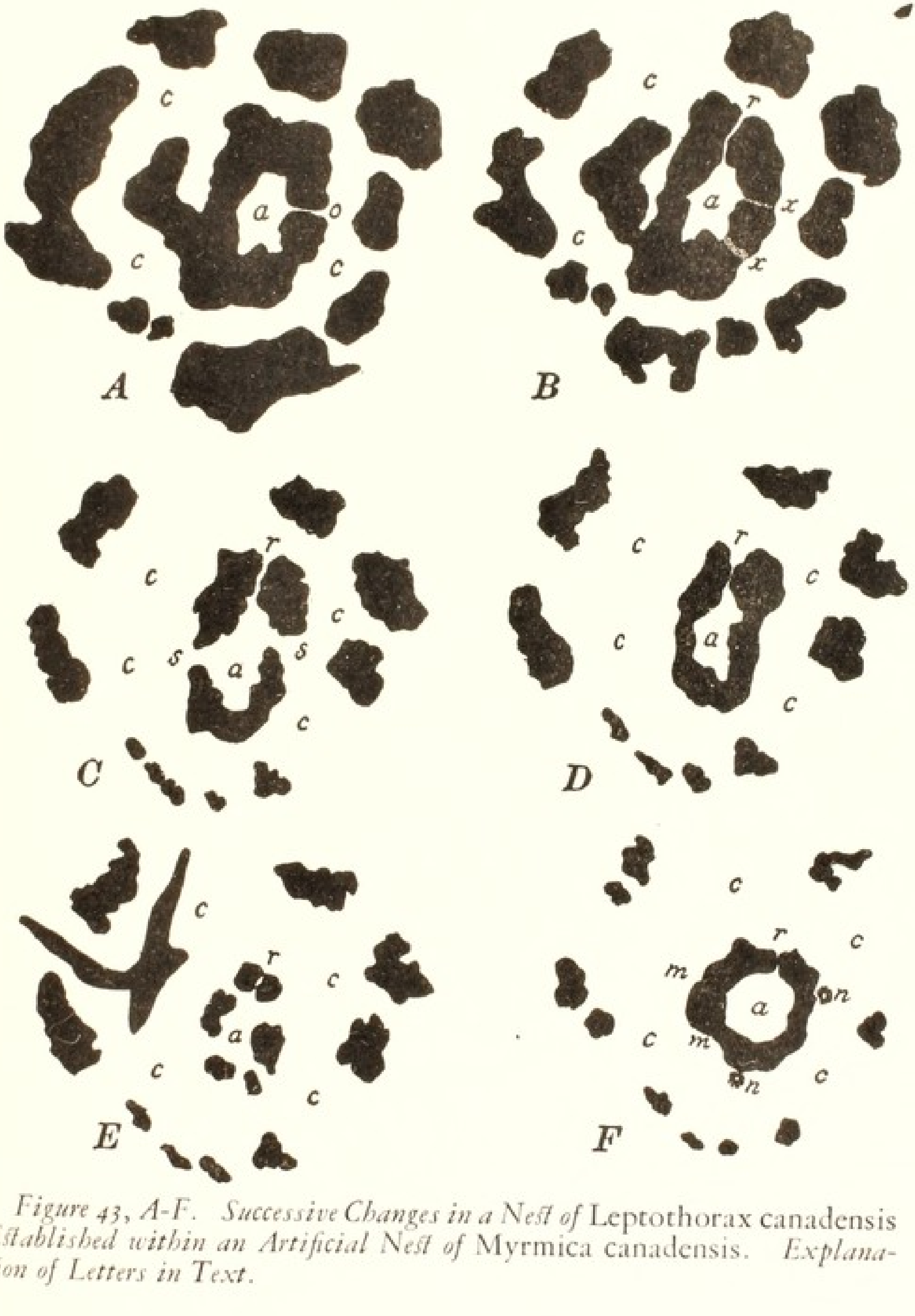

Figure 43, A-F. Successive Changes in a Nest of Leptothorax canadensis *Established within an Artificial Nest of* Myrmica canadensis. *Explanation of Letters in Text.*

their little companions, and two of them in single file shouldered their way through the narrow passage, *r*, enlarging it as they proceeded. As soon as the head of the first Myrmica appeared in the chamber, the Leptothorax, which had been attending to their morning toilet, to that of their larvæ and to the careful arrangement of their eggs, turned to meet the intruders. For an instant I fully expected to see a fierce battle, but I had misjudged the Leptothorax character. To my surprise the Myrmica and her companion on entering the chamber were received with a profusion of shampooing. The large Myrmicas, though sadly crowding the occupants of the little chamber, settled down comfortably and appeared to experience all the sensuous satisfaction of a couple of jaded roués who have dropped into a Turkish bath. The naturalist of a past generation would probably have interpreted the behavior of Leptothorax under these circumstances as a polite act of hospitality on the part of a defenseless but intelligent creature. Today there would be little hesitation in interpreting it as merely a machine-like reflex called into activity by its customary stimulus, the presence of the Myrmicas. That the truth lies somewhere between these two conceptions, though nearer that of reflex than of intelligent action, was apparent from the subsequent behavior of the Leptothorax. These ants undoubtedly had some dim desire to remove the Myrmicas from their nest, for from time to time a Leptothorax was seen to pull with her mandibles at the fore leg or antenna of one of the intruders, as if to remind her that there are limits to polite hospitality. This action was never performed by the Leptothorax while foraging in the Myrmica galleries, but it was regularly performed whenever, as on this and several subsequent occasions, any Myrmica broke into the central chamber. The direction of the tugging was not very definite or constant. Often when a Myrmica thrust its head through the wall, the tugging was indeed towards the interior of the chamber, as if to draw the intruder in. But as the small ant was not able to move the large Myrmica, and as it could not under the circumstances tug in any other direction, the action could hardly be regarded as anything more than a gentle means of persuading the intruder to leave. This tugging was the only act even approaching hostility witnessed between the two species. The Myrmicas never showed the slightest irritation towards the Leptothorax, never seized them in their mandibles, nor even menaced them. They seemed rather to look upon the little creatures with gentle benevolence, much as human adults regard little children. They never passed their little guests without the antennal greeting, and the Leptothorax shampooed their hosts with comical assiduity.

The two Myrmica workers whose intrusion into the Leptothorax chamber led to the foregoing observations finally departed, only to give a second party of Myrmicas an opportunity to make a large breach in the wall at *xx*. They entered the chamber at 1.20 p.m. and were received in the same gracious manner as the first party, and in turn departed after being as politely requested to leave. The Leptothorax then at once set to work to repair their dilapidated wall. At 1.30 a worker went out into the adjoining gallery, picked up a pellet of earth and placed it in the breach. Again and again she returned and gathered earth, often going to a distance of one or two inches from the chamber for suitable pellets. Another worker soon began to assist in repairing the breach from the inside, taking the pellets for this purpose from the inner wall of the chamber. Then the first worker walked around the nest, entered it through the passageway at *r* and began to clean herself, while a third worker went out through the breach and continued the work on the outside till the wall was completed. This was accomplished by 3 p.m.

At 4 p.m. a little water was poured under a corner of the glass where the Myrmicas had congregated in greatest numbers. This additional moisture induced them to move with their whole brood to the middle of the nest. Here they soon began to break through the walls of the Leptothorax cell in two places (Fig. 43 C *s s*). Two Myrmicas again settled down in the cell and underwent the usual shampooing. As soon as they had departed the little ants again set about repairing the walls as before. Sometimes three or four of them worked at the same breach. During the progress of the work they frequently went from two to three inches into the Myrmica galleries in search of the requisite earth. At the same time a few workers toiled from the inside of the cell, and these were soon joined by the queen, working as busily as any of her progeny. Occasionally a worker, after building for some time on the outside, would slip through the breach, turn around and build from the inside. Twice Myrmicas rushed up to the spot *s* (on the right side in Fig. 43 C) and commenced tearing down the wall. They easily took out pieces of earth eight or ten times as large as those which the little Leptothorax workers were putting in with so much care and difficulty. But the infraction of the Myrmicas did not escape the attention of the inquilines. They interrupted their repairs to shampoo and kiss the interlopers and again they tugged them by a leg or an antenna, sometimes in one direction, sometimes in another. And again I was forced to conclude that the Leptothorax workers wished to dissuade their big hosts from trespassing on their property. At any rate, the Myrmicas changed their plans and retreated to another part of the nest, just as the other parties had done on former occasions. The Leptothorax then continued their repairs. By 6 p.m. the walls had been rebuilt and the cell had the appearance of Fig. 43D. The original entrance, *r*, had been much narrowed so as to exclude all but the slender-bodied occupants of the chamber.

At 7 o'clock on the following morning (August 28) the Leptothorax nest was found *in statu quo*, except that the queen had laid three more eggs during the night. By noon, however, the Myrmicas had again broken into the cell, so that at 4:30 p.m. the wall was torn down in several places. Nevertheless, the ever alert guest ants had piled up the earth so that the Myrmicas could scarcely squeeze between it and the glass roof-pane. The inroads of the Myrmicas had been so extensive, however, that even as late as 7 p.m. the nest presented the appearance of Fig. 43 E.

By 7 a.m. on the following day (August 29) the nest had been almost entirely rebuilt, as shown in Fig. 43F. The Leptothorax must have labored during most of the night. They had remodeled the nest, giving it a circular form, whilst apparently retaining the old opening at *r*. Besides this opening they had two others at *n n*, which were underground passages. The ants could be seen diving into these and anon reappearing within the circular chamber, the bottom of which had been sunk still deeper in the soil. The neat little nest now contained ten eggs. From day to day the Myrmicas had been widening their galleries, as is readily seen by comparison of Fig. 43A to F, so that only small pillars of earth remained to support the roof-pane around the Leptothorax cell.

On succeeding days essentially the same conditions as those described above were repeated with slight differences in detail. For the sake of completing the history of the double nest, the observations extending from August 30 to September 4 are condensed in the following notes:

August 30. The round cell, which remained undisturbed all day yesterday, was still intact at 8 o'clock this morning. By noon, however, the Myrmicas had torn down its wall in several places, and three of them were found in the cell, submitting to a vigorous shampoo. By 8 o'clock in the evening the circular nest had been rebuilt. The opening at *r* had been closed and a new one opened at *m* (upper left-hand corner of cell in Fig. 43F).

August 31. Almost an exact repetition of yesterday's performance.

September 1. This morning the reconstructed Leptothorax cell is smaller. Its upper entrance, *m*, and the two subterranean entrances, *n n*, have not been changed. The ants have sunk the pupæ and eggs to a greater depth in the earthen floor of the nest, so that they are almost in contact with the board. The nest was not molested by the Myrmicas during the day.

September 2. The cell this morning has further decreased in size but is still intact. Its cavity is not more than 7 mm. in diameter, so that the Leptothorax family is much crowded. The two subterranean entrances at *n n* are still in use but the upper entrance has been shifted to *m* (lower left-hand corner of cell in Fig. 43 F). The Myrmicas still leave the cell unmolested.

September 3. Today, too, the Leptothorax were left in peaceful possession of their cell. Many of them went out into the galleries from time to time to shampoo the Myrmicas and solicit food, which they then distributed to their queen and to the few workers remaining at home. During the day the lower entrance at *m* was closed so that the wall of the nest was everywhere in close contact with the roof-pane. The ants still entered and left the chamber through the two underground entrances at *n n*.

September 4. At 8 a.m. the Leptothorax nest was unchanged, but by noon its circular walls had grown perceptibly thinner, as the Myrmica workers had again taken to removing the earth from the outer surfaces. The nest was now shaped like a volcano with sloping sides and the guest ants inhabiting the crater. By 5 p.m. the Myrmicas had made two breaches in the walls. The nest remained in this condition throughout the evening.

The fact that the Leptothorax changed their entrances from time to time, and, as shown by the figures, kept perfecting the form of their cell, thereby making it easier to guard and rebuild and more difficult for the Myrmicas to demolish, is evidence of the remarkable psychic plasticity of these ants. Similar behavior on the part of ants that have been repeatedly disturbed by other species is recorded by different observers. Forel (1894, p. 8) brought a large formicary of *Cataglyphis altisquamis* from Algiers and gave it an opportunity to establish itself in a garden near Zürich. The African ants were much annoyed by the incursions of *Lasius niger* and *Tetramorium cæspitum*, and although they at first adhered to their Algerian custom of maintaining a large open entrance to their nest, they learned during the course of the summer to narrow the opening gradually. Finally they plugged it up completely with grains of earth and made only a small temporary orifice whenever they strolled out on sunny days. Wasmann (1897, pp. 69, 70) mentions a colony of *Formica sanguinea* that resorted to similar tactics in protecting itself from the repeated inroads of a neighboring colony of *F. pratensis*. All these observations go to show that Bethe's conception (1898) of ants as *mere* "reflex machines" cannot be entertained.

Being obliged to leave Colebrook I took advantage of the cold morning of September 5, when the ants were inactive, to transfer them all to a glass jar containing some earth. From this date till October 1, I was traveling about and was therefore compelled to suspend observations on the compound nest. On returning to Austin, Texas, October 1, the ants were again transferred to a Lubbock nest, but to my dismay I found only the queen and a single worker of the Leptothorax remaining. The eggs, the two male pupæ, and the other workers of this ant, together with nearly all the larvæ and pupæ of the Myrmica, had disappeared. The Leptothorax queen was very uneasy and wandered about outside the Myrmica nest. On the following day she disappeared.

OBSERVATIONS ON LEPTOTHORAX EMERSONI DURING 1901

ON RETURNING to Colebrook during the summer of 1901 I at once undertook a more systematic search for Myrmica-Leptothorax colonies. The original colonies had been found at an elevation of about 1500 ft. After vainly examining all the hilltops in the vicinity, I found hundreds of the nests almost at the very door of the house in which I was living. Only a few rods away and at the foot of a rock-strewn orchard, a broad meadow spreads out between the wooded hills. Before the memory of the oldest men now living in Colebrook this meadow was the bottom of a lake which the early residents had created by damming a stream. The meadow is still too damp to be explored with comfort without wearing rubber boots. It yields an abundant crop of hay during the summer, but grasses and sedges are not its only vegetation. It is bright in places with glowing cardinal-flowers (*Lobelia cardinalis*) and purple fringed orchids (*Habenaria fimbriata*), not to mention humbler plants like the dwarf cornel (*Cornus canadensis*), the cinquefoil (*Potentilla canadensis*) and the partridge berry (*Mitchella repens*). The expanse is dotted over with a few large boulders covered with moss and other vegetation and almost submerged in the peaty soil. There are a few stumps in the last stages of ligneous decay, some fragments of drift-wood and a very few flat-stones lying more loosely on the surface. Much of the soil is thrown into hummocks formed by tufts of coarse grass or great clumps of moss (*Polytrichum commune*)—surely a most unfavorable locality in which to look for ants, so unfavorable in fact, that I had never given it a thought in this connection till my friend Dr. C. S. Bacon one day invaded it with me in search of botanical specimens. Then I found that the whole meadow, some twenty acres in extent, was so thickly studded with Myrmica-Leptothorax nests that it could best be described as one vast colony, probably comprising more millions of these ants than there are inhabitants in the Chinese empire! Subsequent walks and rides in Litchfield County convinced me that meadows like the one I had explored and not hilltops, are the typical nesting sites of the two ants.

In the meadow at Colebrook three different types of structure could be recognized in the Myrmica-Leptothorax nests. First, there were the nests in old logs that had been floated into the meadow during freshets. The ants simply occupied the inosculating cavities that had been made by insect larvæ or carpenter ants (*Camponotus noveboracensis*). These galleries, as is customary with stump- or log-inhabiting ants in the United States, extended for some distance into the underlying soil. Second, there were nests under stones or flat pieces of wood and presenting several superficial galleries or chambers connected with others extending down into the soil to a depth of five to eight inches. Third, and far and away the most abundant, were the nests in the peaty soil of the hummocks and in the layer of mossy earth covering the boulders. The favorite nesting places, however, were the clumps of *Polytrichum*. In these the ants had made a perfect net-work of galleries and chambers, mainly in the earth threaded by the roots of the plants

(Fig. 44). The fine soil from the excavations had been carried up between the stems of the moss till it formed small mounds a few inches in diameter and conspicuous only in new-mown portions of the meadow. The summits of these mounds were perforated by one or more entrances. The burrows did not extend to a greater depth than four to eight inches, at any rate in the earth overlying the boulders. In all cases the walls of the burrows had con-

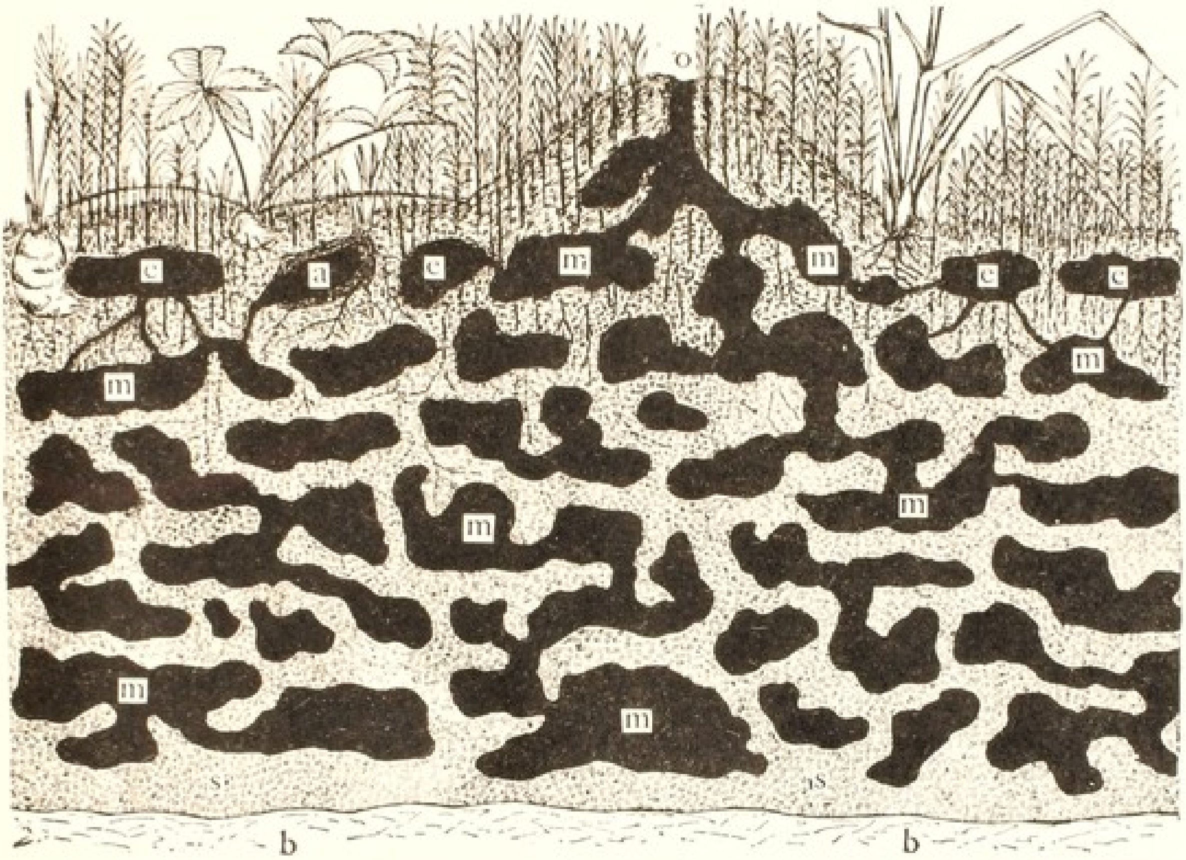

Figure 44. Compound Nest of Myrmica canadensis *and* Leptothorax emersoni *in Peat Covering a Boulder and Overgrown with Moss (Polytrichum);* o, *Entrance;* m, *Chambers Inhabited by Myrmica;* e, *Nests of* L. emersoni; a, *One of These Nests in Root-Stock of Cinquefoil (Potentilla);* b, *Surface of Boulder.*

siderable consistency owing to the felted rootlets which held the peaty soil together.

The consociation of the Myrmica and Leptothorax was so constant that of the many nests I examined—often thirty or forty in the course of a single afternoon—very few, and certainly not more than five percent, of those in the meadow at Colebrook, contained Myrmicas only. In other localities, however, as many as thirty percent were to be found without the small inquilines. In all cases the presence of both species could be easily ascertained, since the Leptothorax almost invariably constructed their nests between the uppermost chambers of the Myrmicas and the surface vegetation or among the most superficial galleries of their host. Often these chambers were in the brown basal portions of the Polytrichum tufts, so that by simply parting the moss with the fingers the tiny Leptothorax nests were at once exposed. They consisted of from one to a dozen or more chambers, varying from one to four c.cm. in capacity and often separated by considerable portions of the Myrmica nest. They were connected with the galleries and chambers of the latter by passages too long and tenuous to admit the robust workers of the host species. I am not certain that there was any communication between the little chambers and the exterior except through the galleries and main exits of the Myrmicas. Where the nests were under flat stones and the relations of the chambers of the two species were much clearer, no independent exits from the Leptothorax chambers could be seen, but when situated in the moss it could hardly be impossible for the guest-ants to work their way up to the outside without passing through the Myrmica galleries. Besides being decidedly superficial, the cells of the inquilines were more numerous near the periphery than directly over the center of the Myrmica nest. Very often the former had carefully hollowed out dead root-stocks of the cinquefoil (*Potentilla canadensis*) (Fig. 44*a*) or buried twigs, thus converting them into neat little chambers. The typical arrangement of the chambers and galleries of the two species is shown in section in the accompanying subdiagrammatic figure (Fig. 44*a* and *e*).

The Myrmica-Leptothorax colonies were found to be in the most populous and flourishing condition during the latter half of August. The rearing of the many winged individuals and of the still more numerous workers is carried on simultaneously by both species. Hence we may infer that their nuptial flights must be nearly or quite synchronous. Nests opened late in August teemed with males and winged females of the Myrmica while the chambers were still crowded with larvæ and pupæ in all stages of development. The cells of the Leptothorax were also packed with tiny pupæ and larvæ in the corresponding stages. The galleries swarmed with brown Myrmica workers intermingled with the tiny brownish yellow workers and dusky males of the Leptothorax. There were very few deälated mother queens of the latter species and not by any means one to each of the little nests or cells. Nor were virgin females produced in considerable numbers like the males and workers. Both species, like most of the ants of the Northern States, produce but a single brood of males and females during the year.

In late August and early September I saw males and winged females of both species running about over the moss and rocks in the meadow but I did not succeed in observing the formation of new colonies. As will be shown later, the winged Myrmica females are familiar, long before leaving the parental nest, with the Leptothorax and their behavior, so that both for this and other reasons to be mentioned presently, there can be no difficuity in the consociation of a fecundated Myrmica female with a fecundated Leptothorax female either while the former is starting her formicary or indeed at any later period in the growth of the colony.

It is not easy to ascertain the exact number of Leptothorax in one of the large compound nests. A census of three of the largest colonies on September 16, at a time when about the maximum number of Leptothorax would be present, gave 77, 116 and 219 respectively. These numbers do not include the males and females most of which had already left the nests.

Although the males and winged females of the Leptothorax leave the nest for the purpose of mating and enabling the latter to enter into fresh consociations with Myrmica colonies, it is not certain that the workers ever leave the nest in which they were born. I have never seen them running about outside, and as they certainly obtain an abundance of food from the Myrmicas within the nest, there is no reason to suppose that they go foraging like their hosts. The latter, of course, resemble in their habits our other species of Myrmica (*scabrinodis*, *punctiventris*, etc.) in being partly predatory and partly aphidicolous. They were frequently seen carrying into the nest the insects, both larval and adult, in which low meadow lands abound. I also found them attending aphids concealed between the equitant leaves of sedges. That food is plentiful is attested by the very populous and flourishing condition of the compound nests, a condition not so frequently attained by our other species of Myrmica which have no commensals to feed.

Even in the natural nests it is easy to observe that the Myrmicas and Leptothorax, although maintaining separate crèches for their offspring, live, nevertheless, on the most friendly terms. They run about together in the galleries and, if the nest is not suddenly or greatly disturbed, it is even possible to see the Leptothorax workers mounting the backs of the Myrmicas and licking them with signs of agitation, as shown by the visible but inaudible stridulatory vibration of their glistening abdomens. But it is only in artificial nests that the intimate relations of the two species can be satisfactorily observed.

For my observations during 1901 I used both Lubbock and Fielde nests.[2] The Lubbock nests are useful because they contain earth and facilitate the formation of artificial compound nests almost exactly like those found under stones and flat pieces of wood. The Fielde nest, in which the earth and the instinct to excavate, which its presence always calls forth in ants, are eliminated, are more satisfactory, however, both for the ants under discussion and for nearly all other species. The artificial nest is placed in a Forel arena, which consists merely of a circular or elliptical wall of dry, powdered plaster of Paris, an inch or more in height, erected on a table and made

---

[2] The construction of these nests is described in my ant book (1910, p. 551).

steep along its inner border with the aid of a putty knife. The ants are unable to scale the rampart of crumbling powder and dislike being covered with it, so that they soon desist from all attempts to escape from the white corral. It is in every way more satisfactory than Lubbock's water-moat. The nest, dug up with a trowel and carried home in a bag, is dumped, earth and all, into the arena. The earth is then spread out so that it may dry quickly, and the ants soon betake themselves with their progeny to the moist, dark chambers of the artificial nest.

Although I have seen colonies of many species of ants abandon their native soil and migrate into artificial nests, I have seen none that accomplished the feat so soon after being placed in the arena as *Myrmica canadensis*. This would seem to indicate that the species is in the habit of often changing its nest and on a moment's notice, a habit that may have been developed in places like damp meadows which are subject to frequent and unforeseen inundation. The migration into the new nest is very instructive. When first placed in the arena the ants wander about aimlessly or establish a dozen different burrows under as many clods of earth from the old nest. Finally one or two ants find the opening to the artificial nest, timidly enter and explore its chambers, and then return to seize some of their larvæ and carry them into the newly discovered apartments. Again and again they return and repeat the act. Their matter-of-fact behavior soon attracts the attention of the aimless and unemployed which now accompany their sisters and finding the accommodations to their liking, forthwith join in the labor. The activity spreads like a contagion, so that often within an hour from the time the ants are placed in the arena, all or nearly all the workers are busily lugging larvæ, pupæ, callows, males, queens and reluctant sister workers into the artificial nest. When the colony has entered the nest its opening may be plugged with a wad of absorbent cotton and the nest removed from the arena, or the entrance may be left open so that the ants may continue to use the arena as a playground. They may, of course, be permitted to do this indefinitely so long as the plaster rampart remains intact.

The Leptothorax were in much less haste than the Myrmicas to establish themselves in the artificial nests. They often remained with some of their brood in little nests in the tufts of moss or under clods of earth in the arena for hours or even days after the Myrmicas had moved into the glass nests. The latter not only carried away their own brood but also many of the Leptothorax larvæ and pupæ. The young of both species were stowed away together and cared for indiscriminately. The Leptothorax workers, however, went back and forth, consorting with the Myrmicas in the new nest and anon returning to their own nests in the arena. Finally the Leptothorax, either because they were compelled to move on account of the drying out of the moss and earth, or because they desired to be nearer the Myrmicas, decided to settle in the glass nest. The migration was rather slow and poorly organized. They drifted, so to speak, one by one with their progeny into the new quarters. During the migration I saw the first cases of deportation. One worker would seize another by the mandibles and raise her from the ground. Both ants were oriented alike, except that the deported individual was curled up. Occasionally the ant to be deported was seized by the mandibles in such a manner that her body was curled around the head at right angles to the body of her porter. I never saw a Myrmica carry a Leptothorax.

On using the Lubbock nest an almost exact repetition of my observation of 1900 was obtained. The ants migrated from the arena into the nest, the Leptothorax lagging behind but finally establishing themselves during the night of August 15-16 in a small cell, which they had excavated in the soil immediately under the roof-pane. The walls of this chamber were being continually broken into or carried away by the Myrmicas as they multiplied or enlarged their galleries. Finally, on the morning of August 20 the walls had been completely removed so that the larvæ and pupæ of the Leptothorax, guarded by a number of workers, were left exposed on all sides in the midst of the Myrmica nest. The Myrmicas had carried away some of the larvæ and pupæ and had deposited them with their own, but the Leptothorax kept most of their pile intact throughout the day. During the ensuing night, however, they excavated another chamber in one of the thick earthen columns in another part of the nest, and by the following morning (August 21) had removed all their progeny, including those that had been kidnapped by the Myrmicas, to these new quarters which were maintained intact for nearly twenty days (till September 10) when the whole colony was transferred to a large Fielde nest.

As the Fielde nest contained no earth, it was, of course, impossible for the Leptothorax to construct cells apart from the Myrmicas. A mixed colony was therefore formed at first, the larvæ and pupæ of the two species being mingled and apparently cared for indiscriminately. Leptothorax workers were seen licking the Myrmica brood as well as their own, and undoubtedly the Myrmicas, unlike most human aristocrats, had not the slightest objection to the co-education of their young with the offspring of beggars. I placed in the nest cells of wood, cork and pith of such size and shape as I conceived might be most suitable for Leptothorax dwellings, but the ants would have nothing to do with such artefacts. For some days this strengthened me in the opinion that I had succeeded in converting the original compound nest into a permanent mixed colony, but I soon found that I was mistaken. While the Leptothorax would have nothing to do with the cells of my manufacture, they soon took of their own accord to the damp sponges that were placed in the nest to insure the right amount of humidity. These were in many ways more like their native soil, moist and porous, with the additional advantage of presenting ready-formed cavities of the right size, communicating with the outside by slender or tortuous passages and enclosed by walls that could not be forced apart or torn asunder by the Myrmicas. The little ants moved such of their larvæ and pupæ as had not hatched or been devoured in the meantime, into these commodious cells—and the compound nest was reëstablished. Thenceforth everything went on, as nearly as could be expected from the conditions, just as in the natural nests. The Leptothorax foraged on the Myrmicas in all parts of the chambers and attended to the exclusive education of their own young, apparently with feelings of the greatest comfort and satisfaction. Even later in the year, after all their larvæ and pupæ had disappeared, they still continued to inhabit the cells in the sponges. They returned to them from time to time to rest from their begging excursions among the Myrmicas. In one of my nests the same cell in a sponge was maintained as a home from the latter part of September 1901 till May 18, 1902, when the colony was released in my garden in Austin, Texas.

Before their release the Leptothorax in this particular nest displayed some traits that made them appear not only as beggars but as thieves. The nest contained several deälated Myrmica queens some of which laid eggs in considerable numbers during March and April. On March 20 I saw a Leptothorax worker (A) leave the little cell in the sponge and run into the adjoining glass chamber where the Myrmicas were guarding their eggs under another slice of moist sponge. She slowly detached one of the eggs from the packet and with signs of great agitation carried it back to her nest. After entering the cell she kept the egg in her mandibles fully ten minutes while exploring every recess as if seeking a suitable place in which to conceal it. Then a large Leptothorax worker (B) entered the cell and took the egg away from A. Thereupon the latter at once departed and went to shampooing the Myrmicas. Soon another Leptothorax (C) entered the cell. B dropped the egg while she licked C's head but as soon as she had completed her caresses she again picked it up and carried it about in the chamber for nearly twenty minutes, exploring every corner in the same manner as A. Then she dropped the egg, preened her legs and antennæ and again took it up. In the meantime C departed and B kept the egg in her mandibles for ten minutes more. Finally she dropped it in the cell and returned to the Myrmicas. March 21 another egg was stolen, and by March 23 the Leptothorax had secured as many as six Myrmica eggs. These were agglutinated to form a packet and were carried about almost continually in the sponge cell. All of these eggs disappeared in the course of a few days and I was compelled to believe that they had been devoured. The thieving continued. By April 10 the Leptothorax had appropriated all the remaining Myrmica eggs, some two dozen all together. By April 30 about half of them had produced larvæ while the other half had been devoured. May 8 most of these larvæ, which showed no signs of growth since hatching, had also disappeared. The last larvæ were seen in the sponge cell May 18, the day on which the colony was released. These observations reminded me that some months previously I had seen a number of small Myrmica larvæ in the Leptothorax cells of another colony. These, too, had disappeared in the course of time. Such observations prove that, at least under artificial conditions, *Leptothorax emersoni* may occasionally revert to behavior like that of the thief ants (*Solenopsis molesta* and *fugax*, Carebara, Pædalgus, etc.).

During 1901 I was able to give greater precision to my observations on the feeding habits of the Leptothorax. There can be no doubt that under normal conditions it obtains its food from the Myrmicas and from them alone. The food is derived from two sources—the body surface of the host and by regurgitation, and it is difficult to ascertain which is the principal source. I had abundant opportunity to corroborate all my earlier statements concerning the shampooing behavior, for the Leptothorax workers and queens were constantly mounting and licking the surfaces of the Myrmicas, and not only the workers of the latter but also the queens and males were subjected to the same treatment. In populous artificial nests as many as four or five Leptothorax may sometimes be seen licking a single Myrmica queen. The licking seems to be a very exciting process as the abdomen of the guest-ant is kept in almost constant stridulatory movement during the operation. There can be no doubt that the little ants obtain some substance from the body-surface of the Myrmica but it is difficult to ascertain its nature. Is it the secretion of cutaneous glands, or is it merely the salivary secretion that has been spread over the Myrmicas by the mutual licking in which they themselves often indulge? Apart from the large pair of epinotal glands described by Nassonov, Lubbock, Janet and others, little is known concerning the cutaneous glands of ants. The epinotal glands, however, seem to be constructed on the pattern of organs that produce a volatile secretion, like the dorsal glands of cockroaches described by Minchin and Haase. The salivary glands of ants are well developed although they have received little study. It is not improbable that they may produce some secretion analogous to the "Futtersaft" of the honey-bee and that they may be of much use in feeding the larvæ. I am confirmed in this opinion by my observations on the peculiar little crickets of the genus Myrmecophila (1900b) which live with species of Formica and Camponotus, and a diminutive, nearly blind cockroach, *Attaphila fungicola* Wheeler (1900a) which inhabits the nests of the Texan leaf-cutting ant (*Atta texana*) and of various South and Central American species (*A. cephalotes*, *Acromyrmex octospinosus*). The behavior of these myrmecophiles shows that the surface of the ant's body must be covered with a greasy, highly nutritious, and possibly also antiseptic secretion, probably derived from the salivary glands of the same ant or of other members of the colony. This secretion is also spread over the eggs, larvæ and pupæ and seems to retard the development of moulds, since the latter tend to grow only on larvæ and pupæ that have been isolated for several days from their nurses. Both Myrmecophila and Attaphila live by licking the surfaces of their hosts; the former remaining on the ground and reaching up to lick the legs and body of the ants, the latter climbing on to the backs of the large Atta soldiers and behaving very much like *Leptothorax emersoni*. Escherich (1902) later described the habits of an Algerian Staphylinid beetle (*Oxysoma oberthueri*) which lives on the dermal secretions of *Cataglyphis viatica*.

But the surface of the Myrmica is not the only source of food for the Leptothorax. If a colony be starved for a few days and then given a dish of sugar and water, the Myrmica workers at once gorge themselves till they are unable to retain all the liquid they have imbibed. They wander about the nest and if examined with a lens, will be seen to be continually regurgitating minute drops which hang suspended for some time in the frame formed by their wide-open jaws. The hanging drop may be eagerly imbibed by some other worker but often the ant is mounted by a Leptothorax. The little insect shampoos the head and clypeus of her host but soon pauses suddenly and for some seconds imbibes the sweet liquid. This she often does even while another Myrmica is partaking of the same drop. Or the Myrmica may regurgitate under the stimulus of the shampooing and thus appear to be feeding the Leptothorax, or the latter may turn to the ventral side of her host and lick her mouthparts and thus induce regurgitation, or at any rate obtain some of the sweet moisture that clings to them.

In 1900 I gained the impression that the Leptothorax never visit the manger themselves nor feed on substances in the nest, but derive their food solely from their hosts. Under normal conditions these observations are correct. In none of my artificial nests, which were well supplied with food, have I seen a Leptothorax drink at the manger or pay the slightest attention to any food placed in the nest. At the same time they are like other ants perfectly able to feed one another and their larvæ by regurgitation. It is possible, however, by changing the conditions, to compel the Leptothorax to obtain their food directly from the manger. Such conditions may be brought about either by starving the whole colony for several days, or by isolating the Leptothorax. The effects of these changes are shown in the following observations:

A colony comprising the sexual forms and several larvæ and pupæ of both species was placed in an artificial nest August 20 and given no food for fully twenty days. During this period both species devoured all their young larvæ and pupæ, leaving only the pupæ that were more or less pigmented and about to hatch. Sept. 10 I placed a small dish of syrup in the nest and within a few minutes its rim was crowded with Myrmicas and Leptothorax eagerly lapping up the syrup side by side. The syrup was left in the nest but on the following days no Leptothorax but only the Myrmicas returned to it. The former confined themselves to their customary source of provisions. In isolated colonies of Leptothorax, however, the habit of going to the manger for food becomes permanently established. Other observations also, to be recorded when I consider the behavior of such colonies, show that these ants can readily obtain their food at first hand.

So far as I was able to observe, both the virgin and the deälated females of Leptothorax behaved in all respects like the workers. The males did not mount and lick the Myrmicas but seemed to depend for their food on the workers and females of their own species. Occasionally, however, they were seen to feed from the manger. It should also be noted that in artificial nests consisting exclusively of Leptothorax workers and females and female Myrmicas the latter behaved in nearly all respects like the workers.

Before considering the conduct of the Leptothorax with ants other than the typical host species, it will be necessary to note its behavior when confined with the same species from another colony, of Leptothorax of one colony confined with Myrmicas from another, and finally of mixtures of Myrmicas from different colonies. These various combinations were made not only with considerable numbers of both species from the natural nests in the same meadow at Colebrook but also with individuals taken from colonies one to three miles apart. The results were the same in all cases: the mutual adaptation was immediate and without the slightest display of hostility. And the same was true when Myrmicas from natural nests containing no inquilines were confined with Leptothorax from other nests. These rapid adjustments must be due to the very mild and timid disposition of the two species and the extraordinary adaptability of the Leptothorax. Were one inclined to be anthromorphic, this behavior might be called "tact."

On but few occasions have I seen anything like mutual hostility in my artificial nests, and I am inclined to attribute it to confinement, improper food and the protracted heat of the Texan autumn. I record these observations in detail as they shed additional light on the behavior of the Leptothorax and make it seem as if this apparently insignificant ant were really the dominant member in the consociation.

About the middle of October one of my nests, containing about sixty workers of each species, began to show signs of demoralization. Little quarrels between the Myrmicas and the Leptothorax became more and more frequent till October 27 and 28 when the mutual hostility reached its climax. The foraging Leptothorax tugged at the antennæ and legs of the Myrmicas in a very vindictive manner. As a rule the Myrmicas endured this treatment with equanimity, often submitting to a shampoo by one Leptothorax while another was tugging at a leg or an antenna. But sometimes the Myrmicas would suddenly seize the Leptothorax by the head or thorax and then as suddenly release and pause to lick them as if to make amends for such unwonted rudeness. As there were several dead Myrmicas, both females and workers, in the nest, but no dead nor dying Leptothorax, I suspected that the inquilines had been killing their hosts. The number of deaths increased daily till November 1 to 3 when among the Myrmicas themselves there were many feuds, often so bitter as to lead to the death of one or both of the combatants. This explained the increasing mortality and exonerated the Leptothorax. The struggles between the two species continued about a week longer when nearly all the Myrmicas were dead and I transferred the Leptothorax to another nest. It was apparent that the aggressive behavior of the Leptothorax had been brought about by the Myrmicas. The latter had turned against one another and the inquilines had, perhaps, imitated the behavior of their hosts. Or the Myrmicas may have failed to respond properly to the blandishments of the Leptothorax as they had failed to behave properly towards one another. Be this as it may, however, I believe that the real cause of the dissensions was the intoxication of the Myrmicas. Their supply of honey and yolk of egg had not been replenished for many days and there were unmistakable signs of fermentation in the mixture. Hence the demoralization.

In another colony consisting largely of female Myrmicas and Leptothorax workers, signs of hostility suddenly developed March 21. A female Myrmica that was trying to enter a Leptothorax nest, was seized by the mandible and later by the middle tarsus. She turned and repeatedly nabbed the inquiline but soon released her uninjured. She walked about seriously incommoded by the Leptothorax which held fast to her tarsus for several hours. Some weeks later (April 30) I observed a similar quarrel in the same nest. One of the female Myrmicas that had retained her wings through the entire winter, objected to being shampooed and ran away whenever a Leptothorax attempted to mount her back. This appeared to irritate the Leptothorax. She seized the Myrmica by one of her fore legs, but suddenly dropped it, and mounting the creature's back with signs of great agitation, seized the right antennal scape, then the left one, then quickly dismounted and again took hold of one of the fore legs. This persistent tweaking excited the Myrmica to such a pitch that she pounced on the little ant and seized her only to drop her almost instantly and run to another part of the nest. The Leptothorax escaped uninjured, but she seemed to have lost for the time any desire to shampoo this particular Myrmica.

In the same nest March 21, there was a severe struggle between two Leptothorax workers. It took place in the sponge cell which had been inhabited so long by the inquilines. They fought like two dogs. Finally one seized the other by the mandibles, carried her out of the chamber to the edge of the sponge and dropped her overboard. Fifteen minutes later the banished Leptothorax returned to the chamber and the struggle was renewed. The ants seemed to be in earnest as they both extruded their stings and sought for weak places in each other's armour. They separated, however, without serious results, and were soon licking the female Myrmicas in the adjoining chamber as if nothing had happened.

Apart from the cases which I ascribed to intoxication, it is impossible to see anything of a serious nature in these combats. They show clearly how difficult it is to ascertain the motives that lead to the unusual behavior of such animals as ants. One observer might be inclined to regard it as a manifestation of the play instinct, while another might interpret it as the result of displeasure or animosity. The difficulty lies in the limited range of expression at the command of organisms so much simpler than ourselves in structure and so very different in psychological endowment.

The fact that in compound nests the Leptothorax are able to procure their own food directly from the manger suggested the possibility of keeping colonies of these ants for some time isolated from the Myrmicas. About two hundred of the inquilines, including a few males and deälated females, with many larvæ and pupæ, taken from several compound nests in the Colebrook meadow, were accordingly removed from their hosts and placed in a large Fielde nest on the morning of September 17. By 7 o'clock in the evening the ants had formed three compact and separate clusters. Two of them were in the damp sponge and contained none of the brood which had been dropped on the glass floor while the ants were being installed in the nest. The remaining cluster was in a piece of earth which had been introduced with a fine lot of ants, larvæ and pupæ. This cluster also neglected the larvæ and pupæ that had fallen out of the nest. The ants in the different clusters passed their time shampooing one another with the most remarkable assiduity, as if compelled to expend on one another the attentions normally lavished on their hosts. None of the workers, ergatoids or queens was seen to feed on the honey and egg-yolk in the manger. One of the males, however, while wandering about the nest, happened on the food and partook of it.

A few days later (September 20) there were five separate clusters of ants in different parts of the two large chambers. Although they were unmolested and had very roomy quarters, they still displayed the tendency to occupy several small chambers instead of a single large cavity. But this tendency soon ceased to manifest itself. On reaching Texas September 26, the ants had all congregated to form with their brood a single mass in a concavity of the damp sponge and thenceforth there was no attempt to form isolated clusters, although the colony was much larger than any single one seen under natural conditions. The ants were in fine condition. The food in the manger, which had been filled before leaving Colebrook, had been devoured.

September 27 the nest was cleaned and provided with a supply of fresh food. The ants were observed daily and were found to behave almost exactly like any other ants in normal single nests. In the chamber exposed to the light there were always from one to half a dozen workers or ergatoids lapping up the food and carrying it back to the dark sponge-chamber. There they fed their hungry sisters whenever they begged for food with rapidly vibrating antennæ. Isolation brought out another form of behavior common to all ants known to me except Polyergus, though it was never manifested by the Leptothorax while associated with the Myrmicas. This is the habit of collecting dead sister ants, little particles of earth, etc. and of depositing them on the liquid food in the manger.

October 5 I placed in the nest three stable flies (*Stomoxys calcitrans*) each cut into a few pieces. The Leptothorax at once mounted the pieces and began to lick them with signs of great agitation. Several of them long and eagerly imbibed the body fluids exuding from the cut surfaces while others devoted themselves to shampooing the outer surfaces of the fragments exactly as if they had been Myrmicas. They licked the heads, legs and wing-membranes of the dead flies, notwithstanding the vibrissæ and coarse bristles, and kept time to the performance with the stridulatory beat of their abdomens. They made no attempt to use their mandibles, which are probably used only for digging and carrying earth, their brood and one another. Later in the day a living Stomoxys, deprived of its wings, was placed in the nest. It walked about trying to avoid the ants which at first seemed to fear the intruder. At last, however, a Leptothorax seized one of the fly's legs; then others came up and pinioned other legs, and soon the insect ceased to move. The stridulation soon summoned other members of the colony and in a short time the whole body of the fly was covered with the little ants, all licking and stridulating as if their lives depended upon it.

Isolation seemed to accentuate another type of behavior, that of deportation. This was rarely exhibited in the compound nests and then only when the Leptothorax were migrating into a new nest. In the isolated colony, however, deportation could be induced at pleasure simply by exposing the sponge chamber to the light and removing the sponge to the food chamber which was then darkened. The ants at first fled in all directions but finally many of those that had discovered the dark chamber returned and carried away the disconcerted workers and queens as well as the brood. By reversing the illumination and returning the sponge to its original place the ants could be made to carry one another back to their old quarters.

During October there was considerable mortality among the members of the colony. The males were the first to succumb, while among the female phases the greatest vitality was exhibited by the queens, ergatoids and largest workers, the least by the small workers. This mortality, though greater than in the compound nests, could not be attributed to the direct effects of isolation but rather to the great number of mites which made their appearance a few weeks after the colony was isolated, and to the drowning of many individuals in the liquid food. It was evident from observation that the ants, though able to feed themselves, were careless or awkward in their movements when they approached the manger. They sometimes toppled over into the liquid, or even ventured to walk on its sticky surface. Such suicidal acts are almost never committed by the Myrmicas or other ants that are in the habit of feeding themselves.

By the end of October most of the pupæ had hatched. The few remaining larvæ were in good condition though they showed hardly any signs of growth. This arrest of development could not be due to isolation as it was quite as conspicuous in the compound nests. By November 2 only fifty-four of the Leptothorax and about two dozen larvæ were still living. This was about a fourth of the original colony and had survived in isolation from the Myrmicas under very artificial conditions for fully six weeks. At this time I introduced some other ants (*Xiphomyrmex spinosus* Pergande) into the nest with results to be recorded below. The colony lived with these strange ants till April 18 when the last Leptothorax died, after having survived fully seven months of isolation from its natural host.

The very considerable plasticity of *Leptothorax emersoni* led me to hope that it might be induced to form compound nests or mixed colonies with other ants besides *Myrmica canadensis*. The experiments performed with this end in view are recorded in the following paragraphs:

1. When placed in nests of such ants as the Ponerine *Stigmatomma pallipes*, the Myrmicines *Pogonomyrmex molefaciens*, *Leptothorax obturator* and *Cyphomyrmex rimosus* and the Formicine *Polyergus bicolor*, with *Formica subænescens* and *F. consocians* as slaves, the *L. emersoni* were promptly attacked and killed before they could enter into an alliance. These results were to be expected from the great differences between the species selected for the experiments and the normal host.

2. As it seemed probable that other species of Myrmica might give more satisfactory results, I selected *M. scabrinodis* subsp. *schencki*, which is common at Colebrook on dry, grassy slopes. On August 18, some earth containing a large Leptothorax nest was placed under the center of the roof-pane of a Lubbock nest and near it a flourishing colony of *schencki* was introduced into the arena. The latter soon began to migrate into the nest carrying their brood and sexual forms into the spaces partly excavated and partly already formed between the small clods of earth under the roof-pane. While engaged in this work they happened on the Leptothorax nest. The attitude of the

two species on first meeting was significant. The Myrmicas were excited and hostile, the Leptothorax calm and conciliatory. They greeted the large ants as they are in the habit of greeting *Myrmica canadensis* workers when they break into the nest, with vibrating antennæ and a willingness to shampoo, but the *schencki* opened their jaws, seized the Leptothorax by the antennæ, head or thorax, dragged them out of their chamber, hurried them through the galleries to the edge of the roof-pane and then dropped them into the arena. No sooner, however, had the Myrmicas turned their backs than the Leptothorax scampered back to their nest under the center of the pane. The rude behavior finally aroused the Leptothorax and they seized the Myrmicas by a leg or an antennal scape and allowed themselves to be carried around the nest motionless and with clenched mandibles. This behavior seems to be resorted to by the Leptothorax whenever it endeavors to coerce another ant into compliance with its desires. Apparently it had some effect even on the truculent Myrmicas, for as the evening wore away I fancied I could detect faint signs of a mutual adaptation between the two species. One Leptothorax even mounted the back of a large Myrmica worker and began to shampoo her thorax, then the sides of her head, till finally, moving around to the ventral side, she ventured to lick the mouthparts. The Myrmica, however, did not assume the spell-bound attitude so characteristic of *M. canadensis* under similar circumstances, but kept her antennæ extended and her mandibles closed, opening them only once or twice, apparently when the titillation was more than usually agreeable. The Leptothorax finally dismounted and, as if emboldened by her success, began to lick some Myrmica pupæ near by. While absorbed in this occupation, another Myrmica came up, seized her by the head and hastily carried her through the nest only to release her near the edge of the roof-pane. A few minutes later I saw a Myrmica shampooed simultaneously by three Leptothorax while she was trying to hold a fourth one in her mandibles. Up to this time none of the inquilines had been injured. This could not be entirely due to the hardness of their integument because a male Leptothorax that was repeatedly seized and carried about by the Myrmicas also escaped uninjured. Apparently the Myrmicas desired to rid themselves of the little pests but were not sufficiently annoyed to destroy them.

Three hours later some changes had taken place in the nest. The Myrmicas had appropriated nearly the whole of the Leptothorax nest but the little ants still held their ground. Nevertheless they showed signs of timidity in the presence of their persecutors and the reactions of the latter were more immediate. They pounced on the Leptothorax wherever and whenever they were encountered, seized them with more vindictive haste than before, and dragged them out of the galleries. Still the Leptothorax escaped uninjured and stubbornly returned to their nest. Within an hour I saw one Leptothorax carried out more than a dozen times by the same or a different Myrmica and as persistently return! While they were being seized, the Leptothorax, for the purpose of resisting ejection, often took hold of any male Myrmica, larva or pupa that happened to be within reach, and the Myrmica worker would be obliged to drag both objects to the edge of the roof-pane. During these struggles a single Leptothorax was killed. But even at this time I saw a Leptothorax shampoo three Myrmicas. One was a dying worker that had been left at the edge of the nest, another was a living worker and the third a winged queen. The last seemed to be well pleased with the operation. Somewhat later a Myrmica worker was seen to kill a male Leptothorax and cast it overboard. At 9:30 o'clock, when I closed my observations for the night, a few of the ejected Leptothorax were still returning to the nest.

At 6:30 o'clock on the following morning the nest showed a decided change. The Leptothorax had been definitely banished. There were six dead workers at the edge of the roof-pane and no living individuals within the nest, which was now entirely occupied by the Myrmicas. The surviving Leptothorax had found an asylum under some dry pellets of earth just beyond the edge of the pane where they were not molested by the Myrmicas. They could not be induced to enter the Myrmica nest even when their own nest was disturbed. They had rescued only three of their larvæ, having been completely dispossessed of their home and remaining progeny by the Myrmicas. The earth in which they were nesting was unpleasantly dry, but they carefully refrained from going under the pane and entering the damp earth which was now being thoroughly explored by the Myrmicas in search of their own larvæ and pupæ.

These observations show very clearly that the formation of a compound nest by *L. emersoni* and *M. schencki* is rendered impossible solely by the conduct of the Myrmicas and not by any unwillingness on the part of the Leptothorax. I deem it probable that compound nests could be formed artificially with the more tractable species of Myrmica, such as *lobicornis*, *detritinodis* and *punctiventris* but as none of these occurs at Colebrook, I was unable to perform the experiment.

3. On returning to Texas I obtained more interesting results with a small predacious ant, *Xiphomyrmex spinosus*, which is but slightly larger than *L. emersoni* and is closely related to the European pavement ant, *Tetramorium cæspitum*, while, so far as its habits are concerned, it occupies about the same situation in the Texan ant-fauna as the various species of Myrmica in the Northern States. It lives in small concealed nests in the earth under the cedars, where the ground after a rain is studded with the emerald spheres of a huge Nostoc.

A single Xiphomyrmex worker was placed in the isolated Leptothorax nest November 2. Whenever the two species met they separated as if startled and ran in opposite directions. The next morning a large ergatoid Leptothorax was carrying the Xiphomyrmex about in the nest. The latter was still alive but had lost a leg during the night. She was soon set down and ran away as rapidly as could be expected. Whenever she encountered a Leptothorax there was the same mutual rebounding as on the preceding day. On the morning of November 4 a large Leptothorax was dragging the Xiphomyrmex about passively by the antennal funicle. The ant soon released her hold and began to lick the Xiphomyrmex all over in the most effusive manner while the latter remained motionless with her feet drawn up. She was rolled over and over by the Leptothorax during the operation and even opened her mandibles while her mouthparts were being licked. Encouraged by this scene I placed five more Xiphomyrmex in the nest. They ran about nimbly and there was the usual rebounding of the two species without other signs of hostility. On the following morning (November 5) six of the Leptothorax were found dead or dying, but I was by no means convinced that this was the result of a struggle. Certainly the Xiphomyrmex never attacked the Leptothorax while I was looking on. They were pulled about by the inquilines either by a leg or an antenna, or even lifted up bodily by the pedicel and carried about the nest or laid down and rolled over and over and licked from head to foot with great gusto and much stridulation. While undergoing this treatment the Xiphomyrmex invariably lapsed into a semicataleptic state from which they recovered gradually, much as many insects do after "feigning death." One Xiphomyrmex that ventured near the Leptothorax brood was seized simultaneously by seven Leptothorax and dragged away by all her legs and an antenna. A deälated female Leptothorax was quite as assiduous as the workers in her attentions to the Xiphomyrmex. November 6 the attitude of the two species towards each other had not changed. The Leptothorax were still dragging the strangers about and licking them by turns. By November 10, however, the behavior had become more friendly. The Xiphomyrmex now lived with the Leptothorax in their nest under the damp sponge and accepted their attentions with equanimity. Sometimes as many as three Leptothorax were to be seen licking a single Xiphomyrmex. The latter were still pulled about by the legs and antennæ but much less frequently and only for short periods. By November 16 pulling ceased altogether and a few days later (November 18) the amalgamation of the two species to form a single mixed colony was completed. Whenever the nest was disturbed the Xiphomyrmex at once hastened to remove the Leptothorax larvæ to a place of safety. They moved more rapidly than the Leptothorax, so that a rather ludicrous appearance was presented, as if the inquilines were waiting for the Xiphomyrmex to do all the work. On this day I saw for the first time a Xiphomyrmex licking a Leptothorax all over. November 22 a Xiphomyrmex was seen feeding a

Leptothorax larva. Both species still visited the manger and the inquilines did not rely on their new hosts for food as might have been expected. During the last days of November the Leptothorax had a very dejected air although the Xiphomyrmex seemed to be in excellent spirits. The mortality of the former species was less than it had been though it still continued. Few of the larvæ remained alive and even these disappeared during the early part of December. The two species continued to live together on the best of terms till April 18, when they died, after the mixed colony had been in existence for fully five months.

OBSERVATIONS ON LEPTOTHORAX GLACIALIS DURING 1906

DURING the summer of 1906, while collecting in Florissant Canyon, near Pike's Peak, Colorado, at an elevation of 8500 feet, I came upon a flourishing colony of *Myrmica brevinodis* spread out under a group of five flat stones on the grassy bank of a stream and containing many workers, a few callow females and males and many larvæ and pupæ of a Leptothorax, which, on account of its very dark color, I at first took to be an undescribed species. Closer examination showed that it might be regarded more properly as a subspecies (*glacialis*) of the New England *emersoni*. The host, too, was found to differ in several minor characters from the eastern form of *brevinodis* and was therefore named var. *subalpina*. That the habits of the western inquiline are somewhat different from those of the eastern type, is indicated by the following notes on the colony kept under observation in an artificial nest from July 17 to August 31.

The artificial nest was of the design which I have described and figured in my ant-book (1910, p. 554, Fig. 286) and consisted of two chambers of the same size, one of which was kept dry and illuminated, the other darkened and kept moist with a slice of sponge soaked in water. The installed colony consisted of the broods of both species, about a hundred Leptothorax workers, a few males and females, and about seventy-five Myrmica workers. The queen of the latter species escaped while the colony was being collected. As soon as the ants and their broods, together with some of the earth in which they had been living, were placed in the lighted chamber, the Myrmicas hastened to transport their own larvæ and pupæ to the dark chamber. The Leptothorax, however, remained behind, and by the following day had hollowed out a small cavity in the earth and had brought into it all their young. This cavity was immediately beneath the glass roof-pane and fully exposed to the light. The Myrmicas kept visiting the Leptothorax continually, but the latter pulled the intruders by the fore-legs or antennæ, and in every way showed the same desire to be left alone in their own habitaculum, as I had observed, under similar circumstances, in the eastern *emersoni*. The Myrmicas endured no end of tweaking and pulling, but nevertheless kept pushing their way into the Leptothorax cavity as if unable to forego the society of their little nest-mates.

Although so jealously guarding their nest against the intruders, the Leptothorax workers did not hesitate to enter the chamber in which the Myrmicas had taken up their abode. There they ran about, accosting the Myrmicas, which had gorged themselves with the sugar water in the manger in one of the corners of the chamber. The Leptothorax mounted their backs, shampooed their bodies and then, turning to the ventral side, promptly placed their tongues in contact with those of their hosts and imbibed the regurgitated sweets. The shampooing, however, was of much briefer duration and much more perfunctory than in the colonies of the typical *emersoni*. Often the *glacialis* worker omitted these manipulations altogether and went at once to the mouth of its host. Sometimes as many as five or six of the little ants would remain standing on the floor of the nest and drink simultaneously from the tongue of a single Myrmica. If the host failed to proffer the droplet of food, the Leptothorax would usually pinch her fore leg or antenna, and this more emphatic and probably more painful appeal rarely failed to elicit the desired response. The Leptothorax undoubtedly obtained all of their food from their hosts, for during the entire six weeks they were under observation, I never found one of them eating from the manger, or even showing the slightest interest in its contents. In the privacy of their own quarters, however, they freely fed one another by regurgitation with the food they had obtained from the Myrmicas.

Since by July 20 the Leptothorax had shown no disposition to move their brood into the dark chamber with the Myrmicas, I undertook to coerce them by exposing their quarters to the bright sunlight. Even this had no effect, till the glass roof-pane became heated, when they slowly and reluctantly took up their larvæ and pupæ and migrated into the dark chamber. Then the entrance between the two chambers was closed. I expected the Leptothorax to establish themselves in one of the larger cavities of the sponge, as had been done by some of my colonies of the typical *emersoni*, but they merely stacked their brood in three piles at the end of the sponge. Here they were, of course, fully exposed to the Myrmica workers and the latter began to visit them assiduously. The presence of the brood, however, caused the Leptothorax to react by pulling and tweaking the fore legs and antennæ of their visitors. By the following day they had brought all their larvæ and pupæ together in a single pile on the side of the sponge opposite that occupied by the Myrmicas and their brood.

July 23 I left Florissant, and for several days traveled about in Colorado, carrying the nest in my luggage. The jarring of the railway train must have had a tendency to mingle the broods of the two species, for during the night of July 23–24, the Leptothorax built a wall of agglutinated sugar crystals about 4 cm. long, parallel with and about a cm. from the edge of the sponge. This wall they were apparently unable to carry up to the roof-pane, so that the long, narrow chamber which they had endeavored to construct, and in which they had placed their brood, was open above and at both ends. The visiting Myrmicas were in no wise restrained by the crystalline rampart, but in their uncontrollable craving to be near the little inquilines kept climbing over it or pushing their way into the openings at the ends.

No change was observed in the relations of the two species till I reached Colorado Springs, July 26, when I found that the Leptothorax had abandoned their useless abode at the edge of the sponge and had moved their brood in under a delicate film of sugar, which they had built inside the food-cup. This film was fastened to the floor and to the vertical wall of the cup, so as to enclose a triangular cavity, which communicated with the outside by means of a single small opening. Structurally this little cell was, of course, an admirable contrivance for preventing the visits of the Myrmicas, but, unfortunately, by August 1st, its sugar wall had been partly dissolved by the moisture in the chamber, and partly eaten by the host ants, so that the little guests and their brood were again exposed on all sides. They now gave up all attempts at keeping their brood sequestered and by August 3, when I arrived in New York, to my surprise both species had collected and mingled their broods together in a single large cavity in the sponge. Henceforth, till all of the pupæ of both species had hatched, the workers of one species did not hesitate to seize and carry the offspring of the other indiscriminately, although up to this time neither had shown the slightest interest in the brood of the other. By reversing the illumination of the chambers and keeping damp sponges in both of them, it was possible to make the ants move back and forth from one to the other, but, although this was repeated on several successive days, the ants always ended by keeping their brood intermingled, either at the edge of the sponge, or in one of the cavities. The original compound nest had, therefore, been converted into a mixed colony. This was quite unexpected, as I had found it extremely difficult to bring about such a result in my colonies of the typical *L. emersoni* and *M. canadensis*. The rapidity of this conversion may have been connected with the condition of the inquiline and host broods, for at the time of its occurrence all the larvæ had become pupæ, and many of them were pigmented and ready to hatch. The presence of eggs or larvæ among the Leptothorax brood would probably have rendered such a fusion of the two colonies impossible.

Early in August a few males and females of the Leptothorax and seven males of the Myrmica made their appearance. The behavior of the inquilines towards the latter was the same as towards the workers. The little ants shampooed these black, winged creatures and licked their mouthparts, but I was unable to ascertain whether any food was regurgitated. The Leptothorax were always on hand whenever a Myrmica male was being fed by a worker of its own species. Sometimes the guests would congregate in numbers and lap up portions of the food as it was passing from the tongue of the worker to that of the male.

August 10 I isolated twenty of the Leptothorax workers and a few of their pupæ in a nest provided with honey and a few dismembered house-flies. The ants lived a few days in a cavity of the sponge till their pupæ had hatched and then wandered aimlessly about the nest. They were never seen to approach the food in the manger and gradually died one by one before the end of the month. This result was very different from that obtained with isolated colonies of the typical *L. emersoni*, for these soon learned to eat from the manger and lived several months as a pure colony.

During August the gaster of one of the larger Myrmica workers in the original nest became unusually distended, and as small packets of eggs were continually appearing and being as rapidly devoured by the workers, I concluded that this unusual individual had become gynæcoid and was trying to function as the queen of the colony. At the end of the month, after all the brood of both species had hatched and the ants had become demoralized, as usually happens when there are no young on which to concentrate their attention, I discontinued my observations. The gynæcoid worker was dissected and found to contain a number of mature eggs.

The foregoing observations indicate that the habits of *L. glacialis* are similar to those of the typical *emersoni*, although differing in two important respects: first, the Colorado form feeds less on the surface secretions of its host and more on regurgitated food; and, second, this ant seems to have lost the ability to secure its food in any other way. If further observations should prove that these peculiarities are common to all colonies of *L. glacialis*, and not an idiosyncrasy of the one I happened to have under observation, or due to the depressing and demoralizing effects of confinement in an artificial nest, we should be justified in concluding that this subspecies has reached an even more advanced stage of symphily or parasitism than the typical form of the Eastern States.

OBSERVATIONS ON LEPTOTHORAX EMERSONI SINCE 1918

WITHIN the past few years the meadow at Colebrook has been drained, so that the number and population of the Myrmica-Leptothorax colonies has been greatly diminished. Probably also the very dry summers of 1917 and 1918 enhanced the unfavorable conditions. On an afternoon in the middle of September 1918 I succeeded in finding only six colonies where in former years I could have found seven or eight times as many. The six colonies were taken to Boston in glass jars and moved as a single colony into an artificial nest during the last days of September. When first collected both the species had young larvæ but owing to the delay in installing the artificial nest, they were nearly all devoured. As soon as the colony was established in its new quarters it was evident that the ants had formed a mixed colony since the Leptothorax showed no inclination to occupy quarters of their own but remained mingled with their hosts even when nesting in the sponge-cavities.

THE CLOSER ALLIES OF LEPTOTHORAX EMERSONI AMONG THE PARASITIC ANTS

WHEN *L. emersoni* was first described, it seemed to represent a unique form of inquilinism, but investigations carried on since 1900 in Europe and the United States show that it is only one of several closely related parasites which are in all probability descended from species of Leptothorax and, with some notable exceptions, still have species of that genus as their hosts. The Leptothoracine genera to which I refer are Myrmoxenus, Epimyrma, Formicoxenus, Symmyrmica, Harpagoxenus and Chalepoxenus. Our present knowledge of the behavior of these various ants may be briefly reviewed.

Myrmoxenus. Since the publication of Ruzsky's description of the single species of this genus, *M. gordiagini*, in 1905, nothing has been learned concerning its behavior. It was originally taken from a colony of *Leptothorax serviculus* Ruzsky in Eastern Siberia.

Epimyrma. Of this genus, established by Emery in 1915, four species are known, all taken in Mediterranean localities, namely *corsica* Emery, from Corsica, *kraussei* from Sardinia, *ravouxi* Ern. André from Southern France and *foreli* Menozzi from Calabria. In regard to the habits of *corsica* and *kraussei* nothing is known, but *ravouxi* was found living with *Leptothorax tuberum unifasciatus* Latr. and *foreli* with four colonies of *L.* (*Temnothorax*) *recedens* Nyl. Vandel (1926) has recently taken *E. ravouxi* in a colony of the latter species of Leptothorax, and since both in the colony found by André and in that found by Vandel deälated mother queens of both species were present, the relationship may be one of xenobiosis.

Formicoxenus. The single species of this genus, *F. nitidulus*, described by Nylander as long ago as 1846, is locally not uncommon over a large portion of Northern and Central Europe. Its small colonies, always associated with *Formica rufa* or its subspecies *pratensis*, nest in the superficial layers of the large mounds of these ants. Its behavior has been studied by Forel (1874), Adlerz (1884), Wasmann (1891, 1915), Donisthorpe (1915), Stumper (1918a, 1918b, 1921) and Stäger (1919, 1923, 1925). In 1908 I published a few notes on its mating habits which I observed in the Upper Engadine. It has long been known that the males of this ant are wingless and very much like the workers in structure (ergatoid), and that mating takes place between brothers and sisters of the same colony (adelphogamy). Until the appearance of Stäger's papers, we had no knowledge of the precise relations of Formicoxenus to its host and the nature of its food, but the enigma is now solved. Although it was known that in artificial nests the inquiline will readily feed independently on insect and saccharine foods, this fact only added to the mystery of its association with such alien hosts as *F. rufa* and *pratensis*. Stumper attempted to show that it must obtain much if not all of its food from the rain water charged with organic substances after percolating through the vegetable débris of which the Formica mounds largely consist. This "Sickerwassertheorie" is rejected by Stäger, because he was able to demonstrate that Formicoxenus really obtains its food in much the same manner as *Leptothorax emersoni*, that is, by mounting the back of its host and appropriating some of the liquid food which it regurgitates or receives from other regurgitating individuals. The host, however, is not so tolerant as *Myrmica canadensis* of its little nest-mates but often attempts to shake them off. Moreover, the *F. rufa* or *pratensis* workers seem to be actually coerced or cowed into letting the Formicoxeni remain among them. When threatened by their hosts, the latter remain quiet, as if "feigning death." They are not, however, indulging in a cataleptic fit but are keenly aware of the danger, for they deliberately and surreptitiously raise the abdomen, turn its apex upward, to the right or to the left, extrude the sting and apply its venom to any exposed and vulnerable point, such as the mouthparts, of the host. This causes the Formica to start back and to desist from following up her attack. The relations between inquiline and host are, therefore, by no means so neutral or indifferent as previous observers have claimed, and the former is quite able to defend itself and to obtain the food which it craves. Stäger's observations show how it is possible for such small greedy creatures to attach themselves to the colonies of such circumspect and irritable ants as *F. rufa* and *pratensis*. Since the inquiline's behavior is neither that of a thieving synœkete, like Lepisma and Myrmecophila, nor that of a symphile, like *Leptothorax emersoni* and Oxysoma, Stäger designates it as "hemisymphilic."

Symmyrmica. This genus, too, comprises but a single species, *S. chamberlini*, which I described in 1904 from specimens taken by Dr. R. V. Chamberlin in Utah in nests of *Manica mutica* Emery (formerly *Myrmica mutica*). The ethological relations of the two species are still unknown. Although Dr. W. M. Mann and I have examined many colonies of *mutica* and other species of Manica in the Western and Northwestern States, we have failed to find any infested with the inquiline. The male, like that of Formicoxenus, is wingless, but the head and thorax are much less like the corresponding parts of the worker and resemble those of the normal winged male of Leptothorax. The male Symmyrmica is clearly, therefore, in a phylogenetically less advanced stage of ergatoidism than the male Formicoxenus.

Harpagoxenus. This genus contains only two species, *H. sublævis* Mayr of Northern and Central Europe and *H. americanus* Emery, of the Atlantic States from Maryland to Massachusetts. Both are rare and local. Their close affinities with Leptothorax, and especially with the subgenus Mychothorax, are very evident, though the workers and females of Harpagoxenus may be readily distinguished by the presence of shallow antennal scrobes at the sides of the frontal carinæ and the prolongation backwards of the latter toward the posterior border of the head. The behavior of the European *sublævis* has been studied by Adlerz in Sweden (1886, 1896) and by Viehmeyer (1908a, 1908b, 1912, 1921) in Saxony. In Sweden the female is represented by workers and wingless, workerlike (ergatoid) but ocellate individuals exclusively, whereas in Saxony true winged females, also occur. The regular host of *sublævis* is *Leptothorax* (*Mychothorax*) *acervorum* Nyl. but it is sometimes found in colonies of *L.* (*M*) *muscorum* Nyl. and there is one dubious record of its occurrence with *L. tuberum* Fabr. Both Adlerz and Viehmeyer have shown that *sublævis* is to be regarded as a dulotic, or slave-making ant. Its behavior is, in fact, much like that of *Formica sanguinea*. The ergatoid female (and the same is probably also true of the deälated female) enters an *acervorum* nest and aggressively takes possession of some of the brood, which later produces the workers that rear the offspring of the intruder, so that a mixed colony is formed. Viehmeyer (1908b) describes the introduction of a *sublævis* ergatoid into a colony of *L. acervorum* as follows: "The experiment gave the same results as the experiments with *F. sanguinea*. The female which was decidedly larger than the Leptothorax workers, ran about the nest in an excited manner and the Leptothorax fled with their larvæ and pupæ. From time to time the latter attacked the female, but she was always the victor in the ensuing conflicts and in the course of the day succeeded in killing all the Leptothorax. Some of them were quite bitten to pieces. The female collected the pupæ and larvæ in a heap, but she displayed less adroitness and eagerness than *sanguinea* queens." The *sublævis* workers also make raids on *acervorum* colonies and carry off their brood, but these raids are made by a small number of individuals and without the concerted organization of *F. sanguinea* and Polyergus. At first, Viehmeyer assumed that *sublævis* must have developed from a predatory stage like that of the thief-ants (*Solenopsis fugax*, etc.) but he later changed his point of view. "At the present time," he says (1921), "I am no longer able to maintain this hypothesis. Since I have been able to show that slavery and social parasitism in *F. sanguinea* arose as independent proclivities within the species and developed in connection with the carnivorous feeding habits, there is no reason, so far as our information goes, for making any other assumptions in regard to Harpagoxenus. In my opinion, therefore, Harpagoxenus, while it was still independent [i.e. non-parasitic], was decidedly carnivorous, but later became a robber of pupæ and eventually specialized exclusively in this kidnapping business till it had attained the extreme stage in which we find it today. Social parasitism kept pace with this development and it alone made it possible to secure the full advantages which this kind of robbery was capable of yielding the species. The advent of social parasitism coincided with the moment when Harpagoxenus began to rear the larvæ and pupæ which it had kidnapped in excess of the number required for food. At the present time, of course, the slave-making ants no longer exhibit such food preferences, but content themselves with what their auxiliaries (slaves) feed them."

Although *americanus*, our North American species of Harpagoxenus, has been known since 1893, it is so scarce and local that little was learned in regard to its behavior till very recently. It is smaller and much darker than *sublævis* and was first taken by Pergande near Washington, D. C. in a nest of *Leptothorax curvispinosus* Mayr. In 1905 I found it in three colonies of the same ant in hollow twigs of elder bushes near Bronxville, N. Y., and in 1925 Sturtevant found it nesting with the same host in an old oak-gall on Naushon Island, Mass. Both Sturtevant (1927) and Creighton (1927) have more recently and independently discovered a number of colonies in various localities near New York City. While the brownish yellow *L. curvispinosus* is undoubtedly the regular host of *americanus*, both of these investigators have taken it also in colonies of the black *L. longispinosus* Roger. Like the Saxon form of *sublævis*, our American species has both winged and ergatoid females, but the latter are rare. The following experiment performed by Sturtevant with a winged queen may be compared with Viehmeyer's experiment with an ergatoid. "On July 31 I removed all but some irregular stumps of the wings of a queen Harpagoxenus (from nest number 9), and placed her in a pure *L. curvispinosus* nest that contained one deälated queen, about 70 workers, and brood. The Harpagoxenus queen was attracted by the brood, but was quickly attacked by the workers. She at once became much excited, and moved so rapidly that the workers did not succeed in grasping her except occasionally by the stumps of wings. She attacked them, but only by 'nipping' at the antennæ or legs—never did she get the 'bulldog grip' that is so characteristic of ants—even of Harpagoxenus workers. These nips were, however, effective, for within half an hour about ten workers had portions of one or both antennæ amputated. Usually the scape was cut in two. The remaining workers in the nest rapidly moved the brood as far as possible from the invading queen—under natural conditions they would presumably have left the nest entirely. The Leptothorax queen did not fare differently from the workers, and ultimately she was so maimed that she died. It seems probable that under natural conditions she too would have migrated. Battles occurred from time to time for several days, until most of the workers were more or less maimed. The Harpagoxenus queen showed interest in the brood only intermittently, but occasionally rested on it. New workers emerged in a few days and on August 4 one of these callows was seen to feed the Harpagoxenus queen by regurgitation. The old workers still attacked her, however, and she grew gradually weaker, until she died August 10. If one may judge from this experiment, the fertilized queen of *H. americanus* enters a nest of pure Leptothorax and appropriates some of the brood. The workers and queen are attacked and emigrate probably to find a new nest, taking much of the brood with them. The intruder is then adopted by the workers that emerge from the brood she has appropriated. It may be surmised that nests numbers 11 and 16 represent cases in which this has just happened. In each of these nests there was present a single deälated Harpagoxenus queen, with a few Leptothorax workers, but no Harpagoxenus workers or pupæ." Creighton was able to observe under very favorable conditions the slave-raids carried out by the workers of *americanus* on both *curvispinosus* and *longispinosus* colonies.

Chalepoxenus. This genus was established by Menozzi as recently as 1922 for a peculiar ant, *C. gribodoi*, which was found in Piedmont, Northern Italy, living in a hollow Rubus stem in company with *Leptothorax tuberum*. The inquiline is closely related to Harpagoxenus and possesses similar antennal scrobes, but the mandibles are toothed, the antennæ are 12- instead of 11-jointed, with a distinct 3-jointed club, and there are no spurs on the middle and hind tibiæ. Menozzi kept the mixed colony, which consisted of a Chalepoxenus queen, a dozen workers and about four times as many Leptothorax workers, in an artificial nest for several days and was able to observe that the Chalepoxeni kept by themselves but occasionally approached the Leptothorax and begged them for food. He believes that the two species really lived in separate portions of the Rubus stem, the host nearer the entrance and in the broader and longer portion of the cavity, while the Chalepoxeni occupied about a centimetre of the blind end. In 1925 Menozzi discovered the male of *C. gribodoi* and concluded that the genus is more closely related to Leptothorax than to Harpagoxenus.

GENERAL CONSIDERATIONS

It will be observed that the hosts of the parasitic species belonging to four of the seven groups we have been considering, namely Myrmoxenus, Epimyrma, Harpagoxenus and Chalepoxenus, belong to the genus Leptothorax, i.e. to the very genus to which they are themselves most closely related. They therefore conform to the general rule according to which most parasitic Aculeate Hymenoptera seem to have been originally congeneric if, indeed, not actually cospecific with their hosts. In a former paper (1919) I have cited a considerable number of parasitic bees, wasps and ants which follow this rule. Nor is it surprising to find that Leptothorax has produced a number of parasitic offshoots, since it is a large, cosmopolitan and very old genus, as shown by the fact that at least five species are known from the Lower Oligocene (Baltic amber). Furthermore, the existing species are sufficiently diverse to be referable to several subgenera (Mychothorax, Temnothorax, Dichothorax, Goniothorax and Leptothorax *sens. str.*). It is not so easy to account for the fact that three of the parasitic species, *L. emersoni*, Formicoxenus and Symmyrmica, live with hosts that are not closely related to Leptothorax. We have no means of determining whether Myrmica, Formica and Manica were the original hosts of these parasites or whether the latter lived originally with species of Leptothorax and became secondarily associated with their present, after the extinction of their former hosts. It is obvious, however, that the present hosts are all much larger than species of Leptothorax and must therefore afford the parasites a much more abundant supply of food. That the consociation of the typical *L. emersoni* and *M. canadensis* may not be of very ancient phylogenetic standing is indicated by the fact that *emersoni* can live for many weeks or even months after separation from its host and that under such conditions the primitive impulse to secure food independently can be easily resuscitated. In the subsp. *glacialis*, however, judging from the single colony observed, the parasitic habits have become so firmly fixed that existence apart from the host is no longer possible, so that a stage has been reached like that of the amazon ants (Polyergus), which are no longer able to feed independently.

The Leptothoracine parasites whose behavior is known, namely *L. emersoni*, Formicoxenus and Harpagoxenus, exhibit rather striking differences. *L. emersoni* is truly symphilic, Formicoxenus, to use Stäger's term, is hemisymphilic, and Harpagoxenus is dulotic; and while there is little difficulty in conceiving of a phylogenetic derivation of the behavior of *L. emersoni* from that of the more hostile Formicoxenus, it is highly improbable that either has passed through a dulotic stage like that of Harpagoxenus. All three are much more probably independent developments, but all may be conceived to have had an aggressively predatory initial stage. And though all these forms were originally bent on obtaining their food from other ants, *L. emersoni* and Formicoxenus specialized in securing theirs by compelling their hosts to regurgitate, while Harpagoxenus, if Viehmeyer is correct, specialized in kidnapping and devouring the brood of certain species of Leptothorax. Thus Harpagoxenus eventually became dulotic and established mixed colonies with its host whereas *L. emersoni* and Formicoxenus from the first evinced no interest in the brood of their hosts and failed therefore to develop beyond the compound nest stage. If Menozzi's interpretation is correct, Chalepoxenus may also be regarded as forming a compound nest rather than a mixed colony with *L. tuberum*. Or, perhaps, the relations between the two species may be more like those I have recently described (1925) in two very interesting Panamanian ants, *Megalomyrmex (Cepobroticus) symmetochus* and *Sericomyrmex amabilis*. These live together quite amicably in the fungus gardens of the latter, but each cares only for its own brood though the larvæ and pupæ of both species lie intermingled in the depressions and crypts of the gardens. Here, too, the inquiline takes no interest in the brood of its host but only in the food supply, i.e. in the fungus which is cultivated by the Sericomyrmex. The conditions in the Megalomyrmex-Sericomyrmex colony are therefore clearly intermediate between a compound nest and a mixed colony and, like the experimentally induced mixed colonies of *L. emersoni* and Myrmica, tend to obliterate the sharp line which Forel (1874) and Wasmann (1891, 1915) have drawn between ants forming compound nests and those forming mixed colonies with their hosts. The former are distinguished by bringing up their own young in different nests connected by galleries, the latter by occupying the same chambers and bringing up their broods in common. It is implied that the different methods of rearing the brood are the important distinctions. Obviously *L. emersoni* and *M. brevinodis* belong with the species that make compound nests, but the relations of these two ants are so intimate that *L. emersoni* would seem to be on the road to forming a mixed colony with its host. As we have seen, such colonies can be actually formed in artificial nests where conditions prevent the construction and occupation of separate chambers, or when the brood of the Leptothorax dwindles or disappears. More experiments and observations are required, however, in order to determine the precise conditions that lead to the formation of the mixed colony. If the absence of the brood of the parasite is an essential factor, it should be possible to "unscramble" a mixed Leptothorax-Myrmica colony, such as was formed in 1918, by introducing plenty of larvæ of the two species. Up to the present time I have not had an opportunity to perform this experiment. Moreover, if the presence of the brood is really the determining condition, trophallaxis may prove to be the factor which inhibits the formation of a mixed colony in the case of Myrmica and Leptothorax. In other words, it is very probable that a given species of ant will prefer the secretions (exudates) of its own brood and that it will keep its relations to its own brood intact even when associating as a symphile with adult ants of another species, unless the larvæ of the host have similarly attractive secretions. In the latter case a mixed colony will result as in the various cases of permanent and temporary social parasitism and dulosis (slavery) among the closely allied species of Formica (*F. sanguinea* and *fusca*) or of Formica and Polyergus, of Strongylognathus and Tetramorium, Harpagoxenus and Leptothorax, etc.

It will also be observed that the majority of the Leptothoracine parasites exhibit certain peculiar morphological modifications as compared with typical non-parasitic ants. In two of the groups, Symmyrmica and Formicoxenus, the males are wingless and more or less ergatomorphic, and in three of them, *L. emersoni*, Formicoxenus and Harpagoxenus an ergatoid female, or ergatogyne, possessing a spermatheca and capable of mating (Adlerz, 1896), is present in addition to the normal winged form. These

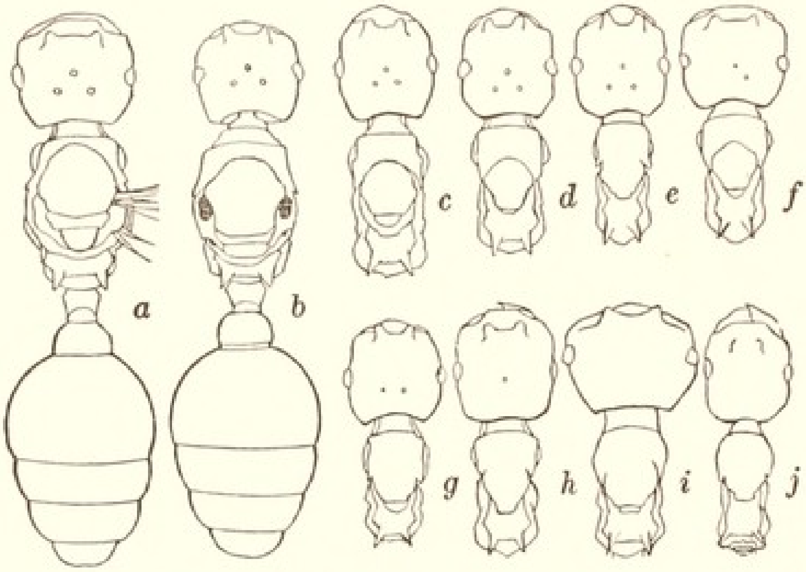

Figure 45. Series of Female and Worker Forms of Leptothorax emersoni, *Dorsal View.* a, *Winged Female;* b, *Ergatoid Female;* c–f, *Triocellate Workers;* g, *Biocellate Worker;* h, *Uniocellate Worker;* i, *Macrergate;* j, *Micrergate. (After Margaret Holliday.)*

peculiarities are probably connected in some way with the parasitic proclivities of the species in which they occur. The absence of wings in the males leads necessarily to adelphogamy, or incestuous mating between the consanguineous males and females of the same colony. Similar conditions have been observed in some other ants, both parasitic (Anergates, Anergatides) and nonparasitic (Ponera, Cardiocondyla) and would seem to be advantageous. All the species in which wingless males occur are rare, diminutive and feeble, and form small colonies which as a rule produce only a few sexual forms. To such ants, the regular marriage flight, owing to the wide aërial dispersion of the males and females, might be distinctly disadvantageous.

The instability of the female and worker phases seems also to be closely connected with peculiarities of habit. Forel (1874) and Wasmann (1895) long ago showed that certain species of Leptothorax (*acervorum*, *muscorum* and *tuberum*) and *Formicoxenus nitidulus* may have females and workers of different types (winged macrogynes and microgynes, wingless ergatogynes and workers proper) and in Formicoxenus, Stumper (1918a, 1918b, 1921) has recently figured and described in detail an almost continuous series of such forms. I had previously observed very similar conditions in *L. emersoni* and as long ago as 1900 was impressed with the fact that the winged females of this ant are produced in small numbers, that the colonies contain several ergatoid females and that the workers vary considerably in size and often possess from one to three ocelli, a condition very unusual in the genus Leptothorax. It seemed to me, therefore, that the reproductive function might be in process of being shifted from the female to the worker phase. In order to test this view I requested one of my former students, Miss Margaret Holliday, to study the various female and worker forms and the structure of their ovaries. Her paper, published in 1903, seems to confirm my opinion. In her examination of 1,000 specimens of *L. emersoni* she was able to distinguish eleven different types among the workers and females, as shown in the following table:

- Females
  - Winged
    - XI Queen
    - X Microgyne
  - Apterous
    - IX Ergatoid
    - Ocellate Workers
      - Triocellate
        - VIII scutellate
          - a) with large scutellum
          - b) with small scutellum
        - VII escutellate
      - Biocellate
        - VI scutellate
          - a) with large scutellum
          - b) with small scutellum
        - V escutellate
      - Uniocellate
        - IV scutellate
          - a) with large scutellum
          - b) with small scutellum
        - III escutellate
    - II Macrergate
    - I Micrergate

The structure of most of these forms is shown in the accompanying sketches (Figs. 45 and 46). The thousand specimens comprised 111 males, 26 winged queens, 10 microgynes, 16 ergatoids, 276 triocellate workers (36 of type VIIIa, 126 of type VIIIb and 114 of type VII), 17 biocellate workers, 8 uniocellate workers, 429 macrergates and 117 micrergates. Specimens of the various types were dissected with the following interesting results: "Throughout the entire series the number of (ovarian) tubules varied between two and three on each side; the receptaculum seminis was observed in all the cases, except two, which were doubtful. The ovaries of the queen were smaller than those of any of the other forms. The number of eggs in each tubule varied both in the two sides of the same ovary and in the ovaries of the different individuals of the same type, as also in those of different types." Miss Holliday remarks that "If Adlerz's statement is correct, that all ants possessing the receptaculum seminis are to be considered as queens, then we have in these one thousand specimens 887 queens, 111 males and two individuals which may be queens, if calculations are based on the results obtained." We might say, therefore, that functionally only two castes of individuals exist in *L. emersoni*, males and females. Unfortunately Miss Holliday did not determine whether sperm was present in the receptaculum of any of the wingless forms so that we are unable to say whether the latter ever mate with the males. The small percentage of males in the colony would seem to indicate that such mating may occur.

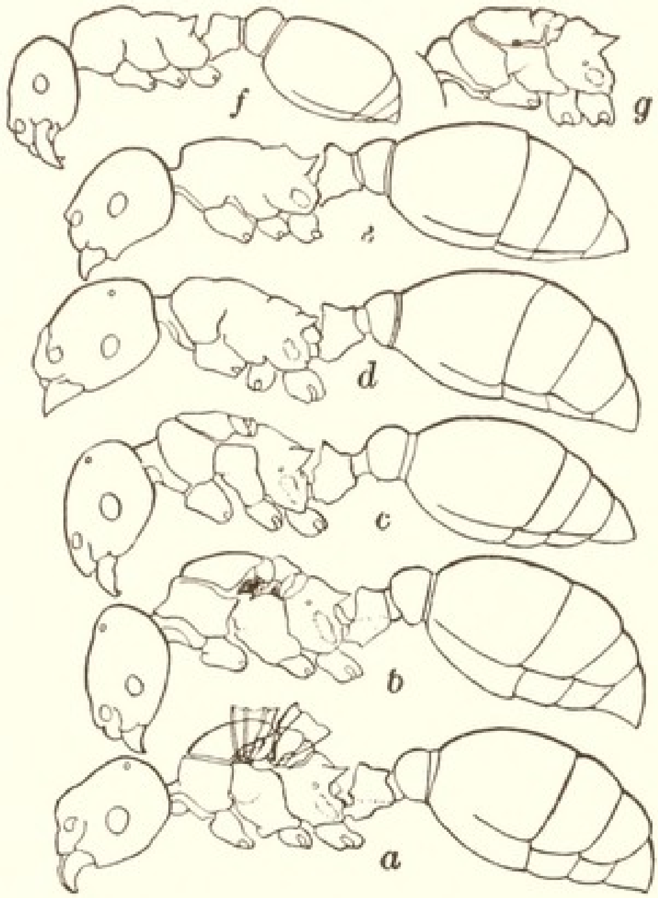

Figure 46. Series of Female and Worker Forms of Leptothorax emersoni *in Profile.* a, *Winged Female;* b, *Ergatoid Female;* c, *Triocellate Worker;* d, *Biocellate Worker;* e, *Macrergate, or Large Worker;* f, *Micrergate, or Small Worker;* g, *Thorax of Ergatoid Form with Sutures for Fore Wings Only. (After Margaret Holliday.)*

In Harpagoxenus the tendency to shift fecundity to the worker phase is clearly shown in the Swedish race of *sublævis* which has replaced the winged with the ergatoid female. The Saxon race of the same species and our American form have not yet reached this regressive stage. The shifting of fecundity to the worker phase is obviously due to the unusually favorable trophic conditions in which both *emersoni* and Harpagoxenus live. Another series of parasitic ants, living under similarly favorable conditions, namely the species of the monotypic genera Anergates, Epœcus, Wheeleriella, Anergatides, Sympheidole and Epipheidole, instead of transferring the reproductive function to the workers and eliminating the queen, have accentuated the fertility of the latter and have suppressed the worker caste altogether. The difference in the two cases represented by *L. emersoni* on the one hand and Anergates, etc., on the other, has evidently been determined by the difference in the parasitic habits. In the former species the worker has to be preserved owing to the way in which the colony derives its food from the host, whereas in the latter the queen replaces the host queen and is therefore fed directly by the host workers. For a similar reason the workers of the thief ants (*Solenopsis fugax* and *molesta*, Pædalgus, Aëromyrma and Carebara) have to be retained, though they are greatly reduced in size as compared with their huge fertile queens, because the workers obtain the food by entering the nests of other ants and termites through tenuous galleries, not unlike those that connect the chambers of the *L. emersoni* and *M. canadensis* nests.

LITERATURE

ADLERZ, G. 1884. Myrmekologiska Studier. I *Formicoxenus nitidulus*. Öfvers. Kongl. Vet.-Akad. Förhandl. 8, pp. 43–64, 2 pls.

——. 1886. Myrmekologiska Studier. II Svenska Myror och deras Lefnadsförhållanden. Bihang till Kongl. Svensk. Vet.-Akad. Handl. 11, 18, pp. 1–329, 7 pls.

——. 1896. Myrmekologiska Studier. III *Tomognathus sublævis* Mayr. Bihang till Kongl. Svensk. Vet.-Akad. Handl. 21, pp. 3–76, 1 pl.

BETHE, A. 1898. Dürfen wir den Ameisen und Bienen psychische Qualitäten zuschreiben. Arch. gesam. Physiol. 70, pp. 15–100, 2 pls., 5 figs.

CREIGHTON, W. S. 1927. The Slave-Raids of *Harpagoxenus americanus*. Psyche 34, pp. 11–29, 2 figs.

DONISTHORPE, H. 1915. British Ants. Plymouth, W. Brendon & Son.

ESCHERICH, K. 1902. Biologische Studien über algerische Myrmekophilen. Biol. Centralbl. 22, pp. 638–663, 4 figs.

FOREL, A. 1874. Les Fourmis de la Suisse. Zürich, Zürcher u. Furrer.

——. 1894. Les Formicides de la Provence d'Oran d'Algérie. Bull. Soc. Vaud Sc. Nat. 30, pp. 1–45, 2 pls.

——. 1921–23. Le Monde Social des Fourmis. Genève, Kundig.

HOLLIDAY, M. 1903. A Study of Some Ergatogynic Ants. Zool. Jahrb. Abth. Syst. 19, pp. 293–328, 16 figs.

MENOZZI, C. 1921. Formiche dei dintorni di Sambiase di Calabria. Boll. Lab. Zool. Gen. Agrar. Portici 15, pp. 24–32, 3 figs.

——. 1922. Nota su un nuovo genere e nuova specie di formica parasita. Atti. Soc. Ital. Sci. Nat. 61, pp. 3–7, 1 fig.

——. 1925. Note Staccate di Mirmecologia. Boll. Soc. Ent. Ital. 57, pp. 17–22, 2 figs.

RUZSKY, M. 1905. Formicariæ Imperii Rossici (In Russian) 799 pp., 176 figs. Kasan.

STÄGER, R. 1919. Erlebnisse mit Insekten. Zürich, Rascher u. Co.

——. 1923. Ergebnisse meiner neuen Beobachtungen an *Formicoxenus nitidulus* Nyl. Zeitschr. wiss. Insektenbiol. 18, pp. 290–292.

——. 1925. Das Leben der Gastameise (*Formicoxenus nitidulus* Nyl.) in neuer Beleuchtung. Zeitschr. Morph. Ökol. der Tiere 3, pp. 452–476.

STUMPER, R. 1918a. *Formicoxenus nitidulus* Nyl. I. Beitrag. Biol. Zentralbl. 38, pp. 160–179, 14 figs.

——. 1918b. Zur Kenntnis des Polymorphismus der Formiciden. Vereinschr. Gesell. Luxemb. Naturfr. 7 pp., 4 figs.

——. 1921. Etudes sur les Fourmis III. Recherches sur l'Ethologie du *Formicoxenus nitidulus* Nyl. Bull. Soc. Ent. Belg. 7, pp. 89–97, 1 fig.

STURTEVANT, A. H. 1925. Notes on the Fauna of Oak Galls in the Woods Hole Region. Psyche 32, pp. 313–314.

——. 1927. The Social Parasitism of the Ant *Harpagoxenus americanus*. Psyche 34, pp. 1–9.

VANDEL, A. 1926. Fourmis françaises rares ou peu connues. Bull. Soc. Ent. France, pp. 196–198.

VIEHMEYER, H. 1908a. Beiträge zur Ameisenfauna des Königreiches Sachsen. Abhandl. naturw. Gesell. Isis Dresden, pp. 55–69, 1 pl.

——. 1908b. Zur Koloniegründung der parasitischen Ameisen. Biol. Centralbl. 28, pp. 18–32.

——. 1912. Ueber die Verbreitung und die geflügelten Weibchen von *Harpagoxenus sublevis* Nyl. Entom. Mitteil. 1, pp. 193–197.

——. 1921. Die mitteleuropäischen Beobachtungen von Harpagoxenus. Biol. Zentralbl. 41, pp. 269–278.

WASMANN, E. 1891. Die zusammengesetzten Nester und gemischten Kolonien der Ameisen. Münster, Aschendorffsche Buchdruckerei.

——. 1895. Die ergatogynen Formen bei den Ameisen. Biol. Centralbl. 15, pp. 606–646.

——. 1915. Das Gesellschaftsleben der Ameisen. Bd. I. Münster, Aschendorffsche Verlagsbuchhandlung.

WHEELER, W. M. 1900a. A new Myrmecophile from the Mushroom Gardens of the Texan Leaf-Cutting Ant. Amer. Natural. 34, pp. 851–862, 6 figs.

——. 1900b. The Habits of *Myrmecophila nebrascensis* Bruner. Psyche, 9, pp. 111–115, 1 fig.

——. 1901. The Compound and Mixed Nests of American Ants. Amer. Natural. 35, pp. 431–448, 9 figs.

——. 1903a. Ethological Observations on an American Ant (*Leptothorax emersoni* Wheeler). Arch. Psych. Neurol. 2, pp. 1–31, 1 fig.

——. 1903b. A Revision of the North American Ants of the Genus Leptothorax. Proc. Acad. Sci. Phila., pp. 215–260, 1 pl.

——. 1904. Three New Genera of Inquiline Ants from Utah and Colorado. Bull. Amer. Mus. Nat. Hist. 20, pp. 1–17, 2 pls.

——. 1905. An Interpretation of the Slavemaking Instincts in Ants. Bull. Amer. Mus. Nat. Hist. 21, pp. 1–16.

——. 1907. Notes on a New Guest Ant, *Leptothorax glacialis*, and the Varieties of *Myrmica brevinodis* Emery. Bull. Wis. Nat. Hist. Soc. 5, pp. 70–83.

——. 1908a. The Ants of Casco Bay, Maine, with Observations on Two Races of *Formica sanguinea* Latreille. Bull. Amer. Mus. Nat. Hist. 24, 1908, pp. 619–645.

——. 1908b. Comparative Ethology of the European and North American Ants. Festschr. f. Forel. Journ. Psych. Neurol. 13, pp. 404–435, 4 pls., 6 figs.

——. 1910. Ants, Their Structure, Development and Behavior. New York, Columbia Univ. Press.

——. 1917. The Mountain Ants of Western North America. Proc. Amer. Acad. Arts Sci. 52, pp. 457–569.

——. 1918. A Study of Some Ant Larvæ, with a Consideration of the Origin and Meaning of the Social Habit among Insects. Proc. Amer. Philos. Soc. 57, pp. 293–343, 12 figs.

——. 1919. The Parasitic Aculeata, a Study in Evolution. Proc. Amer. Philos. Soc. 58, pp. 1–40, 6 tables.

——. 1925. A New Guest-ant and Other New Formicidæ from Barro Colorado Island, Panama. Biol. Bull. 49, pp. 150–181, 8 figs.

THE ANT COLONY AS AN ORGANISM

A LECTURE PREPARED FOR DELIVERY AT THE MARINE BIOLOGICAL LABORATORY, WOODS HOLE, MASS., AUGUST 2, 1910, AND PUBLISHED IN THE *Journal of Morphology*, VOL. 22, 1911

Une autre hypothèse pourrait considérer la ruche, la fourmilière et la termitière comme un individu unique, mais encore ou déjà disseminé, un seul être vivant qui ne serait pas encore ou qui ne serait déjà plus coagulé ou solidifié et dont les divers organes, formés de milliers de cellules, bien qu'extériorisées et malgré leur apparente indépendance resteraient toujours soumis à la même loi centrale. Notre corps aussi est une association, un agglomerat, une colonie de soixante trillions de cellules, mais de cellules qui ne peuvent pas s'éloigner de leur nid, ou de leur noyau, et demeurent, jusqu'à la destruction de ce nid ou de ce noyau, sédentaires et captives. Si terrible, si inhumaine que paraisse l'organisation de la termitière, celle que nous portons en nous est calquée sur le même modèle. Même personalité collective, même sacrifice incessant d'innombrables parties au tout, au bien commun, même système defensif, même cannibalisme de phagocytes envers les cellules mortes ou inutiles, même travail obscur, acharné, aveugle, pour une fin ignorée, même ferocité, mêmes spécialisations pour la nutrition, la reproduction, la respiration, la circulation du sang, etc., mêmes complications, même solidarité, mêmes appels en cas de danger, mêmes équilibres, même police intérieure.

MAETERLINCK,
"LA VIE DE TERMITES"

As a zoölogist, reared among what are now rapidly coming to be regarded as antiquated ideals, I confess to a feeling of great diffidence in addressing an audience so thoroughly versed in the very latest as well as the very oldest biological facts, methods and hypotheses. I feel, indeed, like some village potter who is bringing to the market of the metropolis a pitiable sample of his craft, a pot of some old-fashioned design, possibly with a concealed crack which may prevent it from ringing true. Although in what I have to say, I shall strenuously endeavor to be modern, I can only beg you, if I fail to come within hailing distance of the advance guard of present day zoölogists, to remember that the range of adaptability in all organisms, even in zoölogists, is very limited.

Under the circumstances, my only hope lies in appealing to our permanent common biological interests and these, I take it, must always center in the organism. But the point of view from which we study this most extraordinary of nature's manifestations, is continually shifting. Twenty years ago we were captivated by the morphology of the organism; now its behavior occupies the foreground of our attention. Once we thought we were seriously studying biology when we were scrutinizing paraffine sections of animals and plants or dried specimens mounted on pins or pressed between layers of blotting paper; now we are sure that we were studying merely the exuviæ of organisms, the effete residua of the life-process. If the neovitalistic school has done nothing else, it has jolted us out of this delusion which was gradually taking possession of our faculties. It is certain that whatever changes may overtake biology in the future, we must henceforth grapple with the organism as a dynamic agency acting in a very complex and unstable environment. In using the term organism, therefore, I shall drop the adjective "living," since I do not regard pickled animals or dried plants as organisms.

As I wish to describe a peculiar type of organism, I may be asked, before proceeding, to state more concisely what I mean by an organism. It is obvious that no adequate definition can be given, because the organism is neither a thing nor a concept, but a continual flux or process, and hence forever changing and never completed. As good a formal definition as I can frame is the following: An organism is a complex, definitely coördinated and therefore individualized system of activities, which are primarily directed to obtaining and assimilating substances from an environment, to producing other similar systems, known as offspring, and to protecting the system itself and usually also its offspring from disturbances emanating from the environment. The three fundamental activities enumerated in this definition, namely nutrition, reproduction and protection seem to have their inception in what we know, from exclusively subjective experience, as feelings of hunger, affection and fear respectively.

Biologists long ago constructed an elaborate hierarchy of organisms. Those of a speculative turn of mind, like Spencer and Weismann, postulated the existence of very simple organisms, the physiological units, or biophores, which, though invisible, were nevertheless conceived as combining the fundamental activities above enumerated. These biophores were supposed to form by aggregation the cells, which may exist as independent organisms in the Protozoa and Protophyta, or to unite with other cells to form more complex aggregates, for which Haeckel's term 'persons' may be adopted. The person may be a single cell-aggregate or consist of complexes of such aggregates as the metameres of the higher animals, for the separate metameres, according to a very generally accepted theory, are supposed to be more or less modified or highly specialized persons. Somewhat similar conditions are supposed to obtain in the composition of the vascular plants. The integration both of the metameric and non-metameric Metazoa may proceed still farther, the simple persons combining to form colonies in which the persons are primarily nutritive and acquire fixed and definite spatial relations to one another, whereas the more specialized animals, like the social insects, may constitute families of mobile persons with reproduction as the 'Leitmotiv' of their consociation. In man we have families associating to form still more complex aggregates, the true societies. Other comprehensive organisms are the biocœnoses, or more or less definite consociations of animals and plants of different species, which the ecologists are endeavoring to analyze. Finally we have philosophers, like Fechner, stepping in with the assertion, that the earth as a whole is merely a great organism, that the planetary systems in turn are colonies of earths and suns and that the universe itself is to be regarded as one stupendous organism. Thus, starting with the biophore as the smallest and ending with the universe as the most comprehensive, we have a sufficiently magnificent hierarchy of organisms to satisfy even the most zealous panpsychist. As biologists we may, for present purposes, lop off and discard the ends of this series of organisms, the biophores as being purely hypothetical and the cosmos as involving too many ultrabiological assumptions. We then have left the following series: first, the Protozoon or Protophyte, second the simple or non-metameric person, third the metameric person, fourth the colony of the nutritive type, fifth the family, or colony of the reproductive type, sixth the biocœnose, and seventh the true, or human society. Closer inspection shows that these are sufficiently heterogeneous when compared with one another and with the personal organism, which is the prototype of the series, but I believe, nevertheless, that all of them are true organisms and not merely conceptual constructions or analogies. One of them, the insect colony, has interested me exceedingly, and as I have repeatedly found its treatment as an organism yielding fruitful results in my studies, I have acquired the conviction that our biological theories must remain inadequate so long as we confine ourselves to the study of the cells and persons and leave the psychologists, sociologists and metaphysicians to deal with the more complex organisms. Indeed our failure to coöperate with these investigators in the study of animal and plant societies has blinded us to many aspects of the cellular and personal activities with which we are constantly dealing. This failure, moreover, is largely responsible for our fear of the psychological and the metaphysical, a fear which becomes the more ludicrous from the fact that even our so-called 'exact' sciences smell to heaven with the rankest kind of materialistic metaphysics.[1]

Leaving these generalities for the present, permit me to present the evidence for the contention that the animal colony is a true organism and not merely the analogue of the person. To make this evidence as concrete as possible I shall take the ant-colony as a paradigm and ask you to accept my statement that the colonies of the termites, social bees and wasps, which the limited time at my disposal does not permit to consider, will be found to offer the same and in some cases even more satisfactory data. I select the ant-colony not only because I am more familiar with its activities, but because it is much more interesting than that of the polyps, more typical and less specialized than that of the honey-bee, less generalized than that of the wasps and bumble-bees, and has been much more thoroughly investigated than the colonies of the stingless bees and the termites.

The most general organismal character of the ant-colony is its individuality. Like the cell or the person, it behaves as a unitary whole, maintaining its identity in space, resisting dissolution and, as a general rule, any fusion with other colonies of the same or alien species. This resistance is very strongly manifested in the fierce defensive and offensive coöperation of the colonial personnel. Moreover, every ant-colony has its own peculiar idiosyncrasies of composition and behavior. This is most

[1] The hierarchy of organisms briefly considered in this paragraph now finds its place in "emergent evolution" which is discussed in my "Emergent Evolution and the Development of Societies," New York, W. W. Norton, 1928.

clearly seen in the character of the nest, which bears about the same relation to the colony that the shell bears to the individual Foraminifer or mollusk. The nest is a unitary structure, built on a definite but plastic design and through the coöperation of a number of persons. It not only reflects the idiosyncrasies of these persons individually and as a whole, but it often has a most interesting adaptive growth and orientation which may be regarded as a kind of tropism. In many species the nest mounds, which are used as incubators of the brood and as sun-parlors for the adult ants, are constructed in such a manner as to utilize the solar radiation to the utmost. In the Alps and Rocky Mountains we find the nests oriented in such a manner that the portions in which the brood is reared face south or east, and as time goes on the nests often grow slowly in these directions, like plants turning to the light, so that they become greatly elongated. This orientation is, in fact, so constant in some species that the Swiss mountaineers, when lost in a fog, can use it as a compass.

Every complete ant-colony, moreover, has a definite stature which depends, of course, on the number of its component persons. And this stature, like that of personal organisms, varies greatly with the species and is not determined exclusively by the amount of food, but also by the queen mother's fecundity, which is constitutional. Certain ants live in affluence but are nevertheless unable to form colonies of more than fifty or a hundred individuals, while others, under the same conditions, have a personnel of thousands or tens of thousands.

One of the most general structural peculiarities of the person is the duality of its composition as expressed in the germ-plasm on the one hand and the soma (body) on the other, and the same is true of the ant-colony, in which the mother queen and the virgin males and females represent the germ-plasm, or, more accurately speaking, the 'Keimbahn,' while the normally sterile females, or workers and soldiers, in all their developmental stages, represent the soma. In discussing the question of the inheritance or non-inheritance of acquired characters the Neodarwinians trace all the congenital modifications of the worker and soldier phases to the queen, just as in the personal organism all the congenital somatic characters are traced to the germ-plasm of the egg. Since the homologue of the reproductive organ of the ant-colony consists of the virgin males and females, and since the males mature earlier than the females, the colony may be regarded as a protandric hermaphrodite. Some colonies, however—and this is probably characteristic of certain species—produce only males or females and are therefore in a sense gonochoristic, or diœcious. And this protandric hermaphroditism and gonochorism, like the corresponding conditions in persons, may be interpreted as a device for, or, at any rate, as an aid in insuring cross-fertilization. The fecundated queen of the ant-colony represents the first link in the 'Keimbahn' and therefore corresponds to the fertilized egg of the personal organism. She produces both the worker personnel and the virgin males and females, just as the fertilized egg produces both the soma and the germ-cells. The colonial soma, moreover, may be differentiated as the result of a physiological division of labor into two distinct castes, comprising the workers in which the nutritive and nidificational activities predominate, and the soldiers, which are primarily protective. Here, too, the resemblance to the differentiation of the personal soma into entodermal and ectodermal tissues can hardly be overlooked.

The structure of the ant-colony thus appears to be very simple as compared with that of its component persons. The question naturally arises as to the particular type of unicellular or personal organism which it most resembles. Undoubtedly, if we could see it acting in its entirety, the ant-colony would resemble a gigantic foraminiferous Rhizopod, in which the nest would represent the shell, the queen the nucleus, the mass of ants the plasmodium and the files of workers, which are continually going in and out of the nest, the pseudopodia.

The ant-colony, of course, like the person, has both an ontogenetic and a phylogenetic development; the former open to observation, the latter inferred from the ontogeny, a comparison of the various species of ants with one another and with allied Hymenopterous insects, and from the paleontological record. The fecundated queen, as I have stated, represents the fertilized egg which produces the colonial organism, but she is a winged and possibly conscious egg, capable not only of actively disseminating the species, like the minute eggs of many marine animals, but of selecting the site for the future colony. Before or after finding this site she discards her wings and henceforth becomes sedentary like the wingless workers which she will produce. The whole colony rests satisfied with the nesting site selected by its queen if the environmental conditions remain relatively constant. If these become unfavorable, however, the colony will move as a whole to a new site. In most species such movements are rather limited, but the nomadic driver and legionary ants are almost continually moving from place to place and must cover a considerable territory during the year. After the queen has selected the nesting site, she immures herself in some earthen or vegetable cavity, lays a number of eggs, supplying them with yolk derived by metabolism from her fat-body and now useless wing-muscles, and feeds the hatching larvæ on her salivary secretion, which, though highly nutritious, is, nevertheless, very limited in quantity, so that the offspring when mature are dwarfed and very few in number.[2] They are in fact, workers of the smallest

[2] This statement must now be modified since E. Meyer has shown (Die Ernährung der Mutterameise und ihrer Brut während der solitären Koloniegründung. Biol. Zentralbl. 47, 1927,

and feeblest caste; but they set to work enlarging the nest, break through the soil or plant tissues, construct an entrance on the surface and seek food for themselves and their famished mother. This food enables her to replenish her fat-body and to produce more eggs. Her expansive instincts and activities now contract, so to speak, and become reduced henceforth to a perpetual routine of assimilation, metabolism and oviposition. She produces brood after brood during her long life which may extend over a period of ten to fifteen years. Her workers assume the duties of foraging, of feeding the larvæ and one another, and of completing the nest. Their size and polymorphism increase with successive broods, till the soldier forms, if these are characteristic of the species, make their appearance. Then the individuals which correspond to the reproductive cells of the personal organism, namely, the virgin males and females develop, and the colonial organism may be said to have reached maturity. Like the personal organism, it may persist for thirty or forty years or, perhaps, even longer without much growth of its soma, since the workers and soldiers of which this consists are exposed to many vicissitudes and live only from three to four years and probably, as a rule, for a much shorter period. If the queen grows too old or dies the colony dwindles and eventually perishes unless her place is taken by one or more of her fertile daughters.

This is the ontogenetic history of most ant-colonies. It is so similar to the phylogenetic history derived from the sources mentioned above that we have no hesitation in affirming that it conforms in the most striking manner to the biogenetic law. The very ancient behavior of the solitary female Hymenopteron is still reproduced during the incipient stage of colony formation, just as the unicellular phase of the Metazoon is represented by the egg. A further correspondence of the ontogeny and phylogeny is indicated by the fact that the most archaic and primitive of living ants form small colonies of monomorphic workers closely resembling the queen, whereas the more recent and most highly specialized ants produce large colonies of workers not only very unlike the queen but unlike one another.

In order to complete the foregoing account it will be necessary to consider some interesting modifications of the usual method of colony formation and growth, especially as these modifications furnish additional and striking evidence in favor of the contention that the ant-colony is a true organism. In some species, after the colony has reached maturity and espe-

---

pp. 264–307) that the colony-founding queens of ants frequently and perhaps as a rule use their own eggs instead of their saliva as food for their first brood of larvæ. This was observed in several European ants (*Messor structor*, *Tetramorium semilæve*, *Formica cinerea*, etc.). It had been previously noticed by J. Huber in the Brazilian fungus-grower, *Atta sexdens* (Ueber die Koloniegründung bei *Atta sexdens*. Biol. Centralbl. 25, 1905, pp. 606–619, 625–635).

cially if the food-supply continues to be abundant, several of the virgin females may be fecundated in the nest, lose their wings and remain as members of the colony. This may, indeed, contain half a dozen and in extreme cases as many as forty or fifty or even more fertile queens. But often the growth of the colonial organism becomes excessive through an increase in the worker personnel and passes over into a form of colonial reproduction, when the young fertilized queens, each accompanied by a band of workers, start new nests in the vicinity of the parental formicary. In this manner a very large and complex colony may arise and extend over many adjacent nests. For some time the new settlements may remain in communication with the home-nest through files of workers, but eventually the daughter settlements may become detached and form independent colonies. The resemblance of this method of reproduction, which is essentially the same as the swarming in the honey-bee, to the asexual reproduction of many unicellular and multicellular organisms by a process of budding, is too obvious to need further comment.

The important rôle of nutrition in the development of the colony will be clear from the foregoing remarks. It becomes even more striking in the methods adopted by the queens of certain parasitic species in starting their colonies. Some European observers and myself have found a number of queen-ants that are unable to found colonies without the aid of workers of allied species. These queens may be separated into four groups, as follows:

1. The queen that enters a colony of an alien species and decapitates its queen or is the occasion of her being killed off by her own workers. The intrusive queen is then adopted by the workers and a compound colonial organism arises, consisting of the germ-plasm of one species and the soma of another. The queen proceeds to lay eggs, which are reared by the alien workers, thus relieving her of all the labor and exhaustion endured by the independent typical ant-queen during the early stages of colony formation. *Pari passu* with the development of the worker offspring of the intrusive queen, the worker nurses grow old and die, so that the colony eventually comes to consist of only one species, the soma of the host being replaced by that of the parasite. This method of colony formation, first observed among our American ants and later among certain European and North African species, I have called temporary social parasitism. Now many of the species, which behave in this manner, have extremely small queens, or queens provided with a peculiar pilosity or sculpture that tend to endear them to the workers of the alien colonies which they invade. If we regard the large fertilized queens of ordinary ants, which are supplied with a voluminous fat-body and wing-musculature, as representing eggs provided with a great amount of yolk, and the diminutive queens of the temporary social parasites as the equivalents of alecithal eggs, we have another striking

resemblance between the personal and colonial organisms, for the large queens, like the yolk-laden eggs of many vertebrates, are produced in small numbers but are able to generate the colonial soma independently, whereas the small queens, which are produced in great numbers, in order that some of them may survive the vicissitudes of a parasitic life, correspond to the small yolkless eggs of many parasites, which have to be deposited in plant or animal tissues in order that the imperfect young on hatching may be surrounded by an abundance of food.

2. The queen of the blood-red slave-maker (*Formica sanguinea*) adopts a different method. She enters the colony of an allied species, snatches up the worker brood and kills any of the workers or queens that endeavor to dispute her possessions. The ants hatch with a sense of affiliation with their foster mother and proceed to rear her eggs and larvæ as soon as they appear. Here, too, the colony is formed by a mixture of two species, but the workers produced by the intrusive queen inherit her predatory instincts and therefore become slave-makers. They keep on kidnapping worker larvæ and pupæ from the nests of the alien species, carry them home, and eat some of them but permit many to mature, so that the mixed character of the colony is maintained. This, however, is not invariably the case, for old and vigorous *sanguinea* colonies may cease to make slave-raids and the slaves may die off and leave a pure colony of the predatory species. The advantages of this method of colony formation are obvious, for the colonial soma, being composed of two species, grows more rapidly and is much more efficient as a nutritive and protective support to the colonial germ-plasm, which is restricted to the predatory species.

3. The colony-founding queen of the amazon ants of the genus Polyergus resorts to a modification of the method adopted by *sanguinea*, as has been shown by Emery's recent observations. She enters the colony of an alien species, perforates its queen's head with her sickle-shaped mandibles and permits herself to be adopted by the workers. She pays no attention to the brood but begins to lay eggs, the larvæ from which are carefully reared by the workers. The Polyergus offspring inherit the pugnacity of their mother, but, like the *sanguinea* workers, have the ability to kidnap the brood of other ants. They are, in fact, slave-makers of a very deft and ferocious type. Like their mother, however, they are unable to excavate the nest, to care for their own young or to take food except from the mouths of the workers that hatch from the kidnapped larvæ and pupæ. The mixture of the two species is therefore obligatory, and the slave personnel, which represents the nutritive and nest-building portions of the colonial soma, has to be maintained throughout the life of the colony.

4. Certain feeble queen ants belonging to a few aberrant genera (Anergates, Wheeleriella) invade populous nests of an alien species and are adopted

in the place of their queens, which are destroyed by their own workers. The parasites then proceed to lay eggs but these give rise only to males and females as the worker caste is entirely suppressed. The colony retains a mixed character, the parasitic species usurping the functions of the germ-plasm, while the host is purely somatic. As there are no means of prolonging the lives of the host-workers and as they do not reproduce, the whole colony is short-lived and the maturation of the parasitic sexual individuals has to be accelerated so that it will fall within the brief life-span of the worker hosts. This condition I have called permanent social parasitism.

These four peculiar types of colony-formation all lead to the formation of compound colonial organisms, comparable to certain compound personal organisms which, with few exceptions, can be produced only by artificial means. In temporary social parasitism the colonial egg can develop its soma only when grafted on to the soma of another species. This soma eventually perishes and the colony then assumes a normal complexion. This condition reminds us of certain tropical plants, like the species of Clusia and Ficus, which develop as epiphytes on other trees but after killing their hosts take root in the soil and thenceforth grow as independent organisms. The slave makers of the *sanguinea*, or facultative type are also unable to develop the soma except when grafted on to the soma of another species, but in this case the cooperation of both somas in nourishing and protecting the germ-plasm is maintained for a much longer period. This kind of colony may be compared with a graft made by uniting the longitudinal half of one plant with that of another so that both take nourishment through their roots. To make the resemblance more complete one of the grafted halves would have to be pruned in such a manner as to prevent flowering. In the amazons, or obligatory slave-makers and the permanent social parasites the alien soma alone has a nutritive function, so that the conditions are like those in ordinary vegetable grafts, in which the stock retains the roots and the scion produces the flowers and fruit.

I have dwelt on the various methods of colony formation not only because they give us an insight into colonial reproduction, but because they throw light on the colonial organism from the standpoint of parasitology. That the four types of queens and their offspring are directly comparable with entoparasitic persons is not so remarkable as the fact that in ants the host and parasite form a mixed organism which could only be obtained with persons by jumbling together the component cells of host and parasite like two kinds of peas shaken in a bottle. Notwithstanding this mixture the parasitic colony not only retains its identity and the anticipatory character of its behavior but castrates the host colony and constrains its soma either to cooperate in many of its activities or to specialize as a purely nutritive or nest-building auxiliary. The host is thus reduced to the status of a nourishing or protective organ of the parasite. This behavior has many striking analogies among persons. Giard long ago called attention to the fact that when the Cirriped Sacculina settles under the abdomen of a male crab and sends its rootlike haustoria into the tissues of its host, the latter undergoes castration, and its narrow abdomen expands to form a protection for the soft-bodied parasite. In other words, the parasite acts as if it were a mass of crabs' eggs and the male crab behaves as if it had changed its sex and develops an abdomen of the female type.

Not only are there ants, like those already considered, that may be regarded as colonial entoparasites, but there are also a number of species that may be called colonial ectoparasites. These form the so-called 'compound nests,' in which two or more species live amicably side by side, or may even mingle freely with one another, but rear their broods in separate nests, thus indicating in the clearest manner the integrity of the colonial organism. This is also shown by the vast number of myrmecophilous insects, which are, of course, ento- or ectoparasitic persons, and behave towards the ant-colony as if it were a rather incoherent and therefore more vulnerable, or exploitable personal organism.

Finally we come to what the neovitalists regard as the most striking autonomic manifestations of the organism, namely the regulations and restitutions, and face the question as to whether these, too, have their counterpart in the colonial organism. I believe that the following facts compel us to answer this question in the affirmative. If the worker personnel be removed from a young ant-colony, leaving only the fertile queen, we find that this insect, if provided with a sufficiently voluminous fat-body, will set to work and rear another brood, or, in other words, regenerate the missing soma. And, of course, any portion of the worker or sexual personnel, that is removed from a vigorous colony will be readily replaced by development of a corresponding portion of the brood. On the other hand, if the queen alone be removed, one of the workers will often develop its ovaries and take on the egg-laying function of the queen. In ants such substitution queens, or gynæcoid workers are not fecundated and are therefore unable to assume their mother's worker- and queen-producing functions. The termites, however, show a remarkable provision for restituting both of the fertile parents of the colony from the so-called complemental males and females. In ants we have a production of fertile from normally infertile individuals, but the incompleteness of the result does not disprove the existence of a pronounced restitutional tendency.

Very striking examples of this tendency are exhibited when colonies are injured by parasitic myrmecophiles. I shall consider only the case of the peculiar beetle *Lomechusa strumosa*, which breeds in colonies of the blood-red slave-maker (*Formica sanguinea*). Though the beetle and its larvæ are treated with great affection, the latter devour the ant larvæ in great numbers, so that little of the brood survives during the early summer months when the colony is producing its greatest annual increment to the worker personnel. The ants seem to perceive this defect and endeavor to remedy it by converting all the surviving queen larvæ into workers. But as these larvæ have passed the stage in their development when such an operation can be successful, the result is the production of a lot of pseudogynes, or abortive creatures structurally intermediate between the workers and queens and therefore useless in either capacity. It is instructive to compare this case with the regeneration of the lens from the iris in the Amphibian eye. In his recent analysis of the stimuli of restitution in personal organisms Driesch reaches the conclusion that "the specificity of what is taken away certainly forms part of the stimulus we are searching for, and it does so by being communicated in some way by something that has relations to *many*, if not *all*, parts of the organism and not only to the neighboring ones." He also says that "each part of the organism assigns its specific share to an unknown something and that this something is altered as soon as a part is *removed* or absolutely *stopped* in its functional life, and that the specific alteration of the something is our stimulus of restitutions." These quotations and Driesch's further discussion of the problem are even clearer in their application to the colonial than to the personal organism, for in the former it is much easier to see how each individual insect "can do more than one thing in the service of restitution" than it is to understand how each cell of the person can do more than one thing in restoring a lost organ.

I fear that I may have wearied you with this long attempt to prove that the ant-colony is a true organism, especially as this statement must seem to some of you to be too trite for discussion, but when an author like Driesch writes a large work in two volumes on the "Philosophy of the Organism" and ignores the colonial organisms altogether, an old-fashioned zoölogist may perhaps be pardoned for calling attention to a well-founded, though somewhat thread-bare, biological conception.

If it be granted that the ant-colony and the colonies of the other social insects are organisms, we are still confronted with the formidable question as to what regulates the anticipatory cooperation, or synergy of the colonial personnel and determines its unitary and individualized course. The resemblance of the ant- or bee-colony to the human state long ago suggested a naive reply to this question. Aristotle naturally supposed the colonial activities to be directed and regulated by a βασιλεύς or ἡγεμών, because these personages managed affairs in the Greek states. After the sex of the fertile individual had been discovered by Swammerdam, the word 'queen' was naturally substituted for βασιλευς, or 'king,' and as queens in human states do not necessarily govern and are often rather anabolic, sedentary and prolific persons and the objects of much flattering attention, the term is not altogether inapt when applied to the fertile females of insect colonies. It has been retained although everybody knows that these colonies represent a form of society very different from our own, a kind of communistic anarchy, in which there is "neither guide, overseer nor ruler," as Solomon correctly observed. In this respect, too, the colony is essentially the same as the personal organism, at least in the opinion of those who do not feel compelled to assume the existence of a 'soul' in the scholastic sense. For it is clear, that to primitive thinkers the soul was supposed to bear the same relation to the person as the βασιλεύς to the insect colony and the king to the human state. This supposition is still held though in a more subtle form, by writers of the present day. Some of them, like Maeterlinck, clothe the postulated controlling agency in a mystical or poetic garb and call it the 'spirit of the hive.' The following passage from the Belgian poet's charming account of the honey-bee will serve to illustrate this method of meeting the problem:

> What is this 'spirit of the hive'—where does it reside? It is not like the special instinct that teaches the bird to construct its well planned nest, and then seek other skies when the day for migration returns. Nor is it a kind of mechanical habit of the race, or blind craving for life, that will fling the bees upon any wild hazard the moment an unforeseen event shall derange the accustomed order of phenomena. On the contrary, be the event never so masterful, the 'spirit of the hive' still will follow it, step by step, like an alert and quickwitted slave, who is able to derive advantage even from his master's most dangerous orders.
>
> It disposes pitilessly of the wealth and the happiness, the liberty and life, of all this winged people; and yet with discretion, as though governed itself by some great duty. It regulates day by day the number of births, and contrives that these shall strictly accord with the number of flowers that brighten the country-side. It decrees the queen's deposition or warns her that she must depart; it compels her to bring her own rivals into the world, and rears them royally, protecting them from their mother's political hatred. So, too, in accordance with the generosity of the flowers, the age of the spring, and the probable dangers of the nuptial flight will it permit or forbid the first-born of the virgin princesses to slay in their cradles her younger sisters, who are singing the song of the queens. At other times, when the season wanes, and flowery hours grow shorter, it will command the workers themselves to slaughter the whole imperial brood, that the era of revolutions may close, and work become the sole object of all. The 'spirit of the hive' is prudent and thrifty, but by no means parsimonious. And thus, aware, it would seem, that nature's laws are somewhat wild and extravagant in all that pertains to love, it tolerates, during summer days of abundance, the embarrassing presence in the hive of three or four hundred males, from whose ranks the queen about to be born shall select her lover; three or four hundred foolish, clumsy, useless, noisy creatures, who are pretentious, gluttonous, dirty, coarse, totally and scandalously idle, insatiable, and enormous.
>
> But after the queen's impregnation, when flowers begin to close sooner and open later, the spirit one morning will coldly decree the simultaneous and general massacre of every male. It regulates the workers' labours with due regard to their age; it allots their task to the nurses who tend the nymphs and the larvæ, the ladies of honour who wait on the queen and never allow her out of their sight; the house-bees who air, refresh, or heat the hive by fanning their wings, and hasten the evaporation of the honey that may be too highly charged with water; the architects, masons, wax-workers, and sculptors who form the chain and construct the combs; the foragers who sally forth to the flowers in search of the nectar that turns into honey, of the

pollen that feeds the nymphs and the larvæ, the propolis that welds and strengthens the buildings of the city, or the water and salt required by the youth of the nation. Its orders have gone to the chemists who ensure the preservation of the honey by letting a drop of formic acid fall in from the end of their sting; to the capsule makers who seal down the cells when the treasure is ripe, to the sweepers who maintain public places and streets most irreproachably clean, to the bearers whose duty it is to remove the corpses; and to the amazons of the guard who keep watch on the threshold by night and by day, question comers and goers, recognize the novices who return from their very first flight, scare away vagabonds, marauders and loiterers, expel all intruders, attack redoubtable foes in a body, and, if need be, barricade the entrance.

Finally, it is the spirit of the hive that fixes the hour of the great annual sacrifice to the genius of the race: the hour, that is, of the swarm; when we find a whole people, who have attained the topmost pinnacle of prosperity and power, suddenly abandoning to the generation to come their wealth and their palaces, their homes and the fruits of their labour; themselves content to encounter the hardships and perils of a new and distant country. This act, be it conscious or not, undoubtedly passes the limits of human morality. Its result will sometimes be ruin, but poverty always; and the thrice-happy city is scattered abroad in obedience to a law superior to its own happiness. Where has this law been decreed which, as we soon shall find, is by no means as blind and inevitable as one might believe? Where, in what assembly, what council, what intellectual and moral sphere, does this spirit reside to whom all must submit, itself being vassal to an heroic duty, to an intelligence whose eyes are persistently fixed on the future?

It comes to pass with the bees as with most of the things in this world; we remark some few of their habits; we say they do this, they work in such and such fashion, their queens are born thus, their workers are virgin, they swarm at a certain time. And then we imagine we know them, and ask nothing more. We watch them hasten from flower to flower, we see the constant agitation within the hive; their life seems very simple to us, and bounded, like every life, by the instinctive cares of reproduction and nourishment. But let the eye draw near, and endeavour to see; and at once the least phenomenon of all becomes overpoweringly complex; we are confronted by the enigma of intellect, of destiny, will, aim, means, causes; the incomprehensible organization of the most insignificant act of life.

Other authors like Driesch, give the postulated controlling agency the sharper outlines of a would-be scientific but in reality metaphysical entity and call it the 'entelechy.' It is true that the entelechy is deduced by Driesch from the autonomic peculiarities of the personal organism, but as the colony has all the essential attributes of the organism, he would undoubtedly assign it an entelechy, which according to the definition would have to be nonspacial, but working into space, nonpsychic, but conceivable only after analogy with the psychic, and non-energetic, but nevertheless capable of determining the specificity of the colonial activities through releasing and distributing energy.

I confess that I find the entelechy quite as useless an aid in unravelling the complex activities of the ant-colony as others have found it in analyzing the personal organism. This angel-child, entelechy, comes, to be sure, of most distinguished antecedents, having been mothered by the Platonic idea, fathered by the Kantian Ding-an-sich, suckled at the breast of the scholastic *forma substantialis* and christened, from a strong family likeness, after old

Aristotle's darling ἐντελέχεια, but nevertheless, I believe that we ought not to let it play about in our laboratories, not because it would occupy any space or interfere with our apparatus, but because it might distract us from the serious work in hand. I am quite willing to see it spanked and sent back to the metaphysical house-hold.

But, speaking seriously, it seems to me that if the organism be inexplicable on purely biological grounds, we should do better to resort to psychological agencies like consciousness and the will. These have at least the value which attaches to the most immediate experience. And even the subconscious and the super-conscious might be more serviceable as explanations than such anaemic metaphysical abstractions as the entelechy. Of course, psychic vitalism is one of Driesch's pet aversions and he will have none of it, but the fact that he is compelled to operate with a 'psychoid' and with an entelechy conceivable only *per analogiam* with the psychic, shows the inconsistency of his position.

Before we can adopt any ultrabiological agencies, however, except in a tentative and provisional manner, an old and very knotty problem will have to be more thoroughly elucidated. I refer to the problem of the correlation and cooperation of parts. If the cell is a colony of lower physiological units, or biophores, as some cytologists believe, we must face the fact that all organisms are colonial or social and that one of the fundamental tendencies of life is sociogenic. Every organism manifests a strong predilection for seeking out other organisms and either assimilating them or cooperating with them to form a more comprehensive and efficient individual. Whether, with the mechanists, we attribute this tendency to chemotropism or cytotropism, or with the psychic neovitalists, interpret it as conscious and voluntary, we certainly cannot afford to ignore the facts. The study of the ontogeny of the person, *i.e.*, the person in the process of making, in the hands of recent experimentalists, has thrown a flood of light on the peculiarities of organization, but the animal and plant colony are in certain respects more accessible to observation and experiment, because the component individuals bear such loose spacial relations to one another. Then too, the much simpler and more primitive organismal type of the colony, as compared with that of the person, should enable us to follow the process of consociation and the resulting physiological division of labor more successfully. In the problem, as thus conceived, we must include, not only the true colony and society, and the innumerable cases of symbiosis, parasitism and biocœnosis, but also the consociation and mutual modification of hereditary tendencies in parthenogenetic and biparental plants and animals, since in all of these phenomena our attention is arrested not so much by the struggle for existence, which used to be painted in such lurid colors, as by the ability of the organism to temporize and compromise with other organisms, to inhibit certain activities of the æquipotential unit in the interests of the unit itself and of other organisms; in a word, to secure survival through a kind of egoistic altruism.[3]

---

[3] Since this paragraph was written I have found that several recent authors have given more explicit expression to a very similar conception of the rôle of cooperation and struggle in the development of organisms. Especially worthy of mention in this connection are Kammerer (Allgemeine Symbiose und Kampf ums Dasein als gleichberechtigte Triebkräfte der Evolution. Arch. f. Rass. u. Ges.-Biol. 6, 1909, pp. 585–608), Schiefferdecker (Symbiose. Sitzb. niederrhein. Ges. f. Natur. u. Heilk. zu Bonn, 13, Juni, 1904, 11 pp.), Bölsche (Daseinskampf und gegenseitige Hilfe in der Entwicklung. Kosmos, 6, 1909); Kropotkin (Mutual aid, a factor of evolution, London, 1902); Morley Roberts (Warfare in the Human Body, London, 1920, and Malignancy and Evolution, London, 1926), and Wallin (Symbionticism and the Origin of Species, Baltimore, 1927).

THE KELEP ANT AND THE COURTSHIP OF ITS MIMIC, *CARDIACEPHALA MYRMEX*

PUBLISHED IN THE *Journal of Heredity*, VOL. XV, 1924

For the woman that God gave him, every fibre
of her frame
Proves her launched for one sole issue, armed and
engined for the same;
And to serve that single issue, lest the genera-
tions fail,
The female of the species must be deadlier than
the male.

RUDYARD KIPLING
"THE YEARS BETWEEN"

THE observations recorded in the following paper were made at the tropical laboratory on Barro Colorado Island in the Panama Canal Zone, an institution concerning which my friend, Dr. David Fairchild, published a very interesting article in a recent number of the JOURNAL OF HEREDITY. He called attention to some of the larger opportunities which might attract serious students of animal and plant life to the station, but he could not, of course, descend to details. During the past summer Dr. Fairchild, his son, Mr. Graham Fairchild, Mr. Nathan Banks, Dr. Curt Richter, Mr. Frederick Burgess, Dr. George C. Wheeler and myself passed several delightful and profitable weeks on the island, where Mr. James Zetek, the custodian of the laboratory, and his assistant, Mr. I. Molino, ministered constantly to our comfort. To say that we were profoundly impressed by the opportunities for investigation afforded by the laboratory, is a mild statement. The incidental observations here recorded were made within a few hundred yards of the building and relate to the performances of a couple of insects selected from an inexhaustible fauna.

THE KELEP

ONE of the insects is the large, rust-red "kelep" ant (*Ectatomma tuberculatum*), which twenty years ago was given a reputation by Mr. O. F. Cook, who observed its habits in Guatemala and conceived that it might be introduced into the Southern States for the purpose of destroying the cotton boll-weevil. The experiment failed and the insect has since been relegated to an undeserved oblivion—undeserved, because it is one of the commonest and most conspicuous ants in Tropical America. I have seen it almost daily in Panama, Guatemala, and British Guiana stalking sedately over the foliage of the bushes along the sun-flecked trails through the jungles or, more frequently, standing on some leaf, with its peculiarly wrinkled head uplifted and its long antennæ outstretched. At such times it presents the appearance of having been smitten suddenly by some brilliant idea, and recalls the ant-prophets in Arpad Ferenczy's recent satirical romance, *The Ants of Timothy Thümmel*. But far from being an even ordinarily intelligent and enterprising insect, the kelep might be more aptly described as one of the most inveterate

Figure 47. The Author Observing the Courtship of Cardiacephala *on Leaves of a Piperaceous Shrub on Barro Colorado Island. Photograph by Dr. D. Fairchild.*

loafers and cowards of the ant world. It sometimes captures small feeble or moribund insects and carries them slowly to its nest, but more frequently it is seen feeding at the large saucer-shaped extrafloral nectaries of the various species of Inga which abound in the jungle (Figs. 49 and 50). This fondness for nectar probably accounts very largely for its presence on cotton plants in Guatemala and elsewhere, since these are known to have well-developed extrafloral nectaries on their involucres.

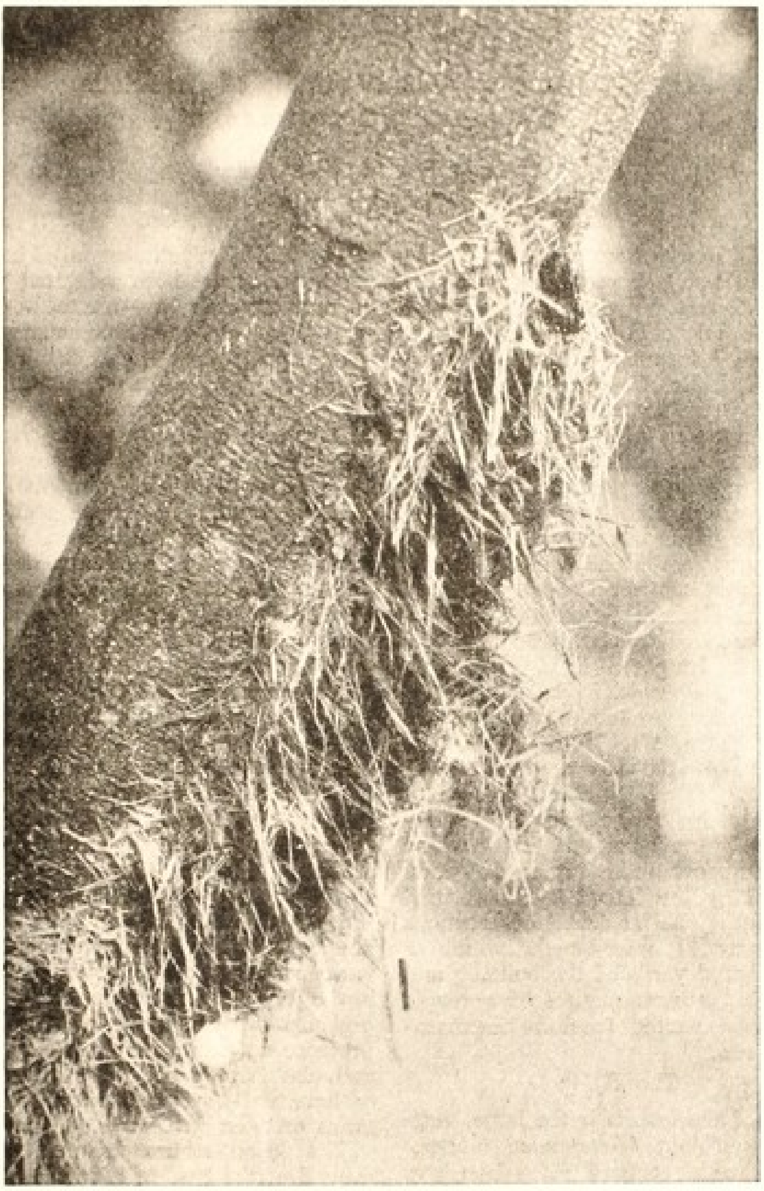

Figure 48. Upper Portion of Felted Tubular Nest Entrance of Kelep Ant (Ectatomma tuberculatum). *(Photograph by Dr. D. Fairchild.)*

The kelep makes its nest in the ground at the base of a small tree, but unlike the more blackish and equally common *Ectatomma ruidum*, which surrounds its nest with a flat earthen crater, *tuberculatum* constructs a singular tubular gallery (Fig. 48), which runs straight up the bark of the tree to a height of two to three feet above the earthen entrance of which it is a continuation. This tube is nearly 1½ inches in diameter and consists of carefully felted, fibrous, vegetable detritus, as shown in Dr. Fairchild's excellent photograph of the upper end of a gallery. When the gallery is torn away from the tree the returning keleps often have some difficulty in finding the opening of their nest in the ground. It is strange that Cook, who saw the nests of this ant in Guatemala and described their earthen chambers (*loc. cit.* p. 6) failed to mention the felted gallery, which is not known to occur in any other species. That it may be a constant feature is shown by the fact that it was always present, both in the nests on Barro Colorado Island and in those which I observed at Kartabo in British Guiana.[1]

CARDIACEPHALA MYRMEX

In company with the kelep, on the same plant and sometimes even on the same leaf, occurs a slender Micropezid fly, which, though somewhat smaller, is so similar when seen in the subdued light of the jungle that it would be described by many entomologists as a true mimic of the kelep. This fly, which Mr. C. W. Johnson has identified as *Cardiacephala myrmex* Schiner, measures 6-8 mm. in length and is ferruginous red, like the kelep, but the head and terminal abdominal segments are shining, iridescent blue. The short, narrow wings have two broad brown cross-bands, with a narrower apical band and a blackish spot near the center. These markings are distinctly seen in Dr. Fairchild's photograph (Fig. 51). The median and hind femora of the very long, slender legs are strongly thickened at the middle. While the insect is resting or running over the leaves the wings are compactly folded over one another on the back of the abdomen. The males and females are quite alike, except in their primary sexual characters, the latter having the tip of the abdomen long and tapering and folded forward under the venter, while the male genitalia have a similar position but are much smaller.

Reference to the literature shows that Schiner described *Cardiacephala myrmex* in 1868 from specimens collected by the "Novara" expedition somewhere in South America. Mr. Johnson has shown me specimens from Bartica, British Guiana, and Van der Wulp in the "Biologia Centrali-Americana" records it from Vera Cruz and Tabasco, Mexico. It is therefore widely distributed in Tropical America. The specific name *myrmex* shows that Schiner

[1] There may be some doubt about the ant's ability to construct the complicated gallery here described. Since certain large tropical spiders make similar structures it is not improbable that the lazy keleps merely appropriate these structures after they have been abandoned by their owners.

was sufficiently impressed by the ant-like appearance of the dried specimens, but these are much less ant-like than the living individuals. Of course, the generic name, established by Macquart as far back as 1843, refers to the heart-shaped head, not to the insect's having its heart in its head, as we might infer from the amorous antics about to be described.

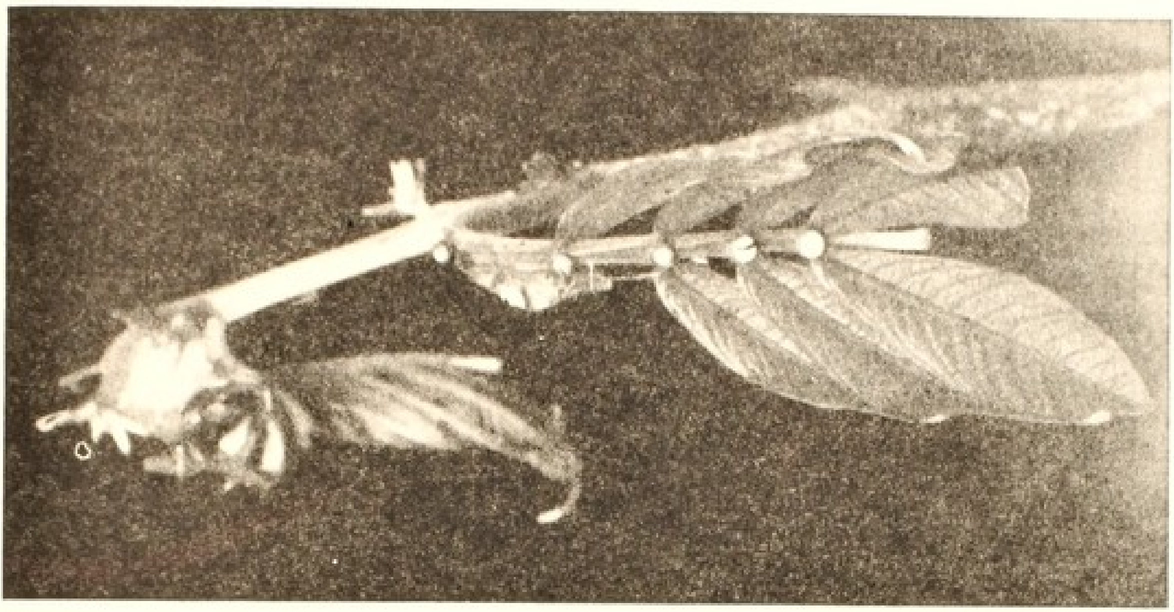

Figure 49. Young Leaf of Inga sp. *Showing Platter-shaped Extrafloral Nectaries along Midrib. (Photograph by Dr. D. Fairchild.)*

This behavior was first witnessed by Mr. Nathan Banks, but was later observed repeatedly by the other workers at the laboratory. During a period of at least two weeks the flies could be seen going through the performance on any sunny morning or afternoon. A dozen or more individuals of both sexes select and for many days use as a playground the large horizontal leaves of some bush growing along the edge of the jungle trails. One bush, partly shown in the photograph (Fig. 47), a vigorous Piperaceous plant, with large cordate leaves, was such a favorite resort which we visited again and again. The flies run about on the upper surfaces of the leaves with rather jerky movements or flit from one leaf to another. They evidently recognize one another by sight. The females are very coy and often drive the males away by making sudden lunges at them when they approach too closely. The males, too, occasionally fight with other males, rising perpendicularly on their long hind legs and facing one another as in the Javan Micropezid described in the sequel.

If carefully observed when alone, the male is sometimes seen to stand still and regurgitate from the tip of his proboscis a small drop of liquid, which he at once swallows, only to produce another drop and withdraw it in turn. This may be repeated several times and is obviously the same as the behavior described by Hewitt and Graham-Smith in the common housefly. In both cases the alimentary canal is distended with liquid and the indecent creatures amuse themselves by alternately regurgitating and swallowing portions of their food.

If the female Cardiacephala is willing to receive the male, he is permitted to approach within a few centimetres. Facing her he then performs a peculiar dance, stepping first to one side and then to the other, swaying his abdomen towards her and at the same time downward till it strikes the surface of the leaf. He may do this three or four times, one might perhaps conjecture with the purpose of enabling the female to estimate his *embonpoint*, or the amount of juice in his crop. Perhaps, however, he is merely displaying to its best advantage the beautifully iridescent surface of his terminal abdominal segments. At any rate, the female, after witnessing this *danse du ventre*, seems

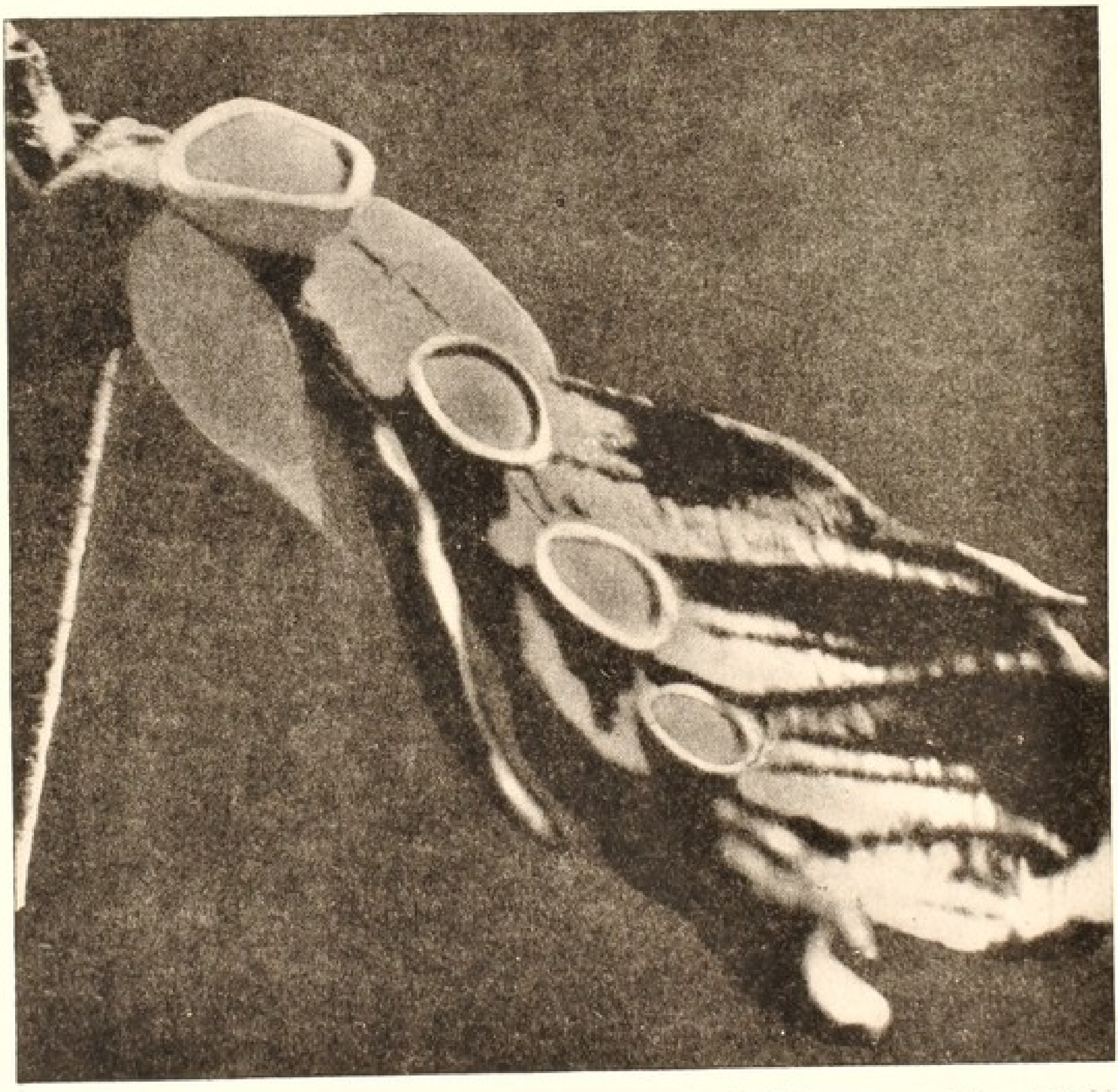

Figure 50. Extrafloral Nectaries on Young Leaf of Inga sp. *More Highly Magnified. (Photograph by Dr. D. Fairchild.)*

to indicate to the male by some very subtle sign, which I have been unable to detect, that she is ready to receive his embrace. She instantly bends her body in an arc by throwing her head back and turning up the tip of her abdomen (Fig. 51). The male is on top of her at once and bringing his proboscis in contact with hers, places a drop of food on it and almost at the same instant inserts his intromittent organ into the tapering apex of her abdomen. The female quickly straightens her body and the pair now remain together, usually for as many as ten to fifteen minutes, the male with his fore tarsi parallel and planted on the sides of the female's prothorax and his other pairs of feet on the leaf. Occasionally he reaches forward with his fore tarsi and scratches the female's eyes, but more frequently he advances his head and proboscis and with a peculiar pecking movement places a minute drop of regurgitated liquid on the upper corner of one of her eyes. She at once reaches up with her forelegs, wipes off the droplet with her tarsi and draws them over her proboscis. These acts on the part of the male and female may be repeated a dozen or more times. In the meantime the couple may run about or stand still for short periods, the female determining the direction to be taken and the stops. Finally, with a sudden kick of her hind legs she dislodges the male and the couple separate. It is probable that the male is kicked off as soon as the female perceives that the supply of liquid food in his crop is exhausted. Sometimes a stray male may come up and dance before a female *in copulâ*, but usually the couple are left alone. After mating the female may in a short time accept another partner. When she does this she is, perhaps, actuated more by hunger than by lust.

COURTSHIP OF OTHER FLIES

Although the courtship and mating of Cardiacephala are extraordinary, even stranger scenes will probably be witnessed by the observer who can devote his attention to the other Central American Micropezids. There are numerous species frequenting the leaves and tree trunks on Barro Colorado Island and I was able to see enough of their behavior to state that each seems to have its own peculiar type of courtship. This is indicated also by the only account of mating Micropezids that I have been able to find in the literature, a note by Jacobson on the Javanese *Nerius fuscus* Wied., hidden away in a taxonomic paper on East Indian Diptera by de Meijere: I here translate the note and reproduce the accompanying sketch (Fig. 52):

I captured the whole lot of 14 specimens together on a "kelor" tree (*Moringa pterygosperma*) in my garden. This tree, which is dying and shows many decayed spots in its trunk, had evidently been visited by a woodpecker that had hacked the bark to pieces in many places. On these spots, where the sap was trickling out, the flies had congregated to lick up the sap, to copulate and oviposit. I will here describe in more detail their peculiar behavior during copulation. Both females and males seem to vary considerably in size. The peculiar behavior consists in the manner in which the preferred males defend their females from rival males. As a rule, these flies run about high on their legs, so that there is a considerable space between their bodies and the bark. Now the males stand in such a position over the females that the latter are completely enclosed by their legs. The females then run with their bodies very close to the bark, that is, in a crouching posture. Whenever the female moves the male follows, usually covering the female with his body. Whenever another male comes too near the pair, the male covering the female makes a sudden sally, with the result that the rival usually at once flies away. All the movements of these flies are more or less jerky. But the rival male is not always ousted and then a very amusing contest ensues. The two males raise their bodies perpendicularly, spread their wings and set them in rapid vibration. Thus with their bodies pressed together they kept pushing one another, one of them often with his fore legs thrown over those of his opponent. The struggle, body to body, is usually of short duration, but I once observed a contest that lasted four minutes and during that period the rivals pushed one another alternately backward. After each sally the male returns to his female, but if he happens to be driven away, the female at once accepts his rival. While the pair are thus running about the bark, the female licks up the sap from its crevices, investigates all its depressions and fissures with her proboscis and if one of them seems suitable, thrusts her pointed abdomen into it and deposits an egg. Copulation occurs very frequently but only for brief periods. During its occurrence the female presses her head against the tree, so that the tip of her abdomen is raised. Copulation then ensues while the male is standing over her.

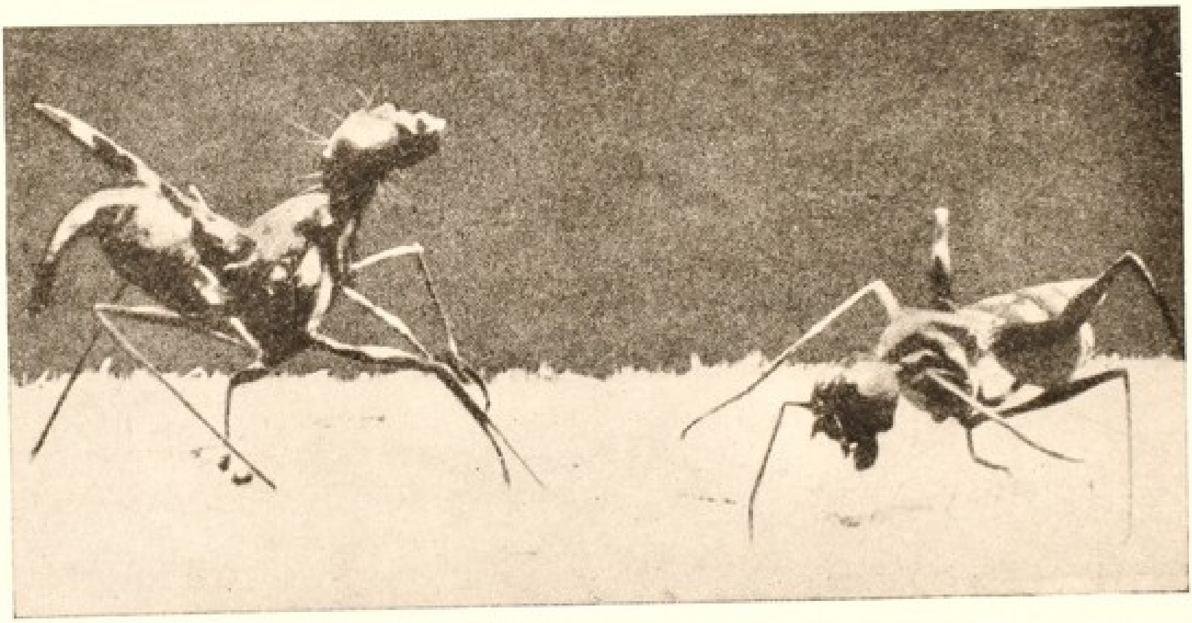

Figure 51. Cardiacephala *Male (to Right) Swinging Abdomen Before Female (to left); the latter Curving Body and Throwing Head Back in Anticipation of Being Fed by Male. (Photograph by Dr. D. Fairchild.)*

A form of courtship more like that of Cardiacephala has been described by Piersol (1907) in another fly, *Rivellia boscii* Desv. which belongs to the family Ortalidæ and occurs in Canada and the Northern States. In this case mating is not preceded by a dance on the part of the male but the female runs about on the leaves in circles, with the male closely following till he touches her abdomen with his proboscis and sooner or later mounts her back and effects connection. The subsequent behavior is described in one of the four pairs observed as follows: "In copula the wings keep in constant motion, while at intervals of three or four minutes a period of greater excitement arrives during which the wings of both are moved more rapidly, and their probosces (*sic*) are alternately extended and retracted. After a few seconds of this excitement a droplet of colorless fluid appears at the end of the proboscis of the male and rapidly increases in size until from one-half to two-thirds of a millimeter in diameter. This is not a bubble but a solid globule. The male now raises his proboscis as high as possible and lurching forward with his body, brings it down with a sweep and transfers the globule to the proboscis of the female which she elevates to receive it. The movement is rapid and very deft. Under movements of the female's proboscis the globule now dwindles and disappears; evidently she eats it. This transference of a globule is repeated many times before the pair separate. The male maintains his position chiefly by grasping the abdomen of the female with the second pair of legs, the first pair resting either on abdomen or thorax." In another pair observed by Piersol, "after handing over the globule the male would dismount of his own choice and run in circles around the female who remained almost stationary. After three or four minutes he would mount, the globule would appear at once and be handed over as usual. This occurred many times in succession."[2]

The above described nuptial performances of Micropezid and Ortalid flies, which live on the juices of plants, acquire a peculiar significance when we consider the even more astonishing behavior of the predaceous flies of the family Empididæ as revealed in a number of short papers by Osten Sacken, Becker, Mik, Girschner, Aldrich and Turley, Howlett, Hamm, Poulton and Gruhl.[3] The investigations of these authors enable us to ar-

[2] My attention is called to this case by the perusal of a paper by O. W. Richards (1927), received while this volume is going through the press. Richards' paper contains a succinct but comprehensive account of insect courtship with a valuable discussion of mating, sexual selection, the coyness of the female, etc.

[3] Although we have a great many species of Empididæ, Aldrich, Turley, Webster, MacAtee and Melander appear to be the only Americans who have written on their behavior; the remaining literature refers exclusively to European forms. As a possible aid to those who may wish to study our species I add the following list of the more important papers in chronological order:

Baron C. R. Osten Sacken, A singular Habit of Hilara. Ent. Month. Mag. (1) 14, 1877, p. 126; Becker, *Hilara sartor* n. sp. und ihr Schleier. Berlin Ent. Zeitschr. 1888, p. 7; J. Mik, Ueber ein spinnendes Dipteron, Sitzb. zool. bot. Ges Wien 1888, p. 97; E. Girschner, Zur Biologie von Hilara. Ent. Nachr. 1889, p. 220; Adam Handlirsch, Beitrag zur Kenntniss des Gespinstes von *Hilara sartor* Beck. Vehr. zool. bot. Ges. Wien 1889, p. 623; J. M. Aldrich and L. A. Turley, A Balloon-making Fly, Amer. Naturalist 33, 1899, pp. 809–812, 3 figs.; J. Mik, Einige Worte uber *Hilara sartor* Beck., Ent. Nachr. 20, 1894, p. 49–53; E. Girschner, Beitrag zur Biologie von Hilara, *ibid.* 20, 1894, p. 61–64; J. Mik, Ein Beitrag zur Biologie einiger Dipteren II Ueber spinnende Hilaren, Wien. Ent. Zeitg. 13, 1894, p. 271–284, Pl. 2, Figs. 8–13; F. M. Webster.

range the species of Empididæ in the following groups which seem roughly to represent advancing stages in courtship:

(1) Both sexes capture prey (usually other small flies) and feed upon them. In this respect they resemble other predaceous, or robber flies, like the Asilidæ, a family from which the Empididæ may be descended. The species of Tachydromia, Hybos and a few Empis (*trigramma*, *punctata* and *scutellata*) belong to this group. Hamm (1908, p. 159) describes the rather simple courtship of *E. trigramma* as follows: "On June 5th at 6.48 P. M., I was looking at a female *trigramma* resting on an elder leaf, when a male alighted about an inch distant from her, fluttered his wings for a few seconds, then raised his anterior legs and waved them about. The female then fluttered her wings and raised her anterior legs and moved them about also, apparently in response. The male then rubbed the anterior tarsi together for some seconds, moving them quickly and at the same time rapidly vibrating his wings, which were maintained in a horizontal position. These actions were repeated with variations by one or the other for the space of three minutes. The pair had now drawn closer so that each was able to touch the other's anterior tarsi in a caressing manner. This they continually did, the male every now and then rapidly vibrating his wings. These actions continued for over two minutes, when the female slightly raised the apex of her abdomen, the male gently flew on her back, and pairing took place immediately. The total time occupied in courtship was, therefore, about five-and-a-half minutes."

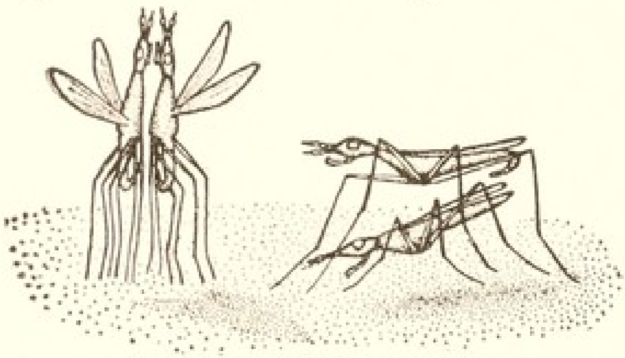

Figure 52. Courtship of Nerius fuscus. *To Left Two Males Fighting; to Right Male Covering Female. (After E. Jacobson, from J. C. H. de Meijere.)*

(2) The male alone captures prey, bites and paralyzes but does not otherwise injure it, and flying up to the female, usually while she is dancing in the air with other females, presents it to her. Mating then takes place on some plant, while the female devours her bridal gift, piercing it in many places, kneading it and imbibing its juices. As soon as this is accomplished

---

Notes and Observations on Several Species of Diptera. Canad. Ent. 30, 1898, pp. 18–19; A. L. Melander, Monograph of the North American Empididæ. Trans. Amer. Ent. Soc. 28, 1902, p. 195–367, 5 pls.; M. Howlett, Note on the Coupling of *Empis borealis*. Ent. Month. Mag. (2) 18, 1907, p. 229–232; A. H. Hamm, Observations on *Empis livida* L., *ibid.* (2) 19, 1908, p. 181–184; A. H. Hamm, Further Observations on the Empinæ, *ibid.* (2) 20, 1909, p. 143–192; W. L. MacAtee, Some Habits of the Empididæ. Ent. News 20, 1909, pp. 359–361; E. B. Poulton, Empidæ and their Prey in Relation to Courtship, *ibid.* (2) 24, 1913, p. 177–180; K. Gruhl, Paarungsgewohnheiten der Dipteran, Zeitschr. Wiss. Zool. 122, 1924, pp. 205–280, 5 figs.

copulation ceases and the prey, now reduced to a crumpled mass, is dropped. This behavior was repeatedly observed by Howlett (1907) in *Empis borealis* and *Hilara maura* and by Hamm (1908, 1909) in *Empis opaca*, *tessellata* and *livida*, *Pachymeria femorata* and *Rhamphomyia sulcata*.

(3) In this group, represented by various species of Hilara, as Poulton (1913, p. 179) states, "the prey or object provided by the male is not devoured by the female, but becomes, as it were, an ornament or plaything providing some indispensable stimulus" to mating. He summarizes Hamm's unpublished observations as follows:

All the species fly over water, and the prey or other object is always picked up from its surface by the male Hilara. The male takes floating insects of all kinds—sometimes specially Diptera, sometimes Aphids—scales off overhanging trees or other fragments of plants. Some of the species will accept almost any floating object, while others seem to restrict themselves to particular insects, such as Aphidæ. When the object is very heavy, the male, after seizing it, spins round with great velocity till the load rises on a cone of water, and is finally lifted from the apex. In Mr. Hamm's experiments, disabled Diptera of the genus Chironomus, etc., stamens of buttercups, and ray florets of daisies strewn on the water were soon taken by the males, and afterwards found in the possession of the females. Pairing invariably occurs upon the wing, but numbers of specimens show that a sweep of the net through the swarm at first catches nothing but males carrying the objects that had been strewn on the water, while a later sweep catches pairs still carrying the same objects. . . . Mr. Hamm's admirable experiments also enabled him to determine that the females carry the objects provided by the males; for although they are never retained when the pairs are captured, the white florets or the yellow stamens can be seen hanging from the lower Hilara of each flying pair, and the lower is invariably the female.

(4) In this group, represented by several species of Hilara, notably *H. maura*, *interstincta*, *aëronetha* and *pruinosa*, according to Girschner (1899) and Mik (1894), and an American *Empis* (*E. aërobatica*), the male catches and kills a minute fly and envelops it in a veil or an ellipsoidal mass of white, frothy or silky substance, which is in all probability a product of his oral, or salivary glands (Fig. 53). This object is given to the female as a bridal gift and is turned about in her feet while she is mating and then dropped. The most interesting account of these nuptial "balloons" or "cocoons" is by Aldrich and Turley (1899), but it appears that their statements may not be altogether accurate, since they describe the female as being on top *in copulâ* and the male as toying with the balloon. According to Poulton, in his review of Hamm's observations, "the cocoon is spun upon the wing, so that the method of its construction cannot be followed. Captured individuals are often found to have extruded a viscid globule—probably the material out of which the cocoon is spun. There can be little doubt that in these extreme cases it is the cocoon itself which acts as a stimulus to the female, although the minute and almost invisible object usually enclosed in it, but sometimes dropped, is the stimulus which incites the male to spin.

Cocoons that have been dropped, probably after pairing, are constantly picked up and used over again by other males."

(5) Apparently the males of some Hilaras, like the species observed by Osten Sacken (1877) and *H. sartor*, observed by Becker (1888), Mik (1888, 1894) and Girschner (1889, 1894) produce a peculiar fish-scale-like silken plaque, without a minute insect as its nucleus, and present it to the female. The observations on these Empidids, however, are incomplete and seem to require reinterpretation in the light of Howlett's and Hamm's investigations.

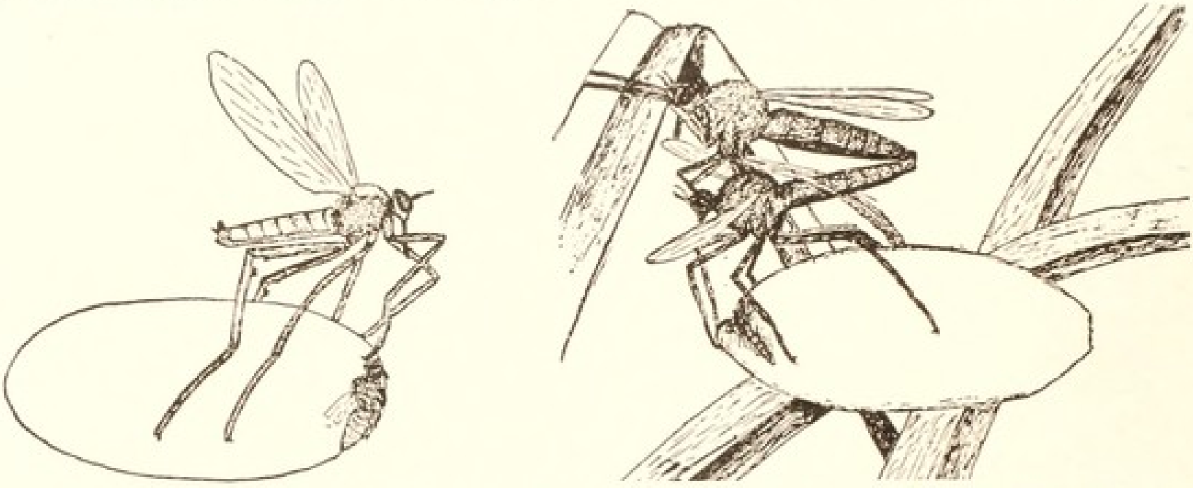

Figure 53. Male of Empis aërobatica *Carrying His Cocoon Containing a Small Fly (to Left); Male and Female (to Right)* in copulâ; *the Female Below Toying with the Balloon. (After J. M. Aldrich and L. A. Turley.)*

FOOD AND SEX INSTINCTS

It will be seen from the foregoing account that in many flies the food and sex appetites are very intimately associated in the female, that she may even become parasitic on the male to the extent of requiring him to feed her and that she may sometimes be satisfied with a substitute, or dummy in the form of some little inedible object that she can play with while mating. The case of *Cardiacephala myrmex* is very interesting because the male feeds the female with regurgitated food, either directly during courtship, or indirectly, by placing it on her head when during copulation he is in such a position as not to be able to reach her mouth with his proboscis. Authors have suggested that this association of the food and sex appetites may arise from the more general and urgent physiological need of the female for concentrated food with which to bring her ovarian eggs rapidly to maturity. We might, therefore, expect among certain insects, which as a class exhibit so many marvellous examples of the greatest economy and parsimony in the utilization of food, that the male would be called upon to provide the necessary pabulum.

We find cases like the ones I have been citing even among the Orthopteroid insects, a complex of orders as primitive in structure and many of their habits as the Diptera are specialized. Thus Hancock, Boldyrev, von Engelhardt, and Fulton, have shown that the male tree-crickets of the genus Oecanthus, both in the United States and Europe, have on the back of the thorax a large gland, the secretion of which is greedily devoured by the female before or after she receives the spermatophore, an act which in these insects takes the place of copulation. That the glandular secretion has a food value is indicated by Fulton's observation of a female Oecanthus nymph in the fifth instar feeding at the gland of a mature male (fig. 54).

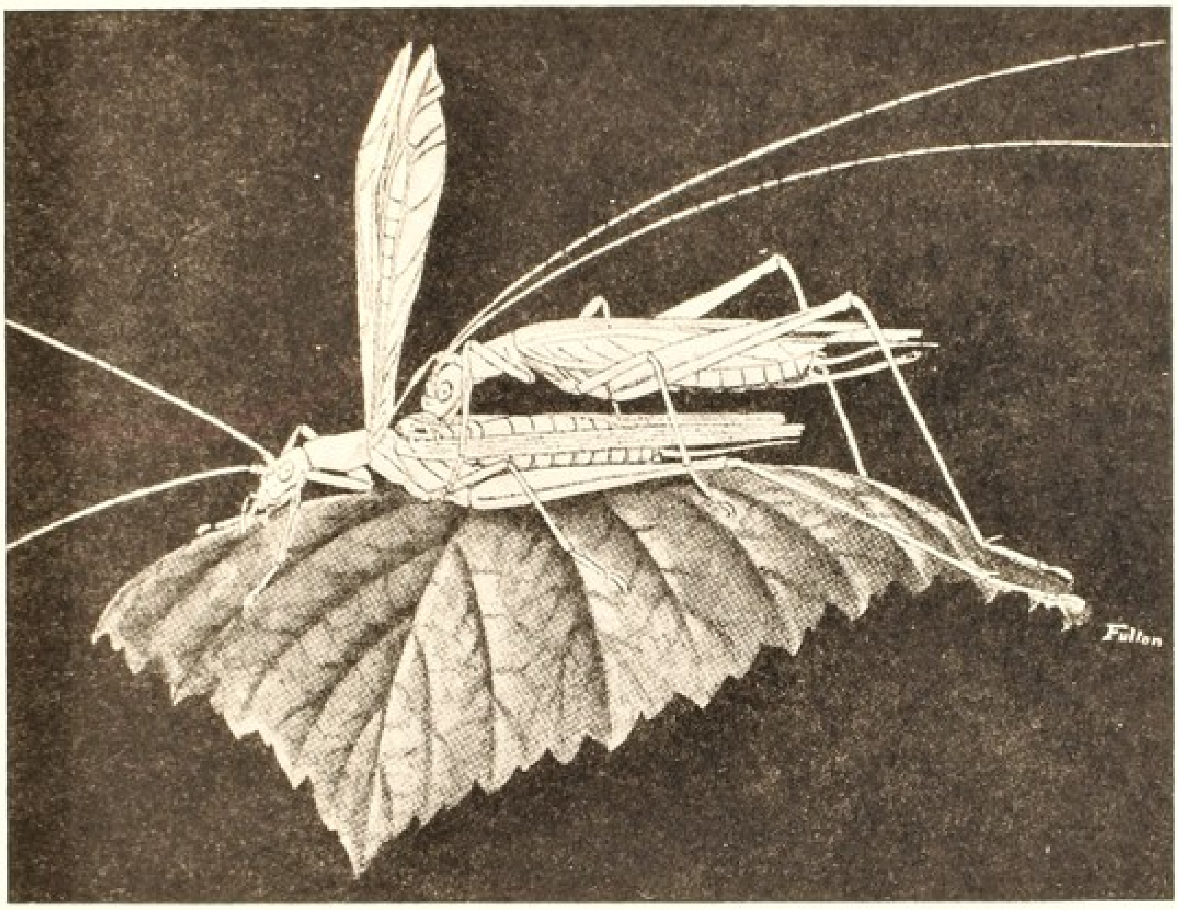

Figure 54. Female of Tree Cricket (Oecanthus niveus) *Feeding on Secretion of Metathoracic Gland of Male Just before Mating. (After B. B. Fulton.)*

An interesting light is shed on the keen appetites of the female Orthoptera and Neuroptera by the following observations summarized by O. W. Richards (1927): "In some forms, such as various Orthoptera (Gerhardt, 1913 and 1914) and Neuroptera (Withycombe, 1922), the male introduces his sperm in the form of a spermatophore, part of which protrudes from the female orifice after pairing. The female always takes advantage of this to eat most of the spermatophore, and in Osmylus (Withycombe, 1922) it is probable that the male remains gripping the female after copulation, in order that she may not eat up the spermatophore before any sperm has left it. In the Locustid grasshoppers (Boldyrev; 1913; Gerhardt *loc. cit.*) one lobe of the spermatophore, the so-called spermatophylax, is devoted to satisfying the female's appetite; by the time it has been eaten, the sperm has been passed into the spermatheca. This type of behavior has been still further specialized in the tree-crickets (Oecanthus), etc." After describing the gland on the metanotum of the male Oecanthus, Richards continues: "The male approaches the female uttering a special song, and eventually she climbs on his back and starts eating the secretion of the gland. After several minutes copulation is effected, but only lasts a short time, the female staying on the male's back both during and for some time after it. As soon as she leaves the male for good, she eats up all that is left of the spermatophore. Boldyrev (1913) has shown that if the female be removed from the gland immediately after copulation, she will eat the whole of the spermatophore before the sperm has left it, and he regards the gland mainly as a protection for the sperm. It is almost certainly also a lure to the female as well as a source of food." The voluminous spermatophore, or seminal sac, of our western, or Mormon cricket (*Anabrus simplex*) and coulee cricket (*Peranabrus scabricollis*) has been described and figured by Snodgrass (1903), Gillette (1905) and Melander and Yothers (1917), and the latter authors have observed the females invariably devouring it within a half-hour after mating.

Finally, in some other Orthopteroids like the Mantids (*Mantis religiosa* and *Stagmomantis carolina*), the nutritive meaning of the male to the female is clearly revealed, for both Fabre, Howard and the Raus have shown that he himself is actually devoured piece-meal by his spouse during or after copulation. I quote part of the passage in which Fabre describes the gruesome spectacle, because it is such a fine example of the master's style and because it makes us wonder what he might have written about Cardiacephala, had he been privileged to witness its courtship on Barro Colorado Island.

We are near the end of August. The male Mantis, a slender and elegant lover, judges the time to be propitious. He makes eyes at his powerful companion; he turns his head towards her; he bows his neck and raises his thorax. His little pointed face almost seems to wear an expression. For a long time he stands thus motionless, in contemplation of the desired one. The latter, as though indifferent, does not stir. Yet the lover has seized upon a sign of consent: a sign of which I do not know the secret. He approaches; suddenly he erects his wings, which are shaken with a convulsive tremor. This is his declaration. He throws himself timidly on the back of his corpulent companion; he clings to her desperately, and steadies himself. The prelude to the embrace is generally lengthy, and the embrace will sometimes last for five or six hours. Nothing worthy of note occurs during this time. Finally the two separate, but they are soon to be made one flesh in a much more intimate fashion. If the poor lover is loved by his mistress as the giver of fertility, she also loves him as the choicest game. During the day, or at latest on the morrow, he is seized by his companion, who first gnaws through the back of his neck, according to use and wont, and then methodically devours him, mouthful by mouthful, leaving only the wings. Here we have no case of jealousy, but simply a depraved taste. I had the curiosity to wonder how a second male would be received by a newly fecundated female. The result of my inquiry was scandalous. The Mantis in only too many cases is never sated with embraces and conjugal feasts. After a rest, of variable duration, whether the eggs have been laid or not, a second male is welcomed and devoured like the first. A third succeeds him, does his duty, and affords yet another meal. A fourth suffers a like fate. In the course of two weeks I have seen the same Mantis treat seven husbands in this fashion. She admitted all to her embraces, and all paid for the nuptial ecstasy with their lives.

Howard's early account of our American Mantis reveals an even more ravenous gluttony on the part of the female and a singular insensibility to pain and dominance of reflex behavior on the part of the male. Writing in 1886 he says: "A few days since, I brought a male of Mantis carolina to a friend who had been keeping a solitary female as a pet. Placing them in the same jar, the male, in alarm, endeavored to escape. In a few minutes the female succeeded in grasping him. She first bit off his left front tarsus, and consumed the tibia and femur. Next she gnawed out his left eye. At this the male seemed to realize his proximity to one of the opposite sex, and began to make vain endeavors to mate. The female next ate up his right front leg, and then entirely decapitated him, devouring his head and gnawing into his thorax. Not until she had eaten all of his thorax except about three millimetres, did she stop to rest. All this while the male had continued his vain attempts to obtain entrance at the valvules, and he now succeeded, as she voluntarily spread the parts open, and union took place. She remained quiet for four hours, and the remnant of the male gave occasional signs of life by a movement of one of his remaining tarsi for three hours. The next morning she had entirely rid herself of her spouse, and nothing but his wings remained. The female was apparently full-fed when the male was placed with her, and had always been plentifully supplied with food." [4]

MATING IN SPIDERS

Descending still further in the scale of Arthropods in search of additional evidence of the close linkage of the food and sex appetites, I may call attention to the male-destroying propensities of female spiders. The courtship of spiders has been carefully studied by many investigators, especially by

[4] O. W. Richards has collected from the entomological literature several cases of interest in connection with those cited above. "In the scorpion-flies, Panorpa, there is a great sexual dimorphism in the salivary glands, those of the males being very large. The male just before pairing, secretes saliva, which hardens into little globules, on the leaf on which the pair are sitting, and while the female makes a meal, he seizes the end of her abdomen with his genitalia and copulates. (Summary in Stitz, 1926.) . . . Goetghebuer (1914) has also recorded that the female of the Ceratopogonid fly, *Johannsenomyia nitida* Mcq., eats the male after copulation; such females are found with the male genitalia still clinging to them, all the rest of him having gone. Edwards (1920) describes similar behaviour in *Serromyia femorata* F., the pair copulating belly to belly with their mouth-parts joined; at the end of pairing the male's juices are sucked out through the mouth."

MacCook, Emerton, G. W. and E. G. Peckham, Montgomery and Petrunkevitch in America, Simon and Berland in France, and Bristowe and Locket in England, and exhibits extraordinary diversity in different species. The Peckhams have called attention to elaborate dances of the males of the jumping spiders (Attidæ) and the preferential display of the more ornamented or more highly colored parts of their bodies and appendages before the females, and similar behavior has been recently described and minutely analyzed by Locket, and Bristowe and Locket in the British hunting spiders

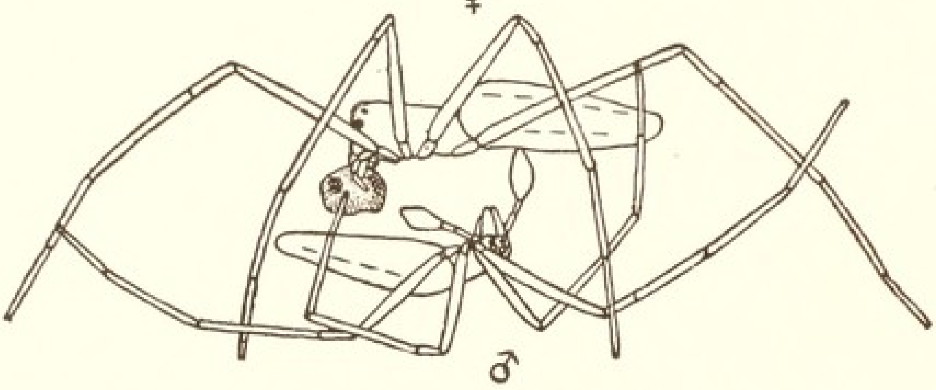

Figure 55. Pisaura mirabilis *Clerck.* in copulâ. *The Female (Above) is Eating a Fly Previously Wrapped up in Silk and Given Her by the Male. (After Bristowe and Locket.)*

of the family Lycosidæ. Their account of the courtship of *Pisaura mirabilis* is extremely interesting from its bearing on the courtship of some of the Empidids and the Cardiacephala described above: "A male was given a fly and placed in a box with a female. He proceeded to enwrap the fly with silk; and then walked about with it in a jerky fashion until presently the attention of the female was attracted, and she approached him. He held out the fly to her and, after testing it with her falces, she seized hold of it. The male then crept to a position *almost beneath the female*, a little to one side, and inserted his right palp. (Fig. 55). After 25 minutes he withdrew his palp and joined the female at the fly, and then, after some curious jerky movements, he inserted his left palp. This was withdrawn after 16½ minutes, but it was applied again for another 6½ minutes, and finally the right palp was applied for 16½ minutes, the total time of mating being 1 hour 11 minutes (G. H. L.). On another occasion the male did not have time to wrap up the fly, but the female leapt down to him and seized it from him. Mating followed, but only one palp was applied (for 18 minutes) before they separated. Throughout the mating the female sucked the fly. One male which was placed with a fly in a case where a female had just been, caught it and wrapped it up at once. On the following day he was given a fly, and enclosed in a case where no female had ever been. He ate the whole of it without making any attempt to enwrap it. Another fly was given him, and this time he was placed in the female's empty case, all trace of her web having been removed, as far as possible, lest this should have some stimulating effect. The result was as before, and he proceeded, after walking about the case for a short time and 'feeling' the ground, to wrap up the fly with silk (G. H. L.). In Tarentula, scent was a sufficient stimulus to make him begin his courting display. In Pisaura, sight does not appear to be so well developed, and the male possesses no epigamic characters, so the Attid or Lycosid kind of courtship would not be so suitable. It is interesting to find that he is also stimulated by the scent of a female to commence his mode of courtship—namely the preparation of food as an offering. (In one case, before the habits of the species were known to us, when the two sexes were placed together in a box, the female leapt upon the male and killed him. No fly has been provided (W. S. B.). *Re* 'giving up his food' to the female, a male has been seen to wrap up the dried remains of a fly he had himself eaten, as his gift to a female!)" According to Bristowe and Locket this singular courtship behavior of *Pisaura mirabilis* has been described by other observers, namely by Van Hasselt in 1889 (Tijdschr. Entom. 32) and Gerhardt in 1924 (Arch. f. Naturg.) "On one occasion Prof. Gerhardt saw two males courting the same female, one with a blue-bottle (Calliphora) and the other with a spider as an offering. The female chose the Calliphora, but whether on account of its greater size it is impossible to say. On another occasion a hungry female jumped at and seized the fly held by a male just as we ourselves observed in one case."

Among the web-spinning spiders Locket finds that the visual courtship display of the Attids and Lycosids is replaced by signals conveyed by the male to the female by vibrating the web. In these species the male is often attacked and devoured after mating but there are many specific differences in the behavior of both sexes, as appears from Locket's summary: "Corresponding to the easily-aroused sexual desires of the females of many species, we find that there is no hostility to the male before mating. Many cases are on record of females eating their mates after coition, but authentic cases of their doing so *beforehand* are rare, and are usually found among species where the breeding season is long (*e.g.* Amaurobius, September to March, or longer, and Tegenaria (Campbell, 1882), August to October and probably longer), and where, consequently, a mature female may not be, at any particular moment, in a state to recognize a male. Apparent exceptions are found in some Argiopidæ, such as *Argiope cophinaria*, studied by MacCook (1890) and notably *Nephila maculata* (Hingston, 1923). The male or males remain on the outskirts of the female's web for some time, and often at first she will not allow them to approach and may attack them. But after a time her hostility wears off, and then she will attack males only after mating. No marked tactile display appears to take place here, and I think that the female becomes ready for the male at a particular stage in the development of the eggs. In cases where the mating period is short, females seem to lose their sexual desires directly after mating and then often attack the male, who, if he escapes, wanders from female to female. Her desires may return, and other males may accomplish mating with her, but for the time being she does not recognize males as such."

All of this peering, in which I have been indulging, into the private affairs of flies, crickets and spiders, will seem to many to be a fine example of the foible of curiosity, the *libido oculorum*, but a little reflection shows that the scattered observations here brought together may have wider implications. In the insects and spiders in which the food and sex appetitions are so closely associated as to conflict, the female must be supplied either with actual nourishment (Cardiacephala, Oecanthus) or with some substitute for it (Empidids) before mating can occur. The bearing of this on certain peculiarities of human behavior has been stressed by Dr. R. Brun who happens to be both an eminent entomologist and a competent psychiatrist. Referring to my account of the Empidids, he says: "From the point of view of economy these cases differ in no respect from the well-known examples of satisfaction by means of substitutes in human instinctive behavior, as *e.g.* when old maids cherish cats or lap-dogs in place of the children they have been denied. This mechanism of substitution is particularly interesting from the biological point of view, because it shows better than any other how very dysteleological Nature may be, for it is scarcely necessary to remark that the object-substitution is quite purposeless, since it renders possible only an apparent satisfaction of the instinct, and thus prevents it from attaining its biological purpose." It is impossible, moreover, to overlook the striking resemblance of the close association of feeding and sex detected by Freud and his disciples in the human "libido," at least in its infantile phases. All the phenomena, indeed, point to more general and more fundamental biological conditions since in all organisms reproduction is an effect of growth and growth an effect of nutrition.

LITERATURE

BOLDYREV, B. T. 1913. Ueber die Begattung und die Spermatophoren bei Locustoidea und Grylloidea Rev. Russe d'Ent. 13, pp. 484–490.

BRISTOWE, W. S., and LOCKET, G. H. 1926. The Courtship of British Lycosid Spiders and Its Probable Significance. Proc. Zool. Soc. London, pp. 217–347, 10 figs.

BRUN, R. 1926. Biologische Parallelen zu Freud's Trieblehre. Experimentelle Beiträge zur Dynamik und Oekonomie des Triebkonflikts. Imago, 31 pp.

COOK, O. F. 1904. Habits of the Kelep, or Guatemalan Cotton-Boll Weevil Ant. Bull. No. 49, U. S. Dep. Agr. Bur. Ent.

DE MEIJERE, J. C. H. 1911. Studien über südostasiatische Dipteren. VI. Tijdschr. v. Ent. 54, p. 344, pl. 20.

ENGELHARDT, V. VON. 1914. Ueber die Hancocksche Drüse von *Oecanthus pellucens* Scop., Zool. Anzeig. 44, pp. 219–227.

FABRE, F. H. 1912. Social Life in the Insect World, Transl. by B. Miall. Century Co., New York.

FULTON, B. B. 1915. The Tree Crickets of New York: Life History and Bionomics. Techn. Bull. No. 42, N. Y. Agric. Exper. Station. 44 pp., 6 pls., 21 text-figs.

GILLETTE, C. P. 1905. The Western Cricket. Bull. 101 Agric. Exper. Stat. Colorado. 16 pp. 2 pls. 1 fig.

GRAHAM-SMITH, G. S. 1913. Flies in Relation to Disease. Cambridge Univ. Press. p. 86.

HANCOCK, J. L. 1905. The Habits of the Striped Meadow Cricket (*Oecanthus fasciatus* Fitch). Amer. Natur. 39, pp. 1–11, 3 figs.

HEWITT, C. G. 1912. House-flies and How They Spread Disease. Cambridge Univ. Press, p. 30.

HOWARD, L. O. 1886. The Excessive Voracity of the Female Mantis. Science 8, p. 326.

LOCKET, G. H. 1923. Mating Habits of Lycosidæ. Ann. Mag. Nat. Hist. (9) 12, pp. 493–502, 5 figs.

LOCKET, G. H. 1926. Observations on the Mating Habits of Some Web-spinning Spiders. Proc. Zool. Soc. London 4, pp. 1125–1146, 4 figs.

MELANDER, A. L., and YOTHERS, M. A. 1917. The Coulee Cricket. Bull. No. 137 State Coll. Washington Exper. Stat. 56 pp. 37 figs.

PIERSOL, W. H. 1907. The Curious Mating Habit of the Fly *Rivellia boscii*. Amer. Natural. 41, pp. 465–467.

RAU, P. and N. 1913. The Biology of *Stagmomantis carolina*. Trans. Acad. Sci. St. Louis, 22, pp. 1–58, 18 pls.

RICHARDS, O. W. 1927. Sexual Selection and Allied Problems in the Insects. Biol. Reviews 2, pp. 298–364, 7 figs.

SNODGRASS, R. E. 1903. The Internal Anatomy of *Peranabrus scabricollis*. Journ. N. Y. Ent. Soc. 11, pp. 183–188.

THE ORGANIZATION OF RESEARCH

ADDRESS OF THE RETIRING VICE-PRESIDENT AND CHAIRMAN OF SECTION F—ZOOLOGICAL SCIENCES—AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE, CHICAGO, 1920, PUBLISHED IN *Science*, N. S., VOL. LIII, 1921

*First of all, it is necessary to rid ourselves once and for all of the notion that organization is in itself a good thing. It is very easy to fall into the notion that growing complexity is a sign of progress, and that the expanding organization of Society is a sign of the coming of the Co-operative Commonwealth. * * * Organization is a marvelous instrument through which we every day accomplish all manner of achievements which would be inconceivable without it; but it is none the less better to do a thing without organization if we can, or with the minimum of organization that is necessary. * * **

In complex modern communities there are so many things that must be organized that it becomes more than ever important to preserve from organization that sphere in which it adds least to, and is apt to detract most from, our field of self-expression—the sphere of personal relationships and personal conduct.

G. D. H. COLE, "SOCIAL THEORY"

Before delivering my paper I wish to confess that I find myself in a somewhat unpleasant predicament, for when I began it and even after sending its title to Professor Allee I was of the opinion that research might, perhaps, be amenable to organization, but after thinking the matter over I was compelled to reverse my opinion, with the result that what I shall say may strike some of you as painfully reactionary. Still I encouraged myself with the reflection that many others have written papers with misleading titles and that I might perhaps put much of the blame for the results on my confrères of Section F for conferring so signal an honor as its chairmanship on one of its tired old bisons from the taxonomic menagerie instead of on one of its fresh young bulls from the Mendelian byre. I might say also, in further justification of myself, that I at least selected the most fashionable and exalted topic I could find, for you must all have observed that at the present time no word occurs with greater frequency and resonance in serious discourse than "organization." Everybody is so busy organizing something or inciting some one to organize something that the word's subtly concealed connotations of control and regulation appear to be overlooked. The purpose of organization is instrumental, as is shown by the derivation of the word, from "organon," a tool, or implement, which is in turn derived from "ergo," to work. It is one of those superb, rotund words which dazzle and hypnotize the uplifter and eventually come to express the peculiar spirit or tendency of a whole period.

These words, which for want of a better term I may call "highbrow," and the conceptions they embody, are so interesting that I will dwell on them for a moment. During the late Victorian period the most high-brow word was "progress." It disappeared and gave place to organization with the World War when we realized that the evolution of our race since the Neolithic Age was not nearly as substantial as we had imagined. Neither the Greeks nor the people of the Middle Ages seem to have had either of these words or their conceptions, though the Greeks, at least, did a fair amount of progressing and organizing.[1] The Mediæval high-brow words were "chiv-

[1] "The notion of cosmic progress was foreign to the Oriental, Greco-Roman and Christian

alry," and "honor," the latter persisting down to the present day in Continental Europe in the German students' duelling code, as a living fossil, or what biologists would call a "relict." Schopenhauer[2] remarked that the duel and venereal diseases were the only contributions to culture the race had made since the classical period, overlooking the fact that the Greeks and the Japanese had their own high-brow words and institutions. Gilbert Murray[3] has shown that the word "aidos," which the Achæan chiefs of the Homeric age so solemnly uttered, was applied to a peculiar kind of chivalry, and the "bushido" of the Japanese was another similar though independent invention. All of these conceptions—progress, organization, chivalry, aidos, bushido—seem to start among the intellectual aristocracy and all imply a certain "noblesse-oblige," for there is no fun in continually exhorting others to progress unless you can keep up with the procession, or organizing others unless you yearn to be organized yourself, just as there is no fun in getting up a duelling or bushido code unless you are willing to fight duels or commit harakiri whenever it is required by the rules of the game.

Of course, the vogue of "organization" was abnormally stimulated by the mobilization of armies and resources for the World War. We acquired the organizing habit with a vengeance and have not since had time to reflect that there may be things in the world that it would be a profanation to organize—courtship, *e.g.*—or not worth organizing—a vacuum, *e.g.*—or things that can not be organized, or if organizable, better left as they are—scientific research, perhaps.

There are at least three different types of organization. One of them we find ready to hand in individual animals and plants, in our own bodies and in animal colonies and societies, *i.e.*, in complexes which organize themselves both onto- and phylogenetically. This is a self-contained type of organization, requiring much time and energy for its consummation and though very intricate and profound still sufficiently plastic and adaptable to trade with time and the environment and to resist a considerable amount of

---

worlds, in which prevailed from time to time beliefs in cycles or of a return to a primitive state or of a lapse from an original state of perfection. In its modern form the notion of progress had its origin among thinkers freed from religious preconceptions and addicted for one reason or another to philosophies of becoming or evolution." B. Croce, "Filosofia della Pratica." 3rd Ed. 1925, p. 188.

[2] "Zwei Dinge sind es hauptsächlich, welche den gesellschaftlichen Zustand der neuen Zeit von dem des Alterthums, zum Nachtheil des ersteren unterscheiden, indem sie demselben einen ernsten, finstern, sinistern Anstrich gegeben haben, von welchem frei das Alterthum heiter und unbefangen, wie der Morgen des Lebens, dasteht. Sie sind: das ritterliche Ehrenprincip und die venerische Krankheit—*par nobile fratrum!*" Schopenhauer, "Parerga und Paralipomena," Ed. Frauenstädt, Vol. 5, 1888, p. 413.

[3] "The Rise of the Greek Epic," 2d Ed. Oxford, Clarendon Press, 1911, pp. 103-112.

thwarting and meddling. For obvious reasons this type appears to us to be so admirable that it influences all our conceptions of organization. If the Greeks had coined a word for organization—the nearest word, orgánosis, seems not to appear till the twelfth century—they would probably have applied it to a second type of cases, in which an agent organizes a complex as an engine for accomplishing certain results. In this sense Mr. Ford would be an organizer of motor cars and in such a sense theologians might speak of the Deity as organizing the universe. This is organization imposed on inorganic or at any rate alien materials. At the present day the word is not used in this sense, since the notion of life in the materials to be organized seems to be so essential. There is, however, a third type, which is intermediate between the two preceding, one in which certain elements of a living complex are permitted or delegated or arrogate to themselves the right to organize the remaining elements, as is seen in innumerable human organizations from a state, church or army to a band of robbers. This type of organization can often be swiftly accomplished, especially if reinforced by the first type, but is necessarily more or less of an artefact and prone to easy and unexpected disintegration. We have this type in mind when we speak of the organization of scientific research, or investigation. It is evident, moreover, that the organization of research up to the present time has developed according to the first type, through a natural division of labor and inclination among investigators and by means of such cooperative *liaison* agencies as learned societies and publications. Even the most pessimistic among us must be lost in admiration at the results thus accomplished during the past few centuries. But the organizers feel that we have been moving too slowly and have been wasting too much time and effort—and they also feel, apparently, that natural, or organic organization of research, like that of the past, affords too little scope for the expression of those instincts of self-assertion and domination, which are so evidently associated with the accumulation of hormones in the older males of all mammals. These hormones commonly produce such an obfuscation of the intellect that even our mature biologists seldom realize that they are headed for the fate of the old rogue elephants and bulls, which, when they try to do too much organizing, are promptly and unceremoniously butted out of the herd by the youngsters.

The phrase "organization of research" is nonsense if we take "research" in its abstract sense, for an abstraction, of course, is one of the things that can not be organized. All we can mean by the term is the organization of the actual processes of research, or investigation, and since these processes are essentially nothing but the living, functioning investigators themselves, organization of research can mean only the organization of the investigators. It would seem desirable, therefore, before attempting such organization to make a behavioristic study of these creatures—either to catch and closely observe a number of them or to steal on them unawares while they are in the full ardor of research—in other words to investigate the investigators. Unfortunately no one has made such a study, which should, of course, precede the making of a card catalogue of the various species, subspecies, varieties, mutations and aberrations of investigators and the enumeration of their genes and chromosomes. And as the investigators themselves seem to be so busy that they have no time to scrutinize their own behavior, or if they do, are either too proud or too bashful to tell us what they find, I am compelled, for the sake of my argument, to attempt such a study and hence to make a brief excursion into psychology. As this is one of the fields in which it is still possible to do a certain amount of loose thinking with impunity, I may hope to return sufficiently intact to proceed with the discussion.

It is often supposed that the investigator enters his laboratory full of instruments and glassware and proceeds, with the use of this equipment, his sense organs and his carefully controlled ratiocinative powers to excogitate the discoveries which our newspaper editors occasionally deign to distort for the benefit of the readers of their Sunday supplements. But every investigator who observes his own activities or those of other investigators knows that this is, to say the least, a very inadequate account of the process, and every psychologist knows that while the proper employment of the senses and the reasoning powers is extremely important, the real "drives" are the instincts, emotions and interests, or what some authors prefer to call in more anæmic terms, the propensities, conative tendencies, sentiments or dispositions. To the biologist, who takes a behavioristic view of the instincts, it is difficult to single out the various drives that initiate, determine and sustain such intricate activities as those leading to scientific discovery and invention, and the psychologists themselves are far from unanimous on this matter. The list submitted in the sequel is, therefore, merely an approximation to the true state of affairs, though it is probably adequate for the purpose I have in mind.

To merit the designation of human instincts, in the conventional sense, tendencies or dispositions must be innate and purposive, common to all the normal individuals of our species, less overlaid or camouflaged by habits and therefore more evident in the young than in the adult and represented by similar though more rudimentary tendencies in the higher mammals. Such instincts seem to be rather numerous and several of them are exhibited by the investigator in a highly specialized form or are at any rate evoked and conditioned by very specific objects or situations. We can recognize:

1. Curiosity, which seems to be clearly manifested in many mammals, like the cow which stares at us across the pasture, and in the open-mouthed

wonder of the child. It is so characteristic not only of individuals but of whole peoples that the Germans often refer to it as a national peculiarity of the Saxons. In the investigator it is commonly insatiable and very intense, because restricted to certain objects and relations, particularly to the causal relations among phenomena. Its importance has been noticed by many writers. McDougall[4] says that in men in whom curiosity is innately strong, "it may become the main source of intellectual energy and effort; to its impulse we certainly owe most of the purely disinterested labors of the highest types of intellect. It must be regarded as one of the principal roots of both science and religion." It is perhaps worthy of note that "inquiry" is often used as a synonym of investigation, and that any problem is most naturally and most concisely stated in the form of an interrogatory sentence.

2. The hunting instinct, which is primarily nutritive in animals and remains so very largely in savages. In children and adults of civilized man it persists in the form of sport and the love of rapid movement in such intensity that it is leading to the extinction of our native faunas and an enormous development of the automobile industry, while in the investigators—the word itself means followers of an animal's spoor—such as zoologists, archeologists and explorers it is too apparent to require discussion. It is not lacking, however, in other investigators, all of whom when too old or too lazy to hunt their accustomed prey in the open, delight to sit and hunt for the opinions of others and especially for confirmation of their own opinions, in comfortably heated libraries.

3. The acquisitive, collecting or hoarding instinct, also primarily nutritive in animals and savages, but modified in children and adults of civilized peoples, in whom it manifests itself in the most extraordinary form of amassing all sorts of objects, from newspaper clippings and cigarbands to meerschaum pipes and shaving mugs. It is unnecessary to dwell on its truly monomaniacal manifestations among zoologists and botanists who collect everything from mites to whales and from bacteria to sequoias. But even those who look down with contempt on the enthusiastic collectors of bird-lice or coprolites are themselves usually addicted to collecting so-called data or statistics. The significant difference between the mere magpie-like collector and the hamster-like investigator lies, of course, in the use made of the accumulated objects.

4. The instinct of workmanship, craftsmanship or contrivance, which also has its phylogenetic roots in the constructive activities of very many animals. In man it begins ontogenetically with the making of mud-pies and may lead to such achievements as the excavation of the Panama Canal or the construction of an airship. It is, as Veblen[5] and others have shown, an

---

[4] "An Introduction to Social Psychology," Boston, Luce & Co., 1910, p. 59.

[5] "The Instinct of Workmanship," N. Y., B. W. Huebsch, 1918.

instinct of the greatest importance. In the investigator it is seen in the inventing of methods and devices and the construction of apparatus and hypotheses, and reaches its highest manifestations in flights of the creative imagination.

The four instincts I have been very briefly considering might be called individual to distinguish them from four others which are more deeply rooted in the social life of the investigator. These are:

5. Emulation. The decision as to whether this may be traced among animals to competition for food or for mates may be left to Jung and Freud and their respective disciples. According to William James,[6] emulation is "a very intense instinct, especially rife with young children or at least especially undisguised. Every one knows it. Nine tenths of the work of the world is done by it. We know that if we do not do the task some one else will do it and get the credit, so we do it." It is powerful and elaborately conditioned in investigators and perhaps the less said about it the better. The word "priority" will conjure up in your minds a sufficient number of emotionally toned ideas to meet the needs of this discussion.

6. What for lack of a better term I shall call the instinct of communication. It seems to have its roots in the behavior of those more or less gregarious or social animals, which apprise one another by signs or sounds of the presence of danger, of food or of certain sexual states. Its manifestations may be said to range from the chirping of crickets, tree frogs and birds to the invention of language and the effusions of poetry and music, both vocal and instrumental. In both the old and the young of our species it appears also as the by no means sex-limited impulse to gossip and divulge secrets, to communicate news and rumors, much information and no little misinformation. It urges the investigator to communicate the results of his activities to learned societies and to publish those results to the world or at least to a select coterie of specialists. The strength of this instinct might be tested by passing stringent laws forbidding certain investigators from attending scientific meetings or publishing anything for long periods of time or during their life-time or even posthumously. The results of such experimental repression might be illuminating but I refrain from speculating on their nature.

7. Closely connected with this instinct of communication is the craving for sympathy and appreciation so clearly exhibited by most highly social animals and so undisguisedly shown by children. Most investigators exhibit such a moderate development of this craving that they seem to be quite satisfied with the good opinion of the workers in their own specialties. But even if more appreciation were demanded the individual investigator would

---

[6] "The Principles of Psychology," N. Y., Holt & Co., Vol. 2, p. 409.

stand little chance of obtaining it, for investigators have become so numerous and the field of their labors has been so vastly expanded through their own enthusiastic efforts and so thickly overgrown with a dense crop of technicalities of their own sowing and cultivation, that most of them can be known only to those who are working in the same or adjoining furrows.

8. The instinct of cooperation—also very evident and of far-reaching significance in gregarious and social animals and manifested in the team-play of young human beings and the innumerable associations of adults. In many investigators this instinct seems to be rather feeble but may still appear at least in the ambition to figure in the rôle of an honest hod-carrier in the erection of some small fragment of the great edifice of human knowledge. In others it may be sufficiently developed to constitute a powerful drive to the invention of labor-saving devices and machinery, methods of preventing disease and increasing longevity and mental and physical efficiency.

This list is probably incomplete, but I believe that it comprises at least the more important drives of the investigator. The special trend of his activities is, no doubt, further determined by his native capacities, but the psychological problem as to whether or not these also constitute drives, as Woodworth[7] maintains and McDougall[8] denies, I shall not attempt to discuss. The point I wish to emphasize is that the specific activities of the investigator depend primarily and preeminently on his instincts, emotions, interests and native endowments.

If we turn now to a survey of investigators in general we find that they can be divided into two classes, usually called theoretical and practical, or pure and applied. The term pure is, to say the least, somewhat priggish, since it seems to imply that its alternative is more or less contaminated, and theoretical and practical are unsatisfactory because all investigation is necessarily both. I prefer, therefore, to designate the two classes as discoverers and inventors, since the former are primarily interested in increasing our knowledge of our environment and of ourselves, the latter in increasing our power over our environment and ourselves. From the very nature of this distinction it follows that the discoverer pursues more general, more theoretical and therefore more remote aims, whereas the inventor, in the very broad sense in which I am using the term, busies himself with more special, more practical and therefore more immediate problems. As both types of investigation are equally essential to the fullest spiritual and economic exploitation of the universe, no society can attain to a high level of culture unless it provides impartially both for its discoveries and its inventors.

There is another classification of investigators which will be useful for the purposes of my argument—namely, into professionals and amateurs. I

[7] "Dynamic Psychology," N. Y., Columbia Univ. Press, 1918, pp. 66 *et seq.*

[8] "Motives in the Light of Recent Discussion," Mind, 29, N. S., 1920, pp. 277–293.

am, of course, using these words in their good sense, not with the evil connotations that have grown up around them. It is clear that both may suffer from certain disabilities, the professional from well-known guild restrictions, the amateur from lack of opportunity or equipment or of the lively interchange of ideas so necessary to the most fruitful type of investigation. Both, too, have their advantages, the professional in the support and advertisement of his guild-fellows, the amateur in the freedom to choose, and delimit his own problems, to work on them in his own way and to publish when he sees fit. These distinctions did not escape that clever old fox, Samuel Butler, who says: [9]

> There is no excuse for amateur work being bad. Amateurs often excuse their shortcomings on the ground that they are not professionals, the professional could plead with greater justice that he is not an amateur. The professional has not, he might well say, the leisure and freedom from money anxieties which will let him devote himself to his art in singleness of heart, telling of things as he sees them without fear of what man shall say unto him; he must think not of what appears to him right and lovable but of what his patrons will think and of what the critics will tell his patrons to say they think; he has got to square every one all round and will assuredly fail to make his way unless he does this; if, then, he betrays his trust he does so under temptation. Whereas the amateur who works with no higher aim than that of immediate recognition betrays it from the vanity and wantonness of his spirit. The one is naughty because he is needy, the other from natural depravity. Besides the amateur can keep his work to himself, whereas the professional man must exhibit or starve.

Contrasting the professional and amateur, to the advantage of the latter, was also a favorite pastime with that irritable old bear, Schopenhauer.[10] He compared the professionals with dogs, the amateurs with wolves, but he was not always consistent zoologically, for he sometimes thought of the professionals as cattle, as *e.g.*, when he says:

> On the whole, the stall-feeding of our professorships is most suitable for ruminants, but those who receive their prey from the hands of Nature, live best in the open.

At present the terms professional and amateur seem to have fallen into disuse among scientists, for reasons that are not far to seek. We know that during the eighteenth and nineteenth centuries, when the books and apparatus necessary for the prosecution of research were so meager as to be within the reach of men of very moderate means, amateurs were able to do a vast amount of important work in all the departments of science. This was particularly true in England and America. In England we have a teacher of music, William Herschel, making great discoveries in astronomy; a stonecutter, Hugh Miller, in geology; a Nottingham cobbler, George Green, in

---

[9] "The Notebooks of Samuel Butler." Edited by H. F. Jones. N. Y., E. P. Dutton & Co., 1917, p. 145.

[10] *Loco citato*, Vol. 6, p. 519.

mathematics; a grocer of Ightham, Harrison, and a jeweller of St. Leonards, W. J. L. Abbott, in archeology, and a country gentleman, Charles Darwin, in biology. There were men like John Hunter, Lyall, Wallace, Galton, Samuel Butler, Lubbock, Bates and a host of other eminent investigators, who really belonged to the class of amateurs. Till very recently whole sciences, such as taxonomy and zoogeography, entomology and genetics were almost entirely in the hands of amateurs. Mendel was an amateur and all the wonderful varieties of our domestic animals and plants were developed, one might almost say invented, by amateurs. The change which has come over the situation is due to the great increase in our knowledge in more recent times and the exuberant growth of our universities, technical schools, museums and research institutions. These have made investigation more and more difficult for the amateur, especially in the inorganic sciences and in physiology, which now demand an exacting preparation and elaborate apparatus, although there are even at the present time a few eminent amateur astronomers and geologists. Amateurs still abound, nevertheless, in zoology and botany, in which it is still possible to carry on much valuable research with very simple equipment. There must be thousands of them, and nothing is more extraordinary than the ignorance of their work on the part of many of our university professionals. I could give a long list of men in the most diverse professions, letter carriers, stage-coach drivers, hosiers, portrait-painters, engravers, parsons, priests, stockyard superintendents, engineers, bankers, country-grocers, country-doctors, army officers, mining prospectors, school teachers and clerks, whose researches have greatly enriched entomology and other departments of zoology. In such vast and complicated sciences as biology and archeology the work of the amateur is so much needed and so worthy of encouragement that we may regard it as one of the greatest defects of our educational system that a youth is ever able to leave the science courses of a high school or college and take up the humblest calling, without a fixed determination to fill at least a portion of his leisure hours with the joys of research.

The disuse of the words professional and amateur is also, no doubt, due to the fact that the two kinds of investigators can no longer be sharply distinguished. Not only are the biologists in our universities and museums frequently recruited from the ranks of the amateurs, but as investigators in those institutions many of them remain amateurs in spirit and merely exercise the teaching and curatorial professions because they can be more conveniently carried on in conjunction with research than more lucrative professions such as undertaking and plumbing. There is no reason to suppose that the number of amateur investigators may not greatly increase under a more favorable form of society. In the ideal commonwealth of the future it may not be in the least surprising to find that the communal furnace-man, after his four-hour day, is conducting elaborate investigations in paleobotany, and that the communal laundress is an acknowledged authority in colloidal chemistry.

Now if the preceding very hasty behavioristic account is accurate we must admit that it would be difficult to find a body of men more unfavorable for purposes of organization, even by a committee of their own class, than the investigators. Many reasons might be given in support of this statement, but I shall consider only the following four:

1. The activities of the investigator depend as we have seen, on an array of instincts, emotions and interests, many of which are so positive that their organization in the sense in which organizers are using the term, is out of the question. It is possible, of course, to overstimulate, repress, pervert and exploit instincts and they are undoubtedly able to organize themselves by long processes of interplay, mutual adjustment and coordination, but even regulation of them *ab extra* is exceedingly difficult. In this matter the experience of the race in its age-long endeavors to regulate and organize such powerful drives as the sexual and parental instincts should be sufficiently illuminating, and the instincts of the typical inventor and discoverer seem to be every bit as imperative. The impossibility of organizing even a small body of investigators can be easily tested. Such bodies exist in our large universities, very small in comparison with the total number of investigators in the country, but large enough, if organized, to determine and control the whole policy of their respective institutions. But if any investigator attempts to organize such a body for such a purpose or for any other of mutual advantage, he will at once find his efforts frustrated or, at any rate circumvented, by a lot of individuals, turgid with peculiar instincts, emotions and purely personal interests and as blind to their collective interests as an equal number of soft-shell clams. Furthermore, it is important to note that the difficulties of organizing are greatly increased by the skeptical and critical attitude of mind which the investigator is bound to cultivate and the defective development of certain dispositions in his constitution, such as the gregarious instinct and the instinct of self-abasement and susceptibility to suggestion, propaganda and leadership, which render other men so prone or at least so accessible to social, religious and political organization.

2. Attempts at organizing investigators must fail because their highly specialized activities depend to such a great extent on their peculiar native aptitudes or capacities. The organizers are willing to admit that they are baffled by the geniuses, but these are dismissed as very rare birds, notwithstanding the fact that their influence on the trend of scientific research is out of all proportion to their numbers. The great majority of investigators appear on superficial acquaintance to be such commonplace, unassuming specimens

of humanity that it would seem that they and society in general could only be greatly benefited by having their problems "assigned" and their investigative efforts directed, controlled and organized. This notion seems to me to be due to a singularly defective insight into the peculiar psychology of investigators. No one who has had long and intimate relations with these men can fail to be impressed with the extraordinary diversity of their aptitudes, and nothing is more evident than that these aptitudes must be permitted to express themselves not only with the greatest freedom, but even in the most whimsically personal manner. Nor can anyone who is running a laboratory fail to notice that he can secure the fullest enthusiasm, devotion and team-play from all his men only on the condition that all considerations are absolutely subordinated to the ideals of research. He knows that some investigators can do their work best with a slow, uniform and apparently never-tiring motion, others with a ravenous, carnivore-like onrush, accompanied by an expenditure of vitality so magnificent that they have to loaf for a considerable period before they can store sufficient energy for another onslaught on their problem, and that there are many others whose investigative activities are of an intermediate and more evenly rhythmical type. Yet men of such diverse aptitudes and habits of work can be easily induced to live in harmony and accomplish much valuable work if any suggestion of such things as punctuality, punching time-clocks and other efficiency and factory devices are most carefully avoided. So sensitive is the investigator to the need of giving expression to his capacities and of doing his work in his own way, that any one who is enough of a martinet to insist on introducing any of the devices to which I have alluded, will at once build up a defence reaction sufficiently powerful to vitiate or inhibit all the research activities of his laboratory. It is for this reason, I believe, that even the vague, tentative suggestions of the organizers are already creating a resentment or at any rate a resistance that would surprise no one who is not bent on behaving like the proverbial bull in a china shop.

3. Whatever may be the value of research to the individual investigator, it is certain that its only social value lies in the discoveries and inventions to which it may lead. The investigative genius may be defined as one who is in a chronic state of discovery or invention, whereas the ordinary investigator approximates genius more or less closely according to the frequency of his creative achievements. Now such essential achievements, both chronic and occasional, can not be included in any scheme of organization for they usually lie outside the purview of the investigator himself or depend on situations over which he has no control. Discovery and invention are in this sense fortuitous or accidental and also involve a time factor which is equally unpredictable and unorganizable. The investigator, if you will pardon my emphatic language, can only do his damnedest and hope that the new truth

will deign to ascend from the subconscious or descend from the lap of the gods. After long and tedious observation or experiment and many disappointments he may or he may not find the discovery or invention flashing suddenly and more or less completely into consciousness or emerging from some happy constellation of events. The plant-physiologist Sachs once told me that his best ideas suddenly entered his mind in the morning while he was lacing his shoes or brushing his teeth. I have noticed in my own case that the few unimportant ideas that strike me as unlike those which ordinarily infest my waking consciousness emerge suddenly while I am passing a certain vacant lot on my morning trip to my laboratory. Not improbably my single cup of breakfast coffee may be a stimulus so timed that the reaction coincides with the vacant lot. I hasten to confess, however, that the outline of this paper was not picked up in a vacant lot, as its miscellaneous contents might lead you to suppose, but came to me, probably after prolonged subconscious incubation, while I was wondering how much coal I could save by using as an "Ersatz" the literature received during the past three years from that noble superorganization of superorganizers, the National Research Council.

4. I have dwelt on the amateurs, because they seem to me to form another insuperable obstacle to the organization of research, at least in the biological field, where they constitute a very large and important "bloc" of investigators. While one might be pardoned for supposing that some of the housebroken or domesticated investigators, who indulge in what is called "institutional" or "industrial" research might be organized after a fashion, it would be unpardonable to suppose that the wild, untamable amateurs would ever submit to such an indignity. These seem to be described as "solitary workers" in some of the literature I have received—why, I can not say. The amateur, as the word implies, is a lover, and all the world loves a lover, no matter how wild, or just because he is wild. Certainly the many members of our numerous natural history, ornithological, entomological, malacological, botanical and mycological clubs, who hold monthly meetings and contribute modestly but effectively to the sum of our knowledge, regard themselves as anything but "solitary" workers. That designation would seem to be more applicable to some of the professionals in our universities and research institutions.

Of course, the organizer who has been stung by the efficiency bug, is troubled by all this diffuse and elusive activity and counters with the assertion that organization would save duplication of effort and direct it to problems of fundamental importance. This takes for granted a knowledge of the fundamental problems on the part of the organizer and a most enviable intuition of the means adapted to their solution, or, at any rate, seems to imply that working on fundamental problems means *eo ipso* making important discoveries and inventions. The contention that we must avoid duplication of effort must have had its origin in a machine shop or a canning plant, for it certainly never originated in the brain of any investigator worthy of the name. That the establishment of the simplest item of our knowledge not only requires duplication, but reduplication and re-reduplication of effort, is too obvious to require discussion, as is also the fact that we always regard the agreement in the results of two or more investigators working independently as presumptive evidence of truth. I would similarly pass over the further implication in the arguments of the organizers, that the only value of an investigator's work lies in the scientific data and conclusions which it contains, and that we are not concerned with its unconscious revelations of habits of thought, personality, etc. The perusal of the works of the great amateur entomologists, Réaumur and Fabre, might be recommended for those whose minds are in such a ligneous, arenaceous or argillaceous condition.

The suggestion that scientific research may be advantageously organized naturally leads one to consider those other great human activities, religion and art, which are also bound up with powerful instincts, emotions and interests. Certainly religion, especially in the form of dogma and ritual, has been so superbly organized *semper ubique et omnibus*, since it first arose in the ghost-fear, daimonism and taboo of our savage ancestors, that it would seem to constitute a wonderful field for the study of both the blessings and curses of organization. It is, in fact, a field in which organization could be readily introduced and maintained owing to the proneness of so many human beings to suggestibility, credulity, the gregarious instinct, the instincts of self-abasement and fear, and of the sentiments of awe and reverence—all of which, be it noted, are singularly feeble or defective in the investigator. The same conclusion would seem to follow from the very different view of some of the Freudians who state that all religions are permeated by a subterranean feeling of guilt and that "this absolutely unfailing presence of the feeling of guilt shows us that the whole structure of religion is erected on a foundation of repression of instinct."[11] That the perfection of organization so characteristic of religion may have been beneficent in other times may be admitted, but the more nearly perfect an organization, the less it is able to adapt itself to changing conditions, and the World War has disclosed to all thinking men the same kind of hopeless, resourceless overspecialization in our ecclesiastical organizations as that with which the biologist is so familiar in archaic, moribund and actually extinct species. At the present time the Church seems to be about as well adapted to piloting the great forces which are impelling society as a two-toed sloth to piloting an airplane or a manatee

---

[11] Cf. O. Rank and H. Sachs, "The Significance of Psycho-analysis for the Mental Sciences." Transl. by C. R. Payne. Nervous and Mental Disease Monographs, No. 23. N. Y., 1916, p. 71.

the Twentieth Century Limited. Like the Edentate and the Sirenian the Church exhibits such feebleness of volition and muscular tonus and such a low ebb of creative energy, that one is inclined to find a modicum of truth in the aphorism which H. G. Wells saw posted by the bolsheviki on one of the houses in Moscow: "Religion is the opium of the people."

What a different picture is presented by that other great field of human activity, in which the instinct of workmanship and the creative imagination attain their finest and most unrestrained expression—the field of art! Its very life seems to depend on freedom from all imposed organization. Hence its plasticity and adaptability in all ages and places, its resilience and prompt resurgence after periods of conventionalization, or overspecialization. Unlike the religious person who seems always to be mistrusting his instincts, or the scientific investigator who is so sophisticated that he ignores them, the artist takes them to his bosom, so to speak, and in all his works tries to persuade the rest of the world to do the same. He thus becomes the ally of creative Nature herself and while himself capable of such control and restraint as are demanded in the harmonious execution of his work, quickly resents the slightest suggestion of restraint or control from the outside. This is so well known that one would find it more entertaining than informing to hear the comments of a lot of painters, sculptors, composers, poets, novelists and actors—and especially of a lot of actresses or prime donne—if some National Art Council had the temerity to suggest that their work could be greatly improved by organization.

The history of science and philosophy is not without significance in connection with the attempts of modern organizers. It is well known that both, after their twin-birth and brilliant childhood among the Greeks, lived through a kind of stupid Babylonian captivity as hand-maidens to the Mediæval Church, which had been so successful in organizing itself that it naturally tried to organize everything else. But science turned out to be such an obstreperous and incorrigible tomboy that she long since regained her freedom, and philosophy, though she had been treated with more consideration, and may still occasionally flirt, no longer, outside of our Jesuit colleges at least, sits down to spoon with theology as she did in the days of St. Thomas of Aquin.

Times have changed so greatly that at present we even have eminent amateurs, like the Rev. Erich Wasmann, S.J., who vie with Haeckel in the boldness of their evolutionary speculations. Scientific research is no longer concerned with the Church but with the two great forces which are contending for the mastery of the modern world, labor and capital. The present plight of the Russian investigators shows us, perhaps, what we may expect when certain communistic ideals of labor are put into practice, and Veblen's account of the evolution by atrophy of the creative artisan of former centuries into the modern factory operative, whose life has been reduced by capital, machinery and efficiency experts to one long hideous routine in some overspecialized task, shows us, perhaps, what we may expect when nothing but money talks.

Even if the investigator could hold aloof and adopt a policy of watchful waiting, till the world is controlled by either labor or capital or, as seems more probable, by some compromise between them, he would still be in an unfortunate position. Since both labor and capital are primarily concerned with production, we should expect both to center their interests on applied research, or invention and to neglect research which is fundamentally concerned with discovery. This would be unfortunate, because the two kinds of research can be most fruitful only in symbiosis, for the neglect of discovery must lead to impoverishment of the theoretical resources of the inventor, and purely theoretical research strongly tends to become socially ineffective. We have as yet, I believe, no concise information in regard to labor's attitude to so-called pure research. The attitude of the capitalist, or business man seems to be much more definite. His activities, like those of the investigator, are bound up with certain powerful, highly conditioned instincts, emotions and interests, some of which have been elucidated by Taussig.[12] He believes that the business man is driven mainly by the acquisitive instinct, centered of course on pecuniary profits, the instinct of domination or predation, the instinct of emulation, in the special form of social emulation, and the instinct of devotion or altruism. Undoubtedly we must recognize also the importance of the instinct of workmanship as a powerful drive in many eminent business men, but both it and the instinct of devotion are, of course, apt to be directed to practical matters or to those which yield immediate returns, such as philanthropy, charity, medicine, etc. Apart from certain notable exceptions, business men may, therefore, be expected to favor invention and to take little interest in discovery, except when it relates to natural resources capable of exploitation.

These considerations lead me to the opinion that so long as our present society endures adequate financial and other support for research in its most comprehensive form will be forthcoming only after the general community has thoroughly grasped the fact that of the four great fields of human endeavor, science, art, religion and philosophy, science is of the most overwhelming social value in the sense that the welfare of every individual, physically, mentally and morally, absolutely depends on its developments, or in other words, on scientific research. To saturate the general public with this conviction is a formidable task and one that can be accomplished only by a slow process of education.

There is also another aspect of the subject which I can best make clear

[12] "Inventors and Money-Makers," N. Y., Macmillan Co., 1915.

by returning to that form of organization which we observe inhering in individual animals and plants and in the societies of the former. Occasionally we find such organisms so highly integrated, differentiated or specialized as seriously to impair their powers of adaptation. When such a condition is reached, the organism either persists without phylogenetic change, if its environment remains stable, or soon becomes extinct, if its environment changes. Most organisms, however, retain a lot of relatively unorganized, or more or less generalized structures and functions as reserves for prospective adjustments to the changing environment. Our own bodies still contain many such primitive elements, like the white-blood corpuscles, the undifferentiated connective tissue, dermal and glandular cells, and in larval insects we find even undifferentiated nerve cells. And we all carry with us in our subconscious a great reservoir of very primitive instincts and tendencies, many of which are as archaic as those of our Palæolithic and anthropoid ancestors. This whole relatively undifferentiated and imperfectly organized equipment must be of the greatest value as a source of future adaptations.

We are also beginning to see that as civilization advances it is necessary to maintain a certain number of our activities in a primitive, unorganized condition and for their exercise to set aside hours of leisure and relaxation, vacations and holidays, so that we can escape from the organized routine of our existence. And as the earth becomes more densely covered with its human populations, it becomes increasingly necessary to retain portions of it in a wild state, *i.e.*, free from the organizing mania of man, as national and city parks or reservations to which we can escape during our holidays from the administrators, organizers and efficiency experts and everything they stand for and return to a Nature that really understands the business of organization. Why may we not regard scientific research, artistic creation, religious contemplation and philosophic speculation as the corresponding reservations of the mind, great world parks to which man must resort to escape from the deadening, overspecializing routine of his habits, mores and occupations and enjoy veritable creative holidays of the spirit? These world parks are in my opinion the best substitute we are ever likely to have for the old theological Heaven, and they have the great advantage that some of us are privileged to return from them with discoveries and inventions to lighten the mental and physical burdens of those whose inclinations or limitations leave them embedded in routine. This is the meaning of that stanza in the witch's song of Faust:

> The lofty skill
> Of Science, still
> From all men deeply hidden!
> Who takes no thought,
> To him 'tis brought,
> 'Tis given unsought, unbidden!

Like other members of society, the scientist, artist and philosopher must always devote considerable time and energy to routine occupations, for their lives, with very rare exceptions, are not completely absorbed in research, speculation and creative activity. They might therefore be expected to react rather unpleasantly to any suggestion of meddling with those occupations in which they feel that they can express their personalities with the greatest freedom and the greatest satisfaction to themselves if not to others. It seems to me that it can only be due to the modesty or indifference of scientific investigators that they have failed to voice their opinions of the organizers. The only utterances I have seen are an admirable paper by Professor Sumner[13] and in another field, that of social theory, a few paragraphs by G. D. H. Cole,[14] which are partly quoted at the beginning of this paper.

---

[13] "Some Perils which Confront us as Scientists," Scient. Monthly, March, 1919, pp. 258–274.
[14] "Social Theory," N. Y., Stokes Co., 1920, p. 185.

THE DRY-ROT OF OUR ACADEMIC BIOLOGY

ADDRESS OF THE PRESIDENT OF THE AMERICAN SOCIETY OF NATURALISTS, BOSTON, DECEMBER 29, 1922, PUBLISHED IN *Science*, VOL. LVII, JANUARY 19, 1923

You beat them and they give out dust like meal sacks. But who could guess that their dust came from corn, and the golden wonder of the summer fields?

NIETZSCHE,
"THUS SPAKE ZARATHUSTRA"

In all institutions which are not ventilated by a keen draught of public criticism, an innocent corruption grows up like a toadstool (for example, in learned corporations and senates).

NIETZSCHE,
"HUMAN ALL TOO HUMAN"

In the modern world the celibacy of the medieval learned class has been replaced by a celibacy of the intellect which is divorced from the concrete contemplation of the complete facts.

A. N. WHITEHEAD,
"SCIENCE AND THE MODERN WORLD"

Truly, as William James once exclaimed to me, apropos of the policy of certain philosophers, *"the natural enemy of any subject is the professor thereof!" It is clear that if these tendencies are allowed to prevail, every subject must in the course of time become unteachable, and not worth teaching. Thus educational systems become the chief enemies of education, and seats of learning the chief obstacles to the growth of knowledge, while in an otherwise stagnant and decadent society these tendencies sooner or later get the upper hand and utterly corrupt the social memory. The power of the professor is revealed not so much by the things he teaches, as by the things he fails or refuses to teach.*

F. C. S. SCHILLER,
"TANTALUS, OR THE FUTURE OF MAN"

OUR society requires its retiring president to close the annual meeting with a discourse or sermon—a task which has become increasingly difficult, for every year the program of the morning and afternoon sessions becomes more abstruse and therefore makes greater demands on our attention and the lingering memories of past presidential rhetoric invite to more odious comparisons. To me the task was the more arduous, because I had been busy for many years in remote fields of entomology in which few of you are interested, and because it fell to me at an inopportune moment, while I was in the very act of laying—if you will pardon a French expression—a volume of some 1,100 pages on ants. This racking oviposition leaves me reduced to a mere blob of *corpora lutea* and so feeble that I can only crawl, in search of a text for my sermon, to the next Encyclopedia Britannica article, which is not "ant-eater," but "Antæus." You will recall Antæus, that mythical F_1 generation hybrid between Poseidon, the Sea, and Gaia, the Earth. His hybrid vigor was so great, we are told, that he not only grew to gigantic stature, but insisted on wrestling with every stranger that happened to pass through his Libyan domain. He was always invincible in these encounters because his strength waxed with each successive contact with his mother Earth. When not engaged in wrestling he was building a monument to his father with the skulls of the vanquished. One day Hercules came along and, knowing the secret of the giant's strength, raised him aloft and strangled him in the air.

We may, perhaps, interpret this exploit of the sun-god Hercules as a mythical expression of the fact that no terrestrial substance can permanently resist evaporation or volatilization by heat, but the accepted and, I believe, more manifest meaning of the myth is that even an agile and vigorous mortal had best keep his feet on the concrete if he wishes to avoid death at the hands of the Hercules of abstraction. That the myth is of rather late origin would seem to be indicated both by this somewhat sophisticated interpretation and by the fact that the slaying of Antæus was not one of the twelve great labors of Hercules, but one of his Parerga, or deeds done by the way. The athletic demigod, while sprinting across the Sahara to get the golden apples of the Hesperides, merely stopped for a few minutes to finish Antæus.

One might conjecture that the myth had been invented by some malicious Athenian potter or weaver, who, happening to live next door to the Academy, had often been annoyed by the "hot air" emanating from that institution, were it not that an Antæus-Hercules wrestling bout is known to have been a brilliant scene in one of the lost dramas of Phrynichus, written about 500 B. C.[1] Nevertheless, the myth remains to this day as one of the most beautiful expressions of the practical man's attitude toward those who place too much confidence in their more abstract intellectual operations.

After securing this text there was difficulty with the title of my sermon. I could not decide whether to call it the "tommy-rot" or the "dry-rot" of our academic biology. I finally chose the latter, because some of our activities so closely resemble the inroads of the fungus *Merulius lacrymans*[2] in old timber, and because it might be amusing to find that the conscientious

---

[1] One may also conjecture that the story of Antæus is a very ancient but much distorted vegetation myth. It certainly resembles the myths of the Phrygian Lityerses and the Lydian Syleus. Both of these vegetation gods compelled strangers to compete with them, the one in the corn-field, the other in the vineyard, and both habitually slew their competitors and were in turn slain by the passing Hercules. See Frazer, "The Golden Bough," abridged ed., 1922, pp. 425, 442.

[2] The wood-rots, and especially *Merulius lacrymans*, are characterized as follows by R. T. and F. W. Rolfe ("The Romance of the Fungus World." Phila., J. B. Lippincott, 1926, p. 117): "By means of the rhizomorphs, these fungi are enabled to climb over brick, stone or metal, in their apparent search for more distant woodwork. Their development, for which water is necessary, sometimes proceeds at an extraordinarily rapid rate. Some, e.g. *Coniophora cerebella*, cannot flourish except in really damp wood, and can thus readily be destroyed, even when they have gained a footing, by drying the wood and ensuring a good ventilation for the future. Others, although requiring moisture for the germination of their spores, can, when established, produce the necessary water themselves. This is the case with *Merulius lacrymans*, the fungus responsible for 'dry-rot.' This requires air for respiration, during which process it takes up oxygen and gives out water, which may thus be produced to the extent of half as much by weight as the original wood. The presence of these drops of water on the hyphæ have been responsible for its name of *lacrymans*='weeping.' This faculty, in conjunction with its frequency of occurrence, and its habit of growth, renders *Merulius lacrymans* probably the most dangerous of any timber-rot, for it can attack the driest wood, and cannot be eradicated by drying or ventilation, unless heat is applied. It affects not only soft woods but also hard woods, including teak, oak and mahogany, which in the space of a few years, or under exceptional circumstances in a much shorter time, may be practically destroyed. The woody tissue permeated by mycelium is left as a spongy mass of brownish material, which absorbs water so as largely to retain its original dimensions while wet. The drying-up of the material produces, however, the well-known 'dry-rot' effect, showing a multiplicity of cracks often disposed more or less at right angles to each other. The power of 'locomotion' of this fungus is really remarkable, for it has been known to travel for yards along thin tubes containing bell-wire; it can climb up a wall from one floor of a building to the next, and it can even penetrate brickwork through the mortar, involving in a common disintegration the walls no less than the woodwork. *Merulius lacrymans* appears to be almost always found in buildings, and very rarely in woods, for which reason it is known to the Germans as 'Hausschwamm,' or house-fungus."

cataloguers of the Widener Library had included my effusion under cryptogamic botany or phytopathology. Imagine the hilarity of some young foot-ball player in the year of our Lord 1952, condemned to bone up for a final exam, and happening on a reprint of this paper reposing unashamed between such monuments of cryptogamic erudition as the 74 folio volumes of Professor Farlow's "Toadstools of God's Footstool" and the 27 quarto volumes of Professor Thaxter's "Laboulbeniales of the Universe"—like a naughty tick pressed between the hide of some royal Siamese she-elephant and that of her suckling daughter![3]

Text and title having been selected, autopsychoanalysis, which, like prayer, is now one of my favorite diversions, revealed the fact that I was suffering from an acute, repressed desire to commit sabotage on our academic biology by hurling a monkey-wrench into its smug machinery. Since, according to the Freudians, such desires simply must be satisfied, and since I may never have another opportunity to hit so many of the wheels with one shot, I can see no reason why I should not obtain all the catharsis to which psychopathology entitles me. My mental condition is, no doubt, partly due to the disappointing spectacle of our accomplishments as more or less decayed campus biologists in increasing the number, enthusiasm and enterprise of our young naturalists. I estimate that at least 25 per cent. of all students graduating from our colleges have had the equivalent of an elementary course in zoology or botany.[4] There must be many thousands of these young men and women in the country and yet, in a prosperous population of 110,000,000, the number with a vital and abiding interest in biological inquiry, even as an avocation, is extremely small. And in our universities, apart from the students preparing to enter medicine, the number indulging in advanced and graduate courses in the science would probably shrink to zero if we failed to provide fellowships or to hold out to them at the end of a long pole that enhaloed bundle of hay, the doctor's degree.

Is this situation due to the moronic ignorance or the satanic machinations of our trustees, presidents and deans? I take down Professor Cattell's illuminating monographs on the taxonomy and behavior of this fauna, but can not find that it is to blame. Is it the fault of the students? Obviously not, for no country produces a greater and more sweetly docile mass of pedagogical cannon-fodder. It would seem, therefore, that the teaching of biology should not be entrusted to those whom Bismarck called the damned professors, or that there is something wrong with us who try to teach the

---

[3] I have since learned that this article was actually catalogued and filed among the literature on fungi in one of our college libraries!

[4] Cf. the very temperate article by Professor H. H. Nininger, "Zoology and the College Curriculum," Scient. Month., 16, 1923, pp. 66–72, an article which I did not see till after the delivery of my address.

science, or with the environment in which we carry on the business. I can not avoid the impression that the problem involves, in varying degrees, all three of these factors. Of course, their adequate discussion would be extremely wearisome. I can only pull out little mycelial tufts of *Merulius lacrymans* here and there and submit them to your inspection as evidence of the dry-rot which seems steadily to be invading the underpinning of biology, at least in some of our eastern universities. If you can bear with me, after a day of strenuous attention to far worthier utterances, I shall first consider very briefly some of the disabilities, both material and personal, under which we seem to be laboring, and in conclusion suggest what I believe might be an ameliorative if not a remedial plan of action.

The hampering effects of the material and environmental conditions under which we strive to inspire the young to become life-long naturalists deserve more attention than they have received. Any one of us who endeavors to grasp with his poor intellect, enfeebled by years of gyration in the academic mill, the stupendous and confusing accumulation of facts, not to mention the assumptions, fictions, hypotheses, theories and dogmas that make up present-day biology, must be staggered by the difficulty of selecting the most appetizing, concentrated and nourishing food for the student just entering the academic cafeteria. Perhaps no other collegiate department is expected to deal with such a vast and heterogeneous wealth of potential pedagogical pabulum. And the difficulty is greatly increased by the fact that one and all of us are highly specialized cooks, who delight in feeding the young on the dishes we ourselves like or that mother used to make and incidentally in showing our fellow cooks what delicious messes we can prepare. The student's metabolism may require plain gruel and toast, but we often insist on filling him up with so many elaborate pastries and salads that we ruin his digestion and, what is a thousand times worse, his appetite. Please bear in mind that I am trying to discuss the very practical business of teaching, not research. I am, of course, a ritualistic, high-church, port-and-sherry-loving Episcopalian in research, but only a poor, Peruna-soaked Methodist when it comes to teaching. I would go to such absurd lengths in helping research that I would even provide a room in the very modest institution to which I belong for any young man who might wish to spend the next ten years of his life investigating, say, the nucleololus of the fourth cell from the end of the last caudal cartilage of the embryo chipmunk, and if his work became very absorbing and his digestion impaired, I should be willing to feed him through a tube in the wall till his head swelled to the size of the room and he believed that he had become the nucleololus of Betelguese, but I should not permit him to see, much less converse, with freshmen. Such a pearl should not be cast before swine.

We might regard it as a great handicap that we academic biologists, unlike our native wood-chucks and muskrats, are compelled to be most active pedagogically during the annual glacial period, but our superior intelligence enables us to cope with that situation. Every autumn we lay in a few cans of soused dog-fish and pickled sea-cucumbers, coop up some guinea-pigs, earth-worms, cockroaches and fruit-flies, throw in a bag of beans and several bales of hay for the botanists—and we are prepared for the worst. We can now proceed to disentangle and unreel the infinite and ineffable complexity of organic reality. We have more than enough for the purpose, for were we not all taught in our childhood by some old maid with ringlets that any little flower, or any little bug, for that matter, plucked from the crannied wall and held in the hand, is sufficient? When the neophyte becomes nauseated with the mess we have provided we can encourage him and incidentally heighten our own prestige by telling him that he is learning to forecast and control the behavior of organic nature, that he may shortly be able to make real live homunculi and regulate their mating habits, and all the pishpash with which, since the Neolithic Age, other priests and other wizards have heartened their constituencies.

More important than the drawbacks I have hinted at are certain types of personality engaged in the business of teaching biology. Since the inquiring scientist insists on poking his nose into every fold of reality, and since biology professors constitute a part, and, in their own estimation at least, an important part of reality, we might expect them not only joyfully to investigate the behavior of their colleagues—they do this already—but also to submit themselves to investigation, with at least a show of good grace. What startling results we might hope to obtain from a thoroughgoing application of the Freudian and Adlerian analyses and the intelligence tests! But even if we concede that the damned professor is an extraordinary being because he has sufficient inertia to specialize for a life-time in a particular department of learning, we must admit that he will grow old like the most ordinary individual of his species. He will gradually take on most or all of the stigmata of gerontic involution, which Dr. G. Stanley Hall has enumerated. At forty, if not sooner, his sense-organs, musculature, endocrines, emotions and memory will begin to atrophy and his intellectual processes will become more and more stereotyped, dogmatic and abstract. From a young Antæus continually gaining fresh strength from each successive contact with concrete reality he will become a creature increasingly infatuated with generalizations, relationships and hypothetical explanations, especially if they are of his own confection, and he will eventually drift into a stage in which words, formulæ and imaginary entities become the very breath of his nostrils. He has been borne aloft to be slowly asphyxiated in the tenuous atmosphere of the unreal. There are, of course, all degrees of the process and it is so gradual that it may completely escape even a professor. One rather mature student, who had spent four years in a divinity school, recently told me that, having outgrown theology, he had entered the course of one of our eminent geneticists, a man capable of twisting one's head off, were one to insinuate that he had ever released his feet from the concrete. A few weeks later the student quietly dropped the course and when asked the reason replied that the professor's mental processes were so similar to those of his decrepit divinity teachers when they held forth on predestination, salvation through grace, infant damnation, and the like, that he had decided not to add a fifth year to his theological training.

Unfortunately we have no intelligence tests for individuals with a mentality of more than 18 years, and biologists are supposed to be older though some of them somehow manage to harmonize a physical age of 40 to 60 with a mentality of 8 to 14. These, however, if really human and endowed with a decorative personality, seem to make the best teachers, probably because they enter most readily into mental rapport with the freshmen and sophomores. It is not from such professors that the Merulius spores proliferate most profusely, but from those who have a physical age of 40 to 60 and a mental age of 80 to 105.

I do not wish to be misunderstood on this matter of aging. Those of us whom the gods have not sufficiently loved to remove early in life all develop what might be called the normal inferiority complex of senescence, but we rationalize and compensate or even overcompensate for it. This is apparent in all the discussions of the subject from the remarks of the aged Cephalus in the prologue to Plato's "Republic" and Cicero's "De Senectute" to the very recent essay of the still delightfully youthful Professor Jennings "On the Advantages of Growing Old." La Rochefoucauld put the matter concisely when he said that "old men are fond of giving good advice in order to console themselves for being no longer able to serve as bad examples." As youngsters we are all filled with a spirit of adventure and long to dominate reality; later, after we have worn down our eye-teeth on its resistant carapace, we try to compromise with it by cajolery, and when this, too, fails, we forsake it and create a reality of our own, a realm of ideas, Platonic, esoteric, inviolable, eternal, in which we can still exercise the meager remnants of our will to power. This type of senescent compensation is most beautifully displayed in the sheltered environment of our universities, and I would not underestimate its enormous value to science and therefore to the race. It is clearly exhibited by old or prematurely old taxonomists, morphologists and geneticists, who derive from static fictions like species, unit characters, genes, etc., a certain feeling of potency, of having their fingers on the very vitals of organic reality. Many of our most revered biological hypotheses are the work of senescents who have been sufficiently industrious and ingenious to make their subconscious compensatory strivings tally with very considerable bodies of facts. It would be interesting to ascertain the precise age, conditions of the sense-organs, endocrines, etc., of men like Darwin, Spencer, Galton, Weismann, Bruecke, Naegeli, Haeckel, Jaeger, Altmann, Wiesner, Haacke, Brooks, Verworn, DeVries, Hatschek and Johannsen, when they first began to operate with pangens, biophors and similar ultra-microscopic flora. We might also need the cephalic index, since certain racial tendencies may be involved. This is suggested by the fact that the French and Italian biologists have rarely shown the slightest interest in the construction of such entities. Are these biologists deficient in imagination or analytical power? Hardly. Or must we assume that the French and Italians, after having produced so many of the great scholastics, have lost confidence in their methods of dealing with the phenomenal world?

Undoubtedly the best culture medium for the academic dry-rot fungus consists of about equal parts of narrow, unsympathetic specialization and normal or precocious senile abstraction; and as this medium is always present in many personalities that find their optimum environment in our universities, the outlook is depressing. A friend who has long been studying our institutions of learning maintains that our only salvation lies in discharging all our faculties and burning or thoroughly disinfecting all the buildings every 25 years. I am somewhat less pessimistic, for although I have seen very little improvement in pedagogical method in our biological departments during the past 35 years, the stress they have laid on research has preserved them from the hopeless mummification that has overtaken some of the other departments.

It seems to me that there are two periods when the young biologist is most susceptible to lethal infection by the Merulius spores that are continually being thrown off by his professors. One is his freshman year, when he should be stimulated to develop an enthusiastic, receptive attitude, the other his graduate year or years, when he may be expected to adopt an independent, adventurous and creative attitude toward his science. Of course, the treatment of advanced students is easy for any professor who will follow the excellent example of the late Professor Roland of Johns Hopkins. The story is told that he was once presented with a list of rules for teaching graduate students and that he crossed out all the items and wrote beneath: "Neglect them!" Despite this very convenient precept, many of us coddle our graduate students till the more impressionable of them develop the most sodden types of the father-complex. Some of us even wear out a layer of cortical neurones annually, correcting their spelling and syntax. One fussy old guru of my acquaintance has destroyed both of his hemispheres, his corpus callosum and a large part of his basal ganglia hunting stray commas, semicolons, dashes, parentheses and other vermin in doctor's dissertations.

Not only do many of us wear out our most valuable tissues converting the graduate students into mere vehicles of our own in[illegible] prepossessions and specialties but nearly all of us fail to excite in them that spirit of adventure which has in the past yielded such remarkable results in the development of our science. The finest example of this lack of vision is seen in the stolid indifference, especially in our eastern universities, to exploration and research in the remoter portions of our own country, in foreign lands and especially in the tropics. We have in the Philippines and at our very doors in the West Indies, Mexico, Central and South America the most marvelous fauna and flora in the world, but we still persuade our traveling fellows to cut more sections in the laboratories of Professor Rindskopf of Berlin or Professor Hammelschwanz of Leipzig, because thirty or forty years ago we were sent to the same *bemooste Häupter*. There was then a certain justification for this procedure because we at least picked up much valuable information from our fellow students in the *Bierstube*. But what shall we say to such dry-rot exhibitions as the following? A few years ago I was asked to secure a young botanist to accompany a biological expedition to the little-known Solomon Islands and therefore begged one of our eminent *exsiccati* to aid me in the quest. To my amazement he actually asked me whether I did not know that New England was covered with luxuriant and almost unknown flora and did not regard it as a crime to dissuade a young botanist from devoting his life to pressing the plants of Cape Cod! And yet the theory which has revolutionized all our thinking was brought to us from the tropics by two naturalist explorers, and for a century those who have presided over higher education in Great Britain, France, Germany and the Scandinavian countries have seized every opportunity to send their young biologists to the tropics. I refrain from wearying you with the long list of gifted European naturalists who, just before the war and throughout the tropics of both hemispheres, were increasing our biological knowledge by leaps and bounds. The neglect of our splendid opportunities has, in fact, become such a scandal that it is known even to our august band of Delphic hierodules[5] in crinolines, the National Research Council.

When we leave the advanced student and turn to the beginner, the picture is even more depressing. To us gerontic schoolmarms in trousers, who have flown from reality and have slowly succumbed to autistic thinking, with defective eye-sight, doughy musculature, brittle ossifications, demoralized intestines, decayed autonomic nervous systems and atrophied interstitials, there comes every year a small army of freshmen—very properly so called—in the late teens and early twenties, burning for impact with reality, with exquisite sense-organs, superb bones, muscles and alimentary tracts, mirific

[5] The definition of "hierodule" in the Century Dictionary is followed by the remark: "Large numbers of such slaves were attached to some foundations, and were either employed about the sanctuary or let out for hire for the profit of the god."

endocrine and autonom... apparatus and a mentality of nine to fourteen years, or thereabouts—and what do we give them? Perhaps we give them what they deserve for coming to us, but it might be more charitable to discuss what we do not give them. What portion of the science of life, that most concrete and most entrancing of all the sciences, ought we to administer to this suckling host of postadolescents? I answer: they should be fed during the first year on the simple oat-meal pap of ecology, but I hasten to declare that I do not mean the "ecology" of the zoologists, and especially of the botanists, of what Mencken calls the silo and saleratus belt of our great republic. For the sake of defining my meaning I shall have to make another tedious digression.

If, as some one has said, mathematics is the science that gives a single name to a great many different things, biology is certainly the science that gives a great many names to the same thing. This is an old story to the taxonomist, who, if he be worth his salt, will not only confer as many names as possible on every animal and plant, and change those of the commonest species every six months, in order to apprise other biologists that he is on the job, but he will also consign as many as possible of the other fellow's names—especially if he dislikes the other fellow—to the synonymy. I admire Haeckel, but I dislike his term "ecology" and have repeatedly pointed out that it belongs in the synonymy with a number of other terms, ranging in order of priority as follows: "natural history" (eighteenth and nineteenth centuries), "ethology" (Isidore Geoffroy St. Hilaire, 1859), "ecology" as "Relationsphysiologie" (Haeckel, 1866, 1869), "Biologie" in the restricted German sense (later nineteenth century to present), "bionomics" (E. Ray Lankester, 1889), "behavior," "comportement," "Gebaren" (past three decades). In this country the inept Haeckelian term, largely as a result of the afore-mentioned silo and saleratus botanists and their zoological camp-followers, has won the day and my adrenals are now too weak to offer further resistance.

Huxley, writing in 1879, apparently distinguished three ontogenetic and phylogenetic stages in the development of biology. He says: "Every country boy possesses more or less information respecting the plants and animals which come under his notice, in the stage of common knowledge; a good many persons have acquired more or less of that accurate, but necessarily incomplete and unmethodized knowledge, which is understood by Natural History; while a few have reached the purely scientific stage, and as Zoologists and Botanists, strive towards the perfection of Biology as a branch of Physical Science. Historically, common knowledge is represented by the allusions to animals and plants in ancient literature; while Natural History, more or less grading into Biology, meets us in the works of Aristotle, and his continuators in the Middle Ages, Rondeletius, Aldrovandus and their contemporaries and successors. But the conscious attempt to construct a complete science of Biology hardly dates further back than Treviranus and Lamarck, at the beginning of this century, while it has received its strongest impulse, in our own day, from Darwin."

This view of the matter is no longer adequate, quite apart from the fact that we are now entering on a fourth stage, a kind of metabiology, embracing biochemistry. The first of Huxley's stages, that of "common knowledge," should have been differently presented, in order to emphasize the practical, or economic source of the science in the activities and lore of the hunter, trapper, woodsman, herdsman, fisherman, husbandman, gardener, herbist, midwife, medicineman, etc. His second stage, that of "natural history," seems also to be presented in an inadequate, if not misleading manner, probably because he was primarily a morphologist and somewhat dazzled by the fresh effulgence of the Darwinian theory of evolution, so that he seems to treat natural history not only as a transitional but also as a transitory phase in the development of biological science. History shows that throughout the centuries, from Aristotle and Pliny to the present day, natural history constitutes the perennial root-stock or stolon of biological science and that it retains this character because it satisfies some of our most fundamental and vital interests in organisms as living individuals more or less like ourselves. From time to time the stolon has produced special disciplines which have grown into great, flourishing complexes, and it has itself changed its name from time to time as the investigators of different periods have been impressed by different aspects of its fundamental tendencies. Aristotle wrote of the "histories" of animals, the naturalists of more recent centuries spoke of their "habits"; we have become more articulate and speak of their "behavior." Even a superficial acquaintance with the voluminous writings on natural history from those of the Stagirite to those of Gessner, Réaumur and Buffon and the naturalists of the first half of the nineteenth century, shows that for obvious psychological reasons human interest in organisms has always centered in their activities or what we now call their reactions to stimuli, their adjustment or adaptations to their environment and to one another. By the latter part of that pedantic century, the eighteenth, such great reserves of observation and experimentation had accumulated in the stolon that it began to bud. Taxonomy, morphology, paleontology, physiology began to shoot up, branch and differentiate, becoming independent specialties, developing their own methods, fictions and hypotheses. In the middle of the nineteenth century, after the great voyages of exploration, the bud chorology, or geographical distribution appeared, and about the same time I. G. St. Hilaire and Haeckel, wishing to emphasize the fundamental importance of adaptation, but mistaking the stolon for a bud, named it "ethology," or "ecology." More recently another dear little bud, genetics, has come off, so promising, so self-conscious, but, alas, so constricted at the base. And future centuries will no doubt witness further gemmation of biological disciplines from the same old natural history stolon.

This is, of course, an extremely imperfect and summary sketch of the development of biological sciences, but it emphasizes the primitive, central and dynamic source of our interest in organisms. Obviously we can offer no criticism of those who prefer to call natural history, or ecology "general" or "external physiology." Burdon Sanderson in 1894 presented the matter very concisely from this point of view in the following passage: "Now the first thing that strikes us in beginning to think about the activities of an organism is that they are naturally distinguishable into two kinds, according as we consider the action of the whole organism in its relation to the external world or to other organisms, or the action of the parts or organs in their relation to each other. The distinction to which we are thus led between the *internal* and *external* relations of plants and animals has of course always existed, but has only lately come into such prominence that it divides biologists more or less completely into two camps—on the one hand those who make it their aim to investigate the actions of the organism and its parts by the accepted methods of physics and chemistry, carrying this investigation as far as the conditions under which each process manifests itself will permit; on the other, those who interest themselves rather in considering the place which each organism occupies, and the part which it plays in the economy of nature. It is apparent that the two lines of inquiry, although they equally relate to what the organism *does*, rather than to what it *is*, and therefore both have equal right to be included in the one great science of life, or biology, yet lead in directions which are scarcely even parallel. So marked, indeed, is the distinction, that Professor Haeckel some twenty years ago proposed to separate the study of organisms with reference to their place in nature under the designation of 'œcology,' defining it as comprising the relation of the animal to its organic as well as to its inorganic environment, particularly its friendly or hostile relations to those animals or plants with which it comes into direct contact. Whether with the œcologist we regard the organism in relation to the world, or with the physiologist as a wonderful complex of vital energies, the two branches have this in common, that both fix their attention, not on stuffed animals, butterflies in cases, or even microscopical sections of the animal or plant body—all of which relate to the framework of life—but on life itself."

The stolonic relationship of natural history, or ecology to the other biological disciplines is of great theoretical and practical significance. Nearly all the important biological problems, especially of a physiological or morphological character, have arisen in the course of simple investigation in natural history and many of the more difficult of them have been turned over to the special disciplines for solution. On the other hand, the ecologist is continually drawing on the methods and resources of physiology, morphology, taxonomy, distribution, etc., in solving his own particular problems of adaptation and behavior. The most interesting and important of them relate, not to the reactions of organisms to their inorganic environment, but to their reactions to one another. As this matter, though very simple, is often misunderstood, you will pardon me for dwelling on it for a few moments. Since all organisms, either of the same or of different species, invariably live in relationships of dependence on or of cooperation with others, the ecologist is justified in regarding the whole living world as an intricate congeries of biocoenoses, or consociations, ranging in complexity from at least two to a great many organisms. Even genetics may be regarded as a department of ecology, which is striving to formulate the precise symbiotic relationships of the gametes to each other in the constitution of the zygote, and their reactions with the environment. Hence the problem of adaptation is not foreign to this discipline though it is at present either ignored, as Bateson implies, or expressed in terms that are unfamiliar to the ecologist and physiologist. Moreover, since human societies are very intimate and elaborate biocoenoses of individuals of the same species, psychology, sociology, economics, anthropology, ethnology, history, ethics, jurisprudence, government, hygiene, medicine, etc., are essentially ecological, for their central problems are behavioristic.

It follows from these considerations also that applied, or economic biology is merely applied ecology, as Forbes, Needham and others have repeatedly stated.[6] Whenever and wherever one of the organisms of a biocoenose happens to be man, we have an economic situation, and it is in the precise determination of the relationships thus developed that ecology celebrates many of its greatest triumphs. I need only refer to the great field

[6] *Cf.* the following passage by Professor J. G. Needham, Science, N. S., 49, 1919, p. 457: "Dr. Howard suggests that we give more time to taxonomy and ecology and less to physiology and genetics. This is a good suggestion. We are all out of balance. Some of our laboratories resemble up-to-date shops for quantity production of fabricated genetic hypotheses. Some of our publications make a prodigious effort to translate everything biological into terms of physiology and mechanism—an effort as labored as it is unnecessary and unprofitable. Why not let the facts speak for themselves? Our laboratories are full of fashions. They go from one extreme to another. In my high school days we learned systems of classification; in my college days we did nothing but dissecting; later came morphology and embryology, then experimental zoology, then genetics, and the devotees of each new subject have looked back upon the old with something like that disdain with which a débutante regards a last year's gown. Natural history and classification are perhaps long enough out of date, so that interest in them may again be revived. I hope so; for these are the phases of biology by means of which a youth is best oriented for more special work. Then, too, they are immensely practical. One has to deal with species, and must be able to recognize them; and all economic procedure is applied ecology."

of parasitology—the work on cestodes, trematodes, trichinæ, hookworm, malaria, yellow fever and all the other insect-borne pathogenic organisms, in bacteriology, phytopathology, economic entomology, etc., all work which does not transcend the concrete natural history, or ecological level. And everything indicates that we are only at the beginning of the revelations and benefits which similar studies have in store for us. Surely the ecologist need not veil his face in modesty even in the presence of a Mendelian formula or a new Drosophila mutation.

Although I have left our lusty young freshmen out in the cold during this long harangue, I have not forgotten them. I repeat: what ought we to give them? I do not believe that we should inform them with the first crack out of the box that they are animals and descended from ape-like ancestors. This must come as a severe shock to any young *Boobus americanus* who has never had an opportunity to make the acquaintance of really high-class apes, like the chimpanzees recently studied by Wolfgang Koehler at the German Anthropoid Station on the Island of Teneriffe. The freshman should be gradually led through a sympathetic study of the lower organisms as marvelous centers of beautiful and dignified processes to a knowledge of his own animal respectability, descent and responsibilities. This, I am convinced, is not to be achieved by taking dead and more or less smelly crayfish, earth-worms, starfish and cockroaches to pieces, because Huxley in 1879 intimated that it might be a meritorious occupation for the young, nor by a too immediate study of living forms so remote in the scale of being as the Protozoa, Coelenterates and plants. It would seem to be preferable to start with living animals somewhere in the middle or higher reaches of organic development—small vertebrates, mollusks, insects, arachnids—and to make them the objects of direct, simple, comprehensive observation and experiment, severely suppressing or subordinating all morphological details which have no immediate bearing on the study of their activities. Necropsies, autopsies and postmortems might be introduced with discretion, but only after the student has acquired an acquaintance with the life-histories and more obvious methods of growth of his organisms—with the aid of moving pictures, whenever necessary—their methods of locomotion, feeding, respiration, excretion, defense and concealment, their reactions to light, temperature, humidity, etc., and especially to one another, *i.e.*, their mating, oviposition, parturition, nidification, parental care, predatory, parasitic, symbiotic, gregarious and social behavior, etc. Simple experiments in genetics, regeneration of lost parts, etc., could be introduced, but without cytological lace and ruffles. The successful teacher of elementary mathematics does not overwhelm and confuse the student with all the known recondite properties of the triangle and circle. The freshman laboratory should be neither an animal morgue nor a herbarium, but a vivarium. Its teaching staff should be numerous, competent, enthusiastic and young and, in order that Merulius infection may be avoided, no old professor or weary research student should be permitted to enter it without a complete change of mental underwear and, I might add, without a few moments of silent prayer or meditation at the door. To the present depauperate glacial fauna of the laboratory, the perpetual rat-guinea-pig-frog-Drosophila *repertoire*, we should add many of the thousands of even more interesting organisms that will live and multiply in confinement, and—although I realize the great difficulties involved—some means must be devised for taking the students into the field more frequently, since it is impossible to reproduce and study the more complex biocœnoses under artificial conditions.

You will probably agree that such a program of freshman work as I have very hastily sketched could in adroit hands yield at least a vital part of the needed preparation, first, for men who will devote the remainder of their collegiate and postcollegiate lives to occupations foreign to biology, and such men, of course, constitute the majority of any freshman class; second, for men who are primarily interested in the "Geisteswissenschaften"—psychology, philosophy, history, economics, law, etc.; third, for men who will enter medicine and may therefore be expected to specialize mainly in morphology and physiology during the remainder of their college course; fourth, for men who may wish to specialize in other departments of applied biology, such as agriculture, forestry, economic zoology and botany, fish and game conservation, etc., subjects to which our present freshman biology is a hopelessly inadequate introduction; fifth, for the biological investigator and teacher, who can not be too quickly persuaded to assume the modern dynamic and experimental attitude toward his science. It is, of course, this new attitude, that many of us older men, trained during the late Victorian morphological boom, have difficulty in assuming, and that makes us so conscious of our inability to participate very effectively in the biological education of the present generation.

There is another suggestion I should like to make, in order that the freshman course may be preserved from the dry-rot, which may invade even the most dynamic type of instruction, and that is the utilization by the instructor of competent amateur naturalists as occasional assistants. This seems never to have been tried, except in some of our summer camps and marine laboratories, and the reason is obvious. The typical professor has about the same liking for the amateur that the devil has for holy water, and the amateur habitually thinks of the professor in terms which I should not care to repeat. You will find a choice collection of them in Mencken's writings. The truth is that the amateur naturalist radiates interest and enthusiasm as easily and copiously as the professor radiates dry-rot. For years

I have taken a malicious delight in introducing amateurs to professors, because the behavior of the latter on such occasions yields a precise quantitative test of the amount of Merulius in their timber. Dear, old, mellow, disinfected professors of the type of Louis Agassiz, Asa Gray, Shaler, Hyatt and Ryder enter at once into sympathetic rapport with the humblest amateur, but the young or those of middle age are almost invariably more or less priggish, condescending or worse. Now there is an opportunity to develop a mutual understanding and respect in both of these parties, so essential to the development of biological science, if the young instructors will only welcome and encourage the cooperation of the amateur in interesting his freshmen. We have all known amateurs who could make an enthusiastic naturalist out of an indifferent lad in the course of an afternoon's ramble and, alas, professors who could destroy a dozen budding naturalists in the course of an hour's lecture. The instructor who would from time to time call in some of our talented ornithologists, herpetologists, entomologists, arachnologists and malacologists to assist him, both in the laboratory and the field, would himself profit greatly, the significant human contacts of the students would be multiplied and the amateur be given just the right environment in which to spread the divine fire of his enthusiasm.

And this brings me in conclusion to what is perhaps the main source of our failure in incubating naturalists, and that is our too highly specialized, or esoteric attitude toward organic nature. Whether we contemplate the whole or only some particular portion of the realm of living things, it eventually tends to become for us merely so much material to be used in the solution of the many tantalizing problems which it suggests. We are, indeed, obsessed by problems. No doubt this is the correct attitude for the seasoned investigator, and no doubt a certain spirit of skeptical inquiry should be cultivated even in freshmen, but surely we should realize, like the amateur, that the organic world is also an inexhaustible source of spiritual and æsthetic delight. And especially in the college we are unfaithful to our trust, if we allow biology to become a colorless, aridly scientific discipline, devoid of living contact with the humanities. Our intellects will never be equal to exhausting biological reality. Why animals and plants are as they are, we shall never know, of how they have come to be what they are, our knowledge will always be extremely fragmentary, because we are dealing only with the recent phases of an immense and complicated history, most of the records of which are lost beyond all chance of recovery, but that organisms are as they are, that apart from the members of our own species, they are our only companions in an infinite and unsympathetic waste of electrons, planets, nebulæ and suns, is a perennial joy and consolation. We should all be happier if we were less completely obsessed by problems and somewhat more accessible to the æsthetic and emotional appeal of our materials, and it is doubtful whether, in the end, the growth of biological science would be appreciably retarded. It quite saddens me to think that when I cross the Styx, I may find myself among so many professional biologists, condemned to keep on trying to solve problems, and that Pluto, or whoever is in charge down there now, may condemn me to sit forever trying to identify specimens from my own specific and generic diagnoses, while the amateur entomologists, who have not been damned professors, are permitted to roam at will among the fragrant asphodels of the Elysian meadows, netting gorgeous, ghostly butterflies until the end of time.

THE TERMITODOXA, OR BIOLOGY AND SOCIETY

READ AT THE SYMPOSIUM OF THE AMERICAN SOCIETY OF NATURALISTS, PRINCETON MEETING, DEC. 30TH, 1919, AND PUBLISHED IN THE *Scientific Monthly*, FEBRUARY, 1920

Cette civilisation, la plus ancienne que l'on connaisse est la plus curieuse, la plus logique, la mieux adaptée aux difficultés de l'existence qui, avant la nôtre, se soit manifestée sur ce globe. A plusieurs points de vue, encore que féroce, sinistre et souvent répugnante, elle est supérieure à celle des abeilles, des fourmis et de l'homme même. * * *

Sans en excepter les abeilles et les fourmis, en ce moment il n'y a pas, je le repète, sur cette terre d'être vivant qui soit tout ensemble aussi loin et aussi près de nous, aussi misérablement, aussi admirablement, aussi fraternellement humain.

Nos utopistes vont chercher, aux limites où l'imagination se décompose, des modèles de sociétés futures, alors que nous avons sous les yeux qui sont probablement aussi fantastiques, aussi invraisemblables, et qui sait, aussi prophétiques que ceux que nous pourrions trouver dans Mars, Vénus et Jupiter.

MAETERLINCK,
"LA VIE DES TERMITES"

Just before the World War we seemed to be on the verge of startling revelations in animal behavior. "Rolf," the Ayrdale terrier of Mannheim, was writing affectionate letters to Professor William Mackenzie of Genoa, and the Elberfeld stallions were easily solving such problems in mental arithmetic as extracting the cube root of 12,167, to the discomfiture of certain German professors, who had never been able to detect similar signs of intelligence in their students. The possibilities of animal correspondence struck me as so promising that I longed to dispatch letters and questionnaires to all the unusual insects of my acquaintance. But dismayed at the thought of the quantity of mail that might reach me, especially from the many insects that have been misrepresented by the taxonomists or maltreated by the economic entomologists, I decided to proceed with caution and to confine myself at first to a single letter to the most wonderful of all insects, the queen of the West African *Termes bellicosus*. During the autumn of 1915 my friend, Mr. George Schwab, missionary to the Kamerun, kindly undertook to deliver my communication to a populous termitarium of this species in his back yard in the village of Okani Olinga. He subsequently wrote me that my constant occupation with the ants must have blinded me to the fact that the termitarium, unlike the formicarium, contains a king as well as a queen, but that the *bellicosus* king was so accustomed to being overlooked, even by his own offspring, that he not only pardoned my discourtesy but condescended to answer my letter. Mr. Schwab embarked for Boston in 1917. Off the coast of Sierra Leone his steamer was shelled by a German submarine camouflaged as a small boat in distress, but succeeded in escaping and what would have been another atrocity, the loss of the king's letter, was averted. It runs as follows:

Dear Sir: Your communication addressed to my most gloriously physogastric consort, was duly received. Her majesty, being extremely busy with oviposition—she has laid an egg every three minutes for the past four years—and fearing that an interruption of even twenty minutes might seriously upset the exquisitely balanced routine of the termitarium, has requested me to acknowledge your expression of anxiety concerning the condition of the society in which you are living and to answer your query as to how we termites, to quote your own words, "managed to organize a society which, if we accept Professor Barrell's recent estimates of geological time, based on the decomposition of radium, has not only existed but flourished for a period of at least a hundred million years."

I answer your question the more gladly, because the history of our society has long been with me a favorite topic of study. As you know, the conditions under which I live are most conducive to sustained research. I am carefully fed, have all the leisure in the world and the royal chamber is not only kept absolutely dark and at a constant and agreeable temperature even during the hottest days of the Ethiopian summer, but free from all noises except the

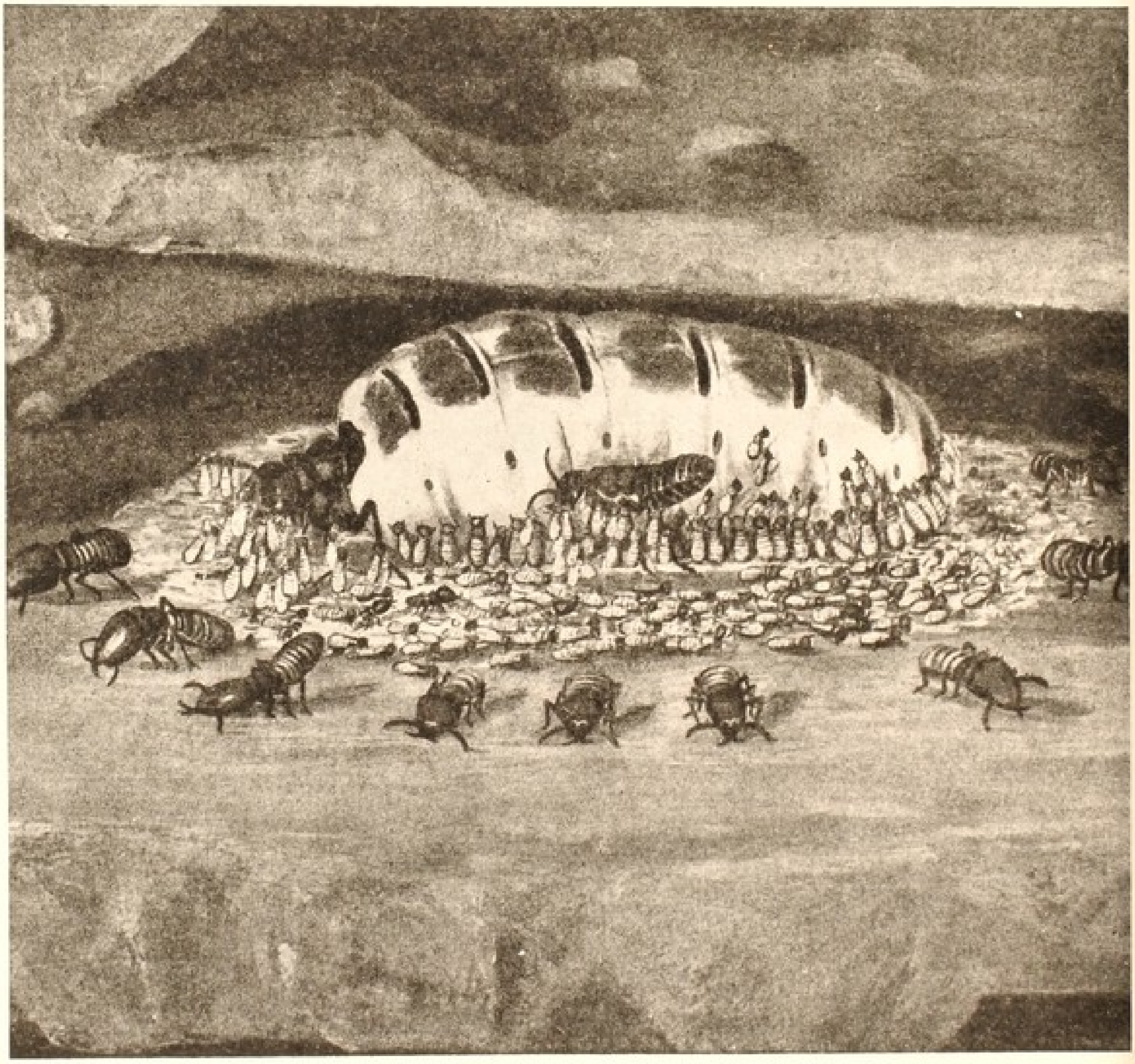

Figure 56. Scene in the Royal Chamber of the African Termes bellicosus *Showing the King (in Centre), Physogastric Queen and the Attendant Soldiers and Workers. (From a Water-Color Drawing by G. Kunze. After Prof. Karl Escherich.)*

gentle rhythmic dropping of her majesty's eggs and the soft footfalls of the workers on the cement floor as they carry away the germs of future populations to the royal nurseries. And you will not wonder at my knowledge of some of the peculiarities of your society when I tell you that in my youth I belonged to a colony that devoured and digested a well-selected library belonging to a learned missionary after he had himself succumbed to the appetite of one of the fiercest tribes of the Kamerun. If I extol the splendid solutions of sociological problems by my remote ancestors, I refrain from suggesting that your society would do well to imitate them too closely. This, indeed, would be impossible. I believe, nevertheless, that you may be interested in my remarks, for, though larger and more versatile, you and your fellow human beings are after all only animals like myself.

According to tradition our ancestors were descended in early Cretaceous times from certain kind-hearted old cockroaches that lived in logs and fed on rotten wood and mud. Their progeny, the aboriginal termites, although at first confined to this apparently unpromising diet, made two important discoveries. First, they chanced to pick up a miscellaneous assortment of Protozoa and Bacteria and adopted them as an intestinal fauna and flora, because they were able to render the rotten wood and mud more easily digestible. The second discovery, more important but quite as incidental, was nothing less than society. Our ancestors, like other solitary insects, originally set their offspring adrift to shift for themselves as soon as they hatched, but it was found that the fatty dermal secretions, or exudates of the young, were a delicious food and that the parents could reciprocate with similar exudates as well as with regurgitated, predigested cellulose. Thenceforth parents and offspring no longer lived apart, for an elaborate exchange of exudates, veritable social hormones, was developed, which, continually circulating through the community, bound all its individuals together in one blissful, indissoluble, syntrophic whole, satisfied to make the comminution and digestion of wood and mud the serious occupation of existence, but the swapping of exudates the delight of every leisure moment. It may be said, therefore, that our society did not arise, like yours, from a combination of selfish predatism and parasitism but from a coöperative mutualism, or symbiosis. In other words, our ancestors did not start society because they thought they loved one another, but they loved one another because they were so sweet, and society supervened as a necessary and unforeseen by-product.

You will admit that no society could have embarked on its career through the ages with more brilliant prospects. The world was full of rotten wood and mud and no laws interfered with distilling and imbibing the social hormones. But in the Midcretaceous our ancestors struck a snag. Not only had all the members of our society begun to reproduce in the wildest and most unregulated manner, but their behavior toward one another had undergone a deterioration most shocking to behold. The priests, pedagogues, politicians and journalists having bored their way up to the highest stratum of the society undertook to influence or control all the activities of its members. The priests tried to convince the people that if they would only give up indulging in the social hormones and confine themselves to a diet of pure mud, they would in a future life eat nothing but rose-wood and mahogany, and the pedagogues insisted that every young termite must thoroughly saturate himself with the culture and languages of the Upper Carboniferous cockroaches. Some suspected that the main value of this form of education lay in intensifying and modulating the stridulatory powers, but for several thousand years most termites implicitly believed that ability to stridulate, both copiously and sonorously, was an infallible indication of brain-power. The politicians and the journalists—well, were it not that profanity has been considered to be very bad form in termite society since the Miocene, I might make a few comments on *their* activities. Suffice it to say that they consumed even more cellulose than the priests and pedagogues and secreted such a quantity of buncombe and flapdoodle that they well-nigh asphyxiated the whole termitarium. Meanwhile in the very foundations of the commonwealth anarchists, syndicalists, I. W. W. and bolsheviki were busy boring holes and filling them with dynamite, while the remainder of society was largely composed of profiteers, grafters, shysters, drug-fiends and criminals of all sizes interspersed with beautifully graduated series of wowsers, morons, feeble-minded, idiots and insane. [At this point the king has introduced a rather trivial note on the word "wowser." This word, he says, was first employed by the termites of Australia but later adopted by the human inhabitants of that continent, to designate an individual who makes a business of taking the joy out of life, one who delights in pouring cold water into his own and especially into other people's soup. The term appears to be onomatopœic to judge from a remark by one of our postcretaceous philologists who asserts that "whenever the wowser saw termites dancing, swearing, flirting, smoking or over-indulging in the social hormones, he sat up on his hind legs, looked very solemn, swelled out his abdomen and said 'WOW!'"]

To such depths, my dear sir, the letter continues, had termite society fallen in the Midcretaceous. The few sane termites still extant were on the point of giving up social life altogether and of returning to the solitary habits of the Palæodictyoptera, but a king, Wuf-wuf IV., of the 529th dynasty, succeeded in initiating those reforms which led our ancestors to complete the most highly integrated social organization on the planet. He has aroused the enthusiastic admiration and emulation of every sovereign down to the present time. I can best describe him by saying that in his serious moments he displayed the statesmanship of a Hammurabi, Moses, Solomon, Solon and Pericles rolled into one and that in his moments of relaxation he was a delightful blend of Aristophanes, Lucian, Rabelais, Anatole France and Bernard Shaw. This king had the happy thought to refer the problems of social reform to the biologists. They were unfortunately few in number and difficult to find, because each was sitting in his hole in some remote corner of the termitarium, boring away in blissful ignorance of the depravity of the society to which he belonged. In obedience to the king's request, however, they were finally rounded up and persuaded to meet together annually just after the winter solstice for the purpose of stridulating about the relations of biology to society. After doing this for ten million years they adopted a program as elegant as it was drastic for the regeneration of termite society, and during the remaining fifteen million years of the Cretaceous they succeeded in putting their plan into operation. I can give you only the baldest outline of this extraordinary achievement.

Our ancient biological reformers started with the assumption that a termite society could not be a success unless it was constructed on the plan of a superorganism, and that such a superorganism must necessarily conform to the fundamental laws of the individual organism. As in the case of the individual, its success would have to depend on the adequate solution of the three basic problems of nutrition, reproduction and protection. It was evident, moreover, that these problems could not be solved without a physiological division of labor among the individuals composing the society, and this, of course, implied the development of classes, or castes. Termite society was therefore divided into three distinct castes, according to the three fundamental organismal needs and functions, the workers being primarily nutritive, the soldiers defensive and the royal couple reproductive. Very fortunately our earliest social ancestors had not imitated our deadly enemies, the ants, who went crazy in the early Cretaceous on the subject of parthenogenesis and developed a militant suffragette type of society, but insisted on an equal representation of both sexes in all the social activities. Our society is therefore ambisexual throughout, so that, unlike the ants, we have male as well as female soldiers and workers. It was early decided that these two castes should be forbidden to grow wings or reproduce and that the royal caste should be relieved from all the labor of securing food and defending the termitarium in order to devote all its energies to reproduction. The carrying out of this scheme yielded at least two great advantages: first, the size of the population could be automatically regulated to correspond with the food-supply, and second, the production of perfect offspring was greatly facilitated.

During the late Cretaceous period of which I am writing our practical geneticists, in obedience to a general demand for a more varied diet, made two important contributions to our social life. The plant breeders found that what was left of the comminuted wood after its passage through the intestines of the worker termites could be built up in the form of elaborate sponge-like structures and utilized as gardens for the growth of mushrooms. Cultivation was later restricted to a few selected varieties of mushrooms which the biochemists had found to contain vitamins that accelerated the growth of the tissues in general and of the spermatocytes and oocytes in particular. And for this reason only the royal caste and the young of the other castes were permitted to feed on this delicious vegetable food. The animal breeders of that age made a more spectacular though less useful contribution when they persuaded our ancestors to adopt a number of singular beetles and flies and to feed and care for them till they developed exudate organs. Owing to the stimulating quality of their exudates these creatures, the termitophiles, added much variety to the previously somewhat monotonous social hormones. This quality, however, made it necessary to restrict the number of termitophiles in the termitarium for the same reason that your society would find it advisable to restrict the cattle industry if your animal breeders had succeeded in producing breeds of cows that yielded highballs and cocktails instead of milk.

It is, of course, one thing to have a policy and quite another to carry it out. The anarchistic elements in our late Cretaceous society were so numerous and so active that great difficulty was at first experienced in putting the theories of the biological reformers into practice, but eventually, just before the Eocene Tertiary, a very effective method of dealing with any termite that attempted to depart from the standards of the most perfect social behavior was discovered and rigorously applied. The culprit was haled before the committee of biochemists who carefully weighed and examined him and stamped on his abdomen the number of his colloidal molecules. This number was taken to signify that his conduct had reduced his social usefulness to the amount of fat and proteins in his constitution. He was then led forth into the general assembly, dismembered and devoured by his fellows.

I describe these mores reluctantly and very briefly, because I fear that they may shock your sensibilities, but some mention of them is essential to an appreciation of certain developments in our society within recent millennia. So perfectly socialized have we now become that not infrequently a termite who has a slight indisposition, such as a sore throat or a headache or has developed some antisocial habit of thought or is merely growing old, will voluntarily resort to the committee of biochemists and beg them to stamp him. He then walks forth with a radiant countenance, stridulating a refrain which is strangely like George Eliot's "O, may I join the choir invisible!" and forthwith becomes the fat and protein "Bausteine" of the crowd that assembles on hearing the first notes of his petition. If you regard this as an even more horrible exhibition of our mores, because it adds suicide to murder and cannibalism, I can only insist that you are viewing the matter from a purely human standpoint. To the perfectly socialized termite nothing can be more blissful or exalted than feeling the precious fats and proteins which he has amassed with so much labor, melting, without the slightest loss of their vital values, into the constitutions of his more vigorous and socially more efficient fellow beings.

Now I beg you to note how satisfactory was our solution of the many problems with which all animals that become social are confronted. I need not emphasize the matter of nutrition, for you would scarcely contend that animals that can digest rotten wood and mud, grow perennial crops of mushrooms on their excrement, domesticate strange animals to serve as animated distilleries and digest not only one anothers' bodies but even one anothers' secretions, have anything to learn in dietetics or food conservation. Our solution of the great problems of reproduction, notably those of eugenics, is if anything, even more admirable, for by confining reproduction to a special caste, by feeding it and the young of the other castes on a peculiarly vitaminous diet and by promptly and deftly eliminating all abnormalities, we have been able to secure a physically and mentally perfect race. You will appreciate the force of this statement when I tell you that in a recent census of the 236,498 individuals comprising the entire population of my termitarium, I found none that had hatched with more than the normal number of antennal joints or even with a misplaced macrochæta. The only anomaly seen was one of no social significance, a slightly defective toenail in three workers. Rigid eugenics combined with rigid enforcement of the regulations requiring all antisocial, diseased and superannuated individuals promptly to join the choir invisible, at the same time solved the problems of ethics and hygiene, for we were thus enabled, so to speak, to ram virtue and health back into the germ-plasm where they belong. And since we thus compelled not only our workers and soldiers but even our kings and queens to be born virtuous and to continue so throughout life, the Midcretaceous wowser caste, finding nothing to do, automatically disappeared. The problem of social protection was solved by the creation of a small standing army of cool-headed, courageous soldiers, to be employed not in waging war but solely for defensive purposes, and the development on the part of the soldiers and workers of ability to construct powerful fortifications. It may be said that the formation of the soldier caste as well as the invention of our cement subway architecture—an architecture unsurpassed in magnitude, strength and beauty, considering the small stature of our laborers and the simple tools they employ—was due to the repeated failures, extending over many million years, of our politicians to form a league of nations with our deadly enemies, the ants. After a recent review of the army and an inspection of the fortifications of my termitarium I agree with several of the kings of the present dynasty who believed that we ought really to be very grateful to our archenemies for their undying animosity.

Such was our society at the beginning of the Eocene, and such with slight improvements in detail, it has remained for the past fifty million years, living and working with perfect smoothness, as if on carefully lubricated ball-bearings. Nor does it, like human society, live and work for itself alone but with a view to the increase and maintenance of other types of life on the planet. On our activities depend the rapid decomposition of the dead vegetation and the rapid formation of the vegetable mould of the tropics. We are so numerous and our operations of such scope that we are a very important factor in accelerating the growth of all the vegetation, not only of the dry savannahs and pampas but even of huge rain-forests like those of the Congo, the Amazon and the East Indies. And when you stop to consider that the animal and human life of the tropics absolutely depends on this vegetation you will not take too seriously the reports of our detractors who are forever calling attention to our destructive activities. One author, I am told, asserts that certain South American nations can never acquire any culture because the termites so quickly eat up all their libraries, and another gives an account of a gentleman in India who went to bed full of whiskey and soda and awoke in the morning stark naked, because the termites had eaten up his pyjamas. How very unfair to dwell on the loss of a few books and a suit of pyjamas and not even to mention our beneficent and untiring participation in one of the most important biocœnoses!

You will pardon me if after this hasty sketch of our history I am emboldened to make a few remarks about your society, and in what I say you will, I hope, make due allowance both for the meagerness of my sources of information and the limitations of my understanding. I must confess that to me your society wears a strangely immature and at the same time senile aspect, the appearance, in fact, of a chimera, composed of the parts of an infant and those of a white-haired octogenarian. Although your species has been in existence little more than one hundredth of the time covered by our evolution, you are nevertheless such huge and gifted animals, that it is surprising to find you in so imperfect a stage of socialization. And although every individual in your society seems to crave social integration with his fellows, it seems to be extremely difficult to persuade him to abate one tittle of all his natural desires and appetites, and every individual resists to the utmost any profound specialization of his structure and functions such as would seem to be demanded by the principle of the division of labor in any perfect society. Hence all the attempts which your society is continually making to form classes or castes are purely superficial and such as depend on the accumulation and transmission of property, and on vocation. And owing to the absence of eugenics and birth-control and to your habit of fostering all weak and inefficient individuals, there is not even the dubious and slow-working apparatus of natural selection to provide for the organic fixation of castes through heredity. So immature is your society in these respects that it might be described as a lot of cave-men and cave-women playing at having a perpetual pink tea or Kaffeeklatsch.

But the senile aspect of your society impresses me as even more extraordinary, because our society—and the same is true of that of all other social insects—is perennially youthful and vigorous, owing to our speedy elimination of the old and infirm. And this brings me to a matter that interests me greatly and one on which I hope we shall have much further correspondence. To be explicit, it seems that though your society has no true caste system, it is, nevertheless, divided into what might be called three spurious castes, the young, the mature and the aged. These, of course, resemble our castes only in number and in consisting of individuals of both sexes. They are peculiar in being rather poorly defined, temporary portions of the life-cycle, so that a single individual may belong to all of them in succession, and in the fact that only one of them, comprising the mature individuals, is of any great economic value to society and therefore actually functions as the host of the two others, which are, biologically speaking, parasitic. To avoid shocking your human sensibilities, I am willing to admit that both these castes may be worth all the care that is bestowed on them, the young on account of their promise and the old on account of past services. And I will even admit the considerable social value of the young and the old as stimuli adapted to call forth the affection of the mature individuals. But, writing as one animal to another, I confess that I am unable to understand why you place the control of your society so completely in the hands of your aged caste. Your society is actually dominated by the superannuated, by old priests, old pedagogues, old politicians and no end of old wowsers of both sexes who are forever suppressing or regulating everything from the observance of the Sabbath and the wearing of feathers on hats to the licking of postage stamps and the grievances and tribulations of stray tom-cats.

I notice that your educators, psychologists and statisticians have much to say on human longevity, and you seem all to crave for nothing so much as an inordinate protraction of your egos. Psychologically, this is, of course, merely another manifestation of your fundamentally unsocial and individualistic appetites. Your writers make much of your long infancy, childhood and adolescence as being very conducive to educability and socialization, and this is doubtless true, but the fact seems to be overlooked that the great lengthening of the initial phases of your life-cycle is also attended by a grave danger, for it also increases the dependence of the young on the adult and aged elements of society, especially on the parents, and this means intensifying what the Freudian psychologists call the father-and mother complexes and therefore also an increased subservience to authority, a cult of the conservative, the stable and the senile. The deplorable effects of intensifying these complexes have long been only too evident in your various religious systems and are already beginning to show in the all too ready acceptance on the part of your society of the visionless policies and confused and hesitating methods of administration of your statesmen.

Unless I am much mistaken this matter of the domination of the old in your society deserves careful investigation. Unfortunately very little seems to be known about senility. In our society it can not be investigated, because we do not permit it to exist, and in your society it is said to be very poorly understood, because no one is interested in it till he actually reaches it and then he no longer has the ability or the time to investigate it. When the social significance of this stage in the human life-cycle comes to be more thoroughly appreciated some of your young biologists and psychologists will make it a subject of exhaustive investigation and will discover the secret of its ominous and persistent domination. It will probably be found that many of your aged are of no economic importance whatever, and that the activities of many others may even be mildly helpful or beneficial, but you will find, as we found in the Midcretaceous, a small percentage, powerful and pernicious out of all proportion to their numbers, who are directly responsible for the deplorable inertia of your institutions, especially of your churches, universities and political bodies. These old individuals combine with a surprising physical vigor a certain sadistic obstinacy which consecrates itself to obstructing, circumventing, suppressing or destroying not only everything young or new, but everything any other old individual in their environment may suggest. The eminent physician who recommended chloroform probably had this type of old man in mind. Certain economic entomologists have advocated some more vigorous insecticide, such as hydrocyanic acid gas. This is, however, a matter concerning which it might be better to defer recommendation till the physiology, psychology and ethology of the superannuated have been more thoroughly investigated.

It has sometimes occurred to me that your social problem may be quite insoluble—that when your troglodyte ancestors first expanded the family and clan into society they were already too long-lived, too "tough" and too specialized mentally and physically ever to develop the fine adjustments demanded by an ideal social organization. I feel certain, nevertheless, that you could form a much better society than the present if you could be convinced that your further progress depends on solving the fundamental, preliminary problems of nutrition, reproduction and social defence, which our ancestors so successfully solved in the late Cretaceous. These problems are, of course, extremely complicated in your society. Under nutrition you would have to include raw materials and fuel, *i.e.*, food for your factories and furnaces as well as food for your bodies. Your problems of reproduction comprise not only those of your own species but of all your domesticated animals and plants, and your social defence problems embrace not only protection from the enemies of your own species (military science) but from the innumerable other organic species which attack your domesticated animals and plants as well as your own bodies (hygiene, parasitology, animal and plant pathology, economic entomology). Like our ancestors you will certainly find that these problems can be solved only by the biologists—taking the word "biologists" in its very broadest sense, to include also the psychologists and anthropologists—and that till they have put their best efforts into the solution your theologians, philosophers, jurists and politicians will continue to add to the existing confusion of your social organization. It is my opinion, therefore, that if you will only increase your biological investigators a hundredfold, put them in positions of trust and responsibility much more often and before they are too old, and pay them at least as well as you are paying your plumbers and bricklayers, you may look forward to making as much social progress in the next three centuries as you have made since the Pleistocene. That some such opinion may also be entertained by some of your statesmen sometime before the end of the present geological age, is the sincere wish of

Yours truly,

WEE-WEE, 43d Neotenic King, of the 8,429th Dynasty of the Bellicose Termites.

On reperusing this letter before deciding, after many misgivings, to read it to so serious a body of naturalists, I notice a great number of inaccuracies and exaggerations, attributable, no doubt, to his majesty's misinterpretation of his own and very superficial acquaintance with our society. His remarks on old age strike me as particularly inept and offensive. He seems not to be aware of the fact that at least a few of our old men have almost attained to the idealism of the superannuated termite, a fact attested by such Freudian confessions as the following, taken from a letter recently received by one of my colleagues from a gentleman in New Hampshire:

> I do not understand how it is that an insect so small as to be invisible is able to worry my dog and also at times sharply to bite myself. A vet. friend of mine in Boston advised lard and kerosene for the dog. This seemed to check them for a time, but what I need is extermination, for I am in my eighty-fourth year.

INDEX

INDEX

A NOTE
ON THE TYPE IN WHICH
THIS BOOK IS SET

The type in which this book has been set (on the Monotype) is Garamont. This face is an adaption by Frederick W. Goudy, of a type designed by Claude Garamond in the sixteenth century. A pupil of Geofroy Tory, Garamond was the foremost type designer and letter cutter of his time (1510–1561). It is believed that he based his letters on the Venetian models although he has introduced a number of important differences, and it is to Garamond that we owe the letter which we know as Old Style. In adapting this type to modern usage Mr. Goudy has not attempted an exact duplication of any of the Garamond models, and he has combined all the characteristics of the original design with the unmistakable Goudy touch.

SET UP, PRINTED AND BOUND
BY THE HADDON CRAFTSMEN, CAMDEN, N. J.
PAPER FURNISHED BY S. D. WARREN CO.,
BOSTON

BORZOI

BOOKS