DEMONS OF THE DUST

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RENÉ-ANTOINE FERCHAULT DE RÉAUMUR
(*From the portrait by Simonneau in the National Library of Paris.*)

DEMONS OF THE DUST

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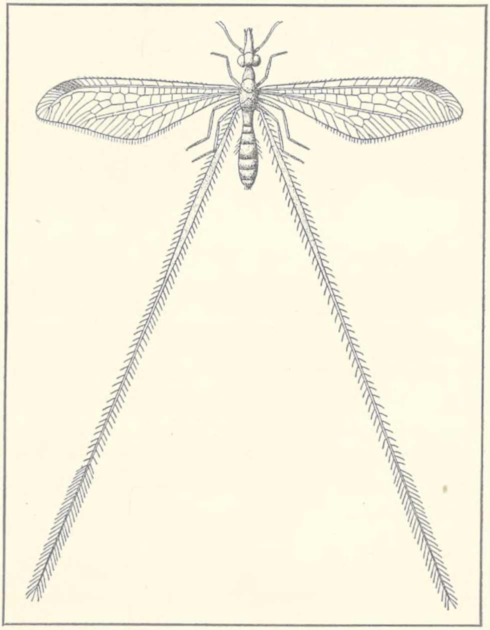

A STUDY IN INSECT BEHAVIOR

W·W·NORTON & COMPANY·INC·PUBLISHERS
NEW YORK

W. W. NORTON & COMPANY, INC.
70 Fifth Avenue, New York

FIRST EDITION

PRINTED IN THE UNITED STATES OF AMERICA
FOR THE PUBLISHERS BY THE VAN REES PRESS

TO

THOMAS BARBOUR

PREFACE

THREE motives seem to have impelled me to write this book. First, there was a kind of Freudian regression to one of my earlier stages, a nostalgia urging me to return to a study of the Diptera, or two-winged flies, which had claimed my attention in youth before I had developed a keener and more stable interest in the social insects. This feeling first came over me in 1917 while observing the worm-lion in the Sierras of California and has led in the intervening years to the monograph on the Vermileoninæ embedded but not, I hope, buried in this volume. Second, after working with this insect and the ecologically very similar ant-lion, I wished to call the attention of zoologists and physiologists to their great value as laboratory animals. Our present laboratory fauna is deplorably scanty, mainly because so few small animals can be kept alive for considerable periods in an artificial environment without a considerable expenditure of time and labor on feeding, maintaining optimal conditions of moisture, temperature, etc. The worm-lion and ant-lion, in addition to being extremely hardy, have the advantage of presenting a host of interesting, unsolved or only partially solved physiological and behavioristic problems. Third, with advancing years and a growing conviction of the value of all science as a *social* undertaking, I felt that a detailed account of the insects which had so long interested me might interest the general reader.

How far the first and second motives may have yielded anything of permanent value must depend, of course, on the judgment of my fellow entomologists. After rereading my manuscript and conversing with friends and colleagues I confess that the third motive has given way to a feeling of perplexity. Some of my colleagues maintain that I have attempted the impossible, that there are only two ways of writing on such a subject as the one I have chosen. Either I should have written as an undefiled specialist in the refined jargon and with the ponderous documentation demanded by the ritual of my caste, or I should have turned to literature and presented the matter with the well-known devices and embellishments of rhetoric, which may perhaps delight, but are sure to mislead the uncritical reader. Any intermediate course, they claimed, can only lead to a compromise distasteful alike to the high-brow scientist and the thrill-seeking, movie-fed public. Some of my councillors suggested, with a just perceptible curl of the lip, that Fabre and his great popular success might be worth emulating. This advice was not reassuring, because, though an ardent admirer of Fabre as an observer, I was aware that his popularity as the "Homer of the insects" was due mainly to his incomparable literary skill, which I could not hope to attain, and partly to his advertisement by certain great littérateurs who had chanced to discover him in his Provençal hermitage when his long life was already drawing to a close. Another factor in his success as a popularizer was the careful avoidance of documentation in his writings. He almost never referred to contemporary entomologists, even to those who had anticipated him in the publication of similar or identical observations, and he rarely cited even such early French authorities as Réaumur, Latreille and Dufour. Now the scholar and the scientist are extremely sensitive in regard to documentation, not only because it is so thrilling to find their own works cited by their friends and enemies, but also because it enables them to judge whether an author has a sufficient knowledge of previous achievements in a particular field and has, or thinks he has, contributed any new facts, inferences or reflections.

If, as seems probable, I have really crashed between two stools in attempting to interest both the entomologist and the general reader, who may be inveigled by the rather sensational title into reading this book, I shall not plead guilty but proceed to rationalize my conduct. There are, in fact, serious and perhaps insurmountable obstacles to popularizing or even semipopularizing entomology in its present state. Quite apart from the disgust experienced by many people at the mere sight of insects, the more we know about their structure and behavior, the more inhuman and demoniac they become. The number of their species, subspecies, varieties and individuals is appalling, and it would have been impossible, during the past two centuries, to weld together the innumerable ascertained and recorded minutiæ of their classification, structure, development and distribution, to make the science of entomology, without the aid of an elaborate technical terminology, or symbolism. Though this terminology is awkward, tortuous and pedantic to a degree, it is, nevertheless, consistent and far more concise and regulated than the vague, emotion-soaked language of ordinary discourse. Fabre was fond of holding the terminology of entomologists up to ridicule, but had he not employed it himself, we should now find it difficult or impossible to identify quite a number of the species which he studied. Since there are no facts or theories in entomology — or for that matter in any biological science — that transcend the understanding of any fairly intelligent lad of fourteen, I feel certain that the chief obstacle to popularization of the life sciences is language, and the obstacle is greater in entomology merely because the distinguishable phenomena are more numerous and have therefore given rise to a more voluminous vocabulary. Santayana's remark that "some language is indispensable to science" is a commonplace, unless the sentence be applied to entomology with the emphasis on 'some' in the American slang sense.

Should these remarks fail to encourage the general reader, and especially one suffering from a fear of Greco-Latin compounds, or what might be called megalologophobia, I would call his attention to the following items:

(1) Many young biologists also suffer from the same complaint but are permanently cured as soon as they begin to manufacture scientific terms of their own. Seasoned biologists, after learning that every organism, object, 'event' or 'essence' is in itself inscrutable and indefinable and that loquacious man is a lineal descendant of the greatest chatterers in the Animal Kingdom, lose all respect for mere words and treat them as they would adhesive labels.

(2) To several very competent biologists working on groups other than insects in laboratories adjacent to my own, the generic and specific terms mentioned in this book are quite as opaque and meaningless as they will be to the general reader. These biologists, however, would react to them differently. Having coined many a big term in their day, my colleagues would merely substitute mental x's and y's for the terms in my text and try to interest themselves in what is said about them. I can see no reason why the general reader should not do the same.

(3) The general reader, unless specially interested, may omit the latter part of the second chapter, which bears somewhat the same relation to the remainder of the book as the catalogue of ships to the remainder of the Iliad. He may also omit several other passages, which have an air of having been written for the annoyance of systematic entomologists.

(4) Since science is a social undertaking, I would beg the reader to coöperate with me to the extent of consulting some good dictionary for the more general terms with which he may be unfamiliar. Many intelligent people spend hours communing with dictionaries and other works of reference for the purpose of solving cross-word puzzles.

Is it expecting too much to ask the general reader to do as much when he is hoping to obtain information from an entomological treatise?

I wish to express my warm thanks to Professor C. T. Brues, Professor E. O. Essig and Dr. F. M. Carpenter for aid in illustrating the volume. I am also greatly indebted to Dr. J. Bequaert and Mr. Nathan Banks for help in looking up literature, to Miss Elsa Thorud for twice very carefully typing the entire manuscript and to Professor Brues and Dr. Bequaert for reading the proof. To the publisher, Mr. W. W. Norton, I am under lasting obligations for valuable suggestions in arranging parts of the manuscript and for his care and pains in making the volume as attractive as possible.

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CHAPTER I

SOME EIGHTEENTH-CENTURY NATURALISTS

TO DEVOTE a whole volume to the consideration of the ant-lions and worm-lions, two small, obscure groups among the myriads of more important insects, at a time when our society is seething with unrest and obsessed by problems of great moment, must seem like a fine example of arrant and useless specialization. These insects, indeed, are quite devoid of any economic significance, for, though predatory, they neither harm us nor endanger the survival of any animal or plant for which we have any use, so that if they were suddenly to become extinct, the fauna and flora of our planet would continue as if they had never existed. As larvæ they are ugly, if not repulsive, and as adult insects they are frail creatures, with short and rather futile lives. The mere fact, however, that they have been favorite objects of study with a long line of thoughtful naturalists for more than two centuries, suggests that they merit careful study. What has impressed all these investigators is first, their extraordinary behavior during their larval stages, and second, the astonishing conformity of this behavior in two groups of insects so remotely related that their earliest common ancestor must have become extinct many millions of years ago. The ant-lions and worm-lions, though they belong to such dissimilar orders as the ancient and primitive Neuroptera and the modern and highly specialized Diptera respectively, exhibit an unusual case of convergent evolution. They illustrate, moreover, in a very interesting manner the long controversy which is still being waged in regard to the correct interpretation of insect behavior. This controversy, as we shall see, revolves about the question as to whether insects are nothing but reflex machines or whether their activities also yield indisputable evidence of a certain adaptability and insight (intelligence) in the employment of individually acquired experience (memory). The structural and functional convergence of the ant-lions and worm-lions is clearly due to living in the same peculiar environment. I propose, therefore, before entering on a more detailed account of these insects, to devote the present chapter to an account of the naturalists who first studied them and the following chapter to a general description of the sand fauna.

The ant-lions and worm-lions seem to have been quite unknown to the ancients. Even Aristotle, who was familiar with so many of the common insects of Greece, fails to mention the ant-lions, though they occur throughout Continental Europe as far north as Finland and are very common in the Mediterranean countries. That the worm-lions were overlooked by the ancients is less surprising, because the three European species of Vermileo and Lampromyia, though confined to the Mediterranean region, are, nevertheless, decidedly local or sporadic. The very existence of these insects, in fact, was not known till the beginning of the eighteenth century.

Curiously enough, the word 'myrmecoleon', now assigned to the ant-lion in the abbreviated form 'Myrmeleon', occurs in the fourth chapter of the Greek version of the Book of Job, in the verse μυρμηκολέων ὤλετο παρὰ τὸ μὴ ἔχειν βορὰν and naturally gave rise to numerous and often very fanciful interpretations among the medieval commentators of the Bible. In the Vulgate the 'myrmecoleon' is supposed to be a tiger and the verse reads *tigris periit quod non haberet prædam,* but in our English Bible it is rendered "The old lion perisheth for lack of prey." The word μύρμηξ seems to have been applied to two very different animals, the ant and some beast of prey, as in the famous passages of Herodotus and Pliny on the gold-digging ants.[1]

Now it was in medieval commentaries on the Book of Job that the singular habits of the ant-lion were first mentioned by Isidore of Seville (Isidorus Hispalensis 560-636) and Gregory the Great (*ca.* 540-604) as early as the sixth and seventh centuries, and by Vincentius Bellovacensis in 1246. There can be no doubt that Isidore refers to the common European ant-lion when he describes the "formicaleo" (the Latinized form of Myrmecoleon) as "a small animal rather hostile to ants, which hides itself in the dust and kills the ants that are carrying grain."[2]

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[1] This subject has been discussed at length by Keferstein (1835).

[2] Even the ant can be identified as one of the South European species of Messor (*barbarus* or *structor*). The entire reference (Book XII, 3) reads as follows: "Dicuntur in Aethiopia esse formicæ ad formam canis quæ arenas aureas pedibus eruunt, quas custodiunt ne quis auferat, captantes ad necem persequuntur. Formicoleon ob hoc vocatus, quia est vel formicarum leo vel certe formica pariter et leo. Est enim animal parvum formicis satis infestum, quod se in pulvere abscondit, et formicas frumenta gestantes interfecit. Proinde autem leo et formica vocatur, quia aliis animalibus ut formica est, formicis autem ut leo est." Since this chapter was written a few additional early references to the ant-lion have come to light. An account of the 'myrmecoleon,' the mythical creature of the Book of Job, is cited by Bodenheimer (1928) as occurring in the 'Physiologus,' which seems to date from the second century of our era. "Eliphas, King of Themen, says: 'The ant-lion has perished, because he has no food.' The Physiologus says that he has the face of a lion and the hinder parts of an ant. His father is a meat-eater, but his mother eats plant food. Now when they beget the ant-lion, they beget him with two peculiarities. He can eat no meat because of his mother's peculiarity and no plant-food because of his father's; he perishes therefore from lack of sustenance." The passage previously cited from Isidore of Seville occurs also in the 'De Universo' of Rhabanus Maurus (*ca.* 776-856). Thomas de Cantimpré (1201-bet. 1263 and 1293) makes some homiletic use of the ant-lion (*see* Bodenheimer, p. 169) and may have derived his information from his teacher, Albert the Great, but

Albert the Great (1193-1280) gives a much better description of the ant-lion and one based on his own observations.[1] Several centuries intervene before we again happen on an account of the insect in the works of Cardanus (1553) and Aldrovandus (1632), and we are disappointed to find that these writers merely rephrase Albert's Latin. This is done very concisely by Cardanus, but Aldrovandus diffusely combines Albert's remarks with the older lucubrations on the meaning of 'myrmecoleon' in the Book of Job. Redtenbacher (1884) was of the opinion that Cardanus' description refers "without doubt" to the worm-lion, but this is certainly an error.[2]

Not till the end of the seventeenth and the beginning of the eighteenth century do we come upon any accurate observations on the ant-lion. Then Vallisnieri in his 'Dia-

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he begins his description of the creature by stating that Adelinus had called it the "mirmicaleon." According to Thorndike (1923), Thomas de Cantimpré refers to the 'Aenigmatum Liber' of Adhelmus, who died in 709 and was the first Englishman of whom there are any literary remains. I have not tried to run this reference down because it is not likely to be funnier than the one cited above from the 'Physiologus.'

[1] De Animalibus Libri XVI (Stadler's Edition, vol. 2, 1920, p. 1586), "*Formicaleon* dicitur leo formicarum qui alio nomine murmycaleon vocatur. Hoc autem animal non est primo formica ut quidem dicunt. Expertus enim sum multotiens et ostendi sociis hoc animal engulas fere habere figuram et absconditur in sabulo semispheram in sabulo fodiens cujus polus est os formicaleonis: et dum formicæ causa lucri transeunt, ipsas capit et devorat et hoc sæpius aspeximus. In hyeme etiam dicitur cibos formicarum diripere eo quod in æstate nihil congregat sibi."

[2] The passage from Cardanus reads as follows: "Insidiatur formicis animal erucæ parvæ simile (sic interpretor Alberti, qui hoc vidit, verba) in sabulo foveam sibi fingens, hemisphærii forma, in cujus apice, quasi polus, foramen existit angustum, ex quo improvisus insultat formicis, easque devorat; hoc formicaleon ab Alberto appellatur." Redtenbacher was misled by the words *animal erucæ parvæ simile* — an animal resembling a small caterpillar, but *eruca* (caterpillar) is an attempt to translate Albert's "engulas", which seems to be a Latinization of "Engerling", the vernacular German name for a Scarabæoid beetle (cockchafer) larva. Since neither the larval Myrmeleon nor the larval Vermileo can properly be called a caterpillar, the word chosen by Cardanus shows that he had never seen either of these creatures. That he was merely citing Albert is clear also from the parenthetical remark *sic interpretor Alberti, qui hoc vidit, verba,* which is omitted in the passage as quoted by Redtenbacher.

logues between Malpighi and Pliny in the Netherworld' (1697, 1700) described both the habits of the larva and its transformation into the imago. The external structure, especially of the latter, is considered in detail, but there are no illustrations. A more adequate account with good figures was published by the anatomist Poupart in 1704 in the Mémoires of the French Academy.[1] This paper was the source of a famous account of the insect published in 1732 by the Abbé Pluche in his 'Spectacle de la Nature,' a work in seven volumes, composed in dialogue form. It passed through several editions during the next half century and was translated into English not long after its appearance by Kelly, Bellamy and Sparrow (1743). Noël Antoine Pluche (1688-1761) was a Jansenist and director of the College of Laon, but was deprived of his position because he refused to adhere to the papal bull "Unigenitus." Through the good offices of Charles Rollin, humanist, historian and rector of the University of Paris, he then became a teacher in the household of Gasville, intendant of Normandy. Later he settled in Paris. Besides the 'Spectacle de la Nature' he published works on the teaching of language, the harmony of the psalms and the gospels and on geography. The philosopher La Mettrie in his 'Essais sur l'esprit et les beaux esprits' gives the following characterization of Pluche: "Without wit, without taste, he is Rollin's pedant. A superficial man, he had need of the work of M. Réaumur, of whom he is only a stale and tiresome imitator

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[1] Vallisnieri in the folio edition of his 'Dialoghi' (1733) accused Poupart of plagiarizing his description of the ant-lion, but Réaumur (1742) showed not only that Poupart made his observations independently but that two other Frenchmen, des Bellettes (1614-1700) and de la Hire had anticipated Vallisnieri in their observations on the insect. Neither of them published, but des Bellettes, who was a member of the French Academy "had studied the ant-lion in his youth in Poitou and had brought it to the attention of our savants", and Réaumur had in his possession a diary written by de la Hire in 1661 and containing notes on the feeding of ant-lions and their ability to fast for seven months.

in the flat little sayings scattered in his dialogues. It was with the works of Rollin as with the 'Spectacle de la Nature,' one made the fortune of the other: Gaçon praised Person, Person praised Gaçon, and the public praised them both." In order that the reader may judge of the aptness of La Mettrie's estimate of Pluche, I quote the greater portion of Kelly, Bellamy and Sparrow's rendering of the eighth dialogue on the ant-lion between the Count and Countess de Jouval, the Prior de Jouval and the Chevalier de Breuil:

"CHEVALIER: After the history of the ant, nothing, in my opinion, can be introduced more naturally than a detail of the Formicaleo; so called, because 'tis the lion, or the most formidable enemy of the whole race of ants.

"COUNTESS: Why can't you call it the *Lion pismire?* We are masters of the terms, at least in our academy.

"CHEVALIER: The term, Madam, which you have given it, is perfectly agreeable; and I'll assure your Ladyship, that for the future I'll never distinguish this little fierce animal by any other title. I was at the Prior's yesterday, where I was obliged with a sight of a very pretty picture, wherein were delineated all the various transformations through which that creature passes. Tho' I have a tolerable idea of the whole train of particulars yet lest I should be troublesome in the repetition, or should forget any material incident, I have committed my thoughts upon the subject to writing, and hope you'll indulge me with the liberty of reading it, especially since the Prior has been pleased to touch it up with his own hand; and that, I presume, you will allow to be a material article.

"COUNTESS: Your apology, Sir, is delivered with such an air of freedom, that it might pass for an introduction to the most entertaining history.

"CHEVALIER: The lion-pismire is much about the length of the common palmer (The Memoirs of the Academy of

Sciences. Mr. Poupart, 1704), or wood-louse; but then 'tis somewhat thicker. It has a very long head, and its body grows round as it lengthens toward the tail. As to its colour, 'tis a dark-grey, and mark'd with black spots. Its body consists of several flat ringlets, which glide over one another. It has six feet, four whereof are inserted in the breast, and two in the neck. Its head is small and flat; from the fore-part shoot out two little horns, which are smooth and hard, about two-twelfths of an inch in length, and bent like hooks at the extremes. Toward the base of these horns it has two small eyes, which are black as jet, very sprightly, and serviceable to the last degree; for it starts at the smallest objects that present themselves before it.

"Other animals are provided with wings, or at least with feet, to enable them to pursue their prey. This, however, is only capable of moving backwards. He never pursues his prey, and would sooner die than advance one step towards it. His prey must come to him, and he has learnt the art of making it fall into the snare he has prepared for it. 'Tis to this artifice alone he owes his subsistence; and altho' 'tis all the knowledge he is endow'd with, yet 'tis sufficient for his purpose.

"He makes choice of a bed of dry sand at the foot of some stone wall, or under some covert, that his work may receive no damage from the injuries of the weather. Not only sand, but the driest he can procure is the best for his purpose; because either a hard ground, or a moist sand, would prove an obstacle to his operations. When he proposes to hollow the trench, or ambuscade, for the ensnaring of his prey, he begins with bending the hinder part of his body, which terminates in a point. After this he plunges it, like a plough-share, into the sand, which he removes by a retrograde motion. And thus, by frequent repetitions, and various little tours, he traces out at last a circular furrow, the diameter whereof exactly corresponds with the depth to which he determines to sink it. Having planted himself in the center of that circle, he plunges himself still deeper into the sand, which he throws up with his horns some little distance from the furrows, always observing a retrograde motion in a spiral line in proportion to the depth he sinks. The reiterated blows with his head make the sand fly out of the circle and by slow degrees evacuate the inner part. This is the artful method he observes in the completion of his trench, which bears a very near resemblance to a cone revers'd, or rather, the internal part of a funnel.

"The furrow which the lion-pismire traces, when he is first hatched, is but very small. However, as he increases gradually in bulk, he makes it more extensive; the cavity whereof may probably be two inches or more in diameter, and much about the same depth. When he has accomplish'd his work, he lies in ambuscade, and conceals himself in such a manner under the sand, that his horns exactly surround the point wherein the bottom of the funnel terminates. Thus he watches for his game, and inevitably ruin attends the ant, the wood-louse, or any other insect, that indiscreetly rambles round the edge of this precipice, which is made shelving and in the sand, too, that such animals as approach it unawares may tumble in. 'Tis in hopes of ensnaring the female ant, that the lion-pismire thus lays the ground-work of his kitchen. She has no wings, as most other insects have, to disengage herself from this fatal den. Other animals, however, as well as she, are ruin'd and undone by the dexterity and address of this insidious hunter. As soon as he perceives, by the fall of a few grains of sand, that some game is near, he retreats a step or two, and by that motion saps the foundation of the sand, which immediately falls down to the bottom with the prey. If such prey be an active animal, if it springs up in an instant, and especially if it has wings, the lion-pismire flirts a quantity of sand all over her. Such a shower of stones must doubtless be shock-ing to so tender an animal as a gnat or ant. Thus blinded, and overwhelm'd by the impetuous storm, that pours down on every side, and carried away by the unstable sand, which rolls from under her feet, the unfortunate insect falls between the two jaws of her enemy, who plunges them in an instant into her body, drags her with violence under the sand, and there regales himself upon his captive. When he has gratified his voracious appetite, and nothing more remains than the carcase, drain'd of all its juices, he takes particular care to remove and conceal it. The sight of a dead body might probably prevent some future visits, and render his habitation a place of ill repute; for which reason he extends the mangled carcase on his horns, and with a sudden jerk throws it about half a foot beyond the edges of the trench. If he finds the trench too much encumbered and filled up by this expedition; or if the aperture becoming too large for the depth, should lose its proper slope, he instantly repairs the whole; he rounds, hollows and clears his den, and then lies upon the catch for some new victim.

"The possession of a hunter, all sportsmen allow, requires abundance of patience; and the lion-pismire is endow'd with as large a share of that quality, as of artifice and deceit. He will sometimes spend whole weeks, nay months together, without motion, and, what is still more surprising, without the least subsistence.

"His abstinence, which is of singular service to him, is so remarkable, that I have known him to live above six months in a box, shut up as close as possible, without anything in it, except a little sand. I have seen several of them accomplish their work as usual; and afterwards metamorphose into nymphs, like others, which I have supported with all imaginable care. It must be acknowledged, however, that such as eat, grow larger, and improve in strength and vigor.

"When this lion-pismire has attained a certain age, and is desirous of undergoing a state of renovation, in order to make his appearance in the last form he is to assume, he then concerns himself no more about his trench; but sets himself to work in the sand and therein strikes out a thousand irregular tracks, which labour he strenuously pursues, in order, no doubt, to throw himself into a violent sweat; after which he plunges headlong into the sand.[1] That glutinous moisture, which by such excessive motion flows from each part of his body, fastens to and unites with all the grains which he touches. With these particles of sand, and the dry'd glue which so consolidates them, he forms a kind of coat or crust, which surrounds and covers every part of him, like a little ball of about five or six twelfths of an inch in diameter; wherein the insect takes care to reserve for himself sufficient room to move with ease and freedom. He is not contented, however, with bare walls, which would doubtless chill him after sweating; but spins out of his own bowels, a thread, which, with respect to the fineness of it, infinitely surpasses that of the silk-worm, whose operations we have already discoursed upon, and viewed with admiration. When he has thus manufactur'd a sufficient quantity, he fastens it first to one place, and then to a second, and glewing them one over another; by virtue whereof he furnishes his little retreat with pearl-colour'd satin hangings, which strike the eye in the most agreeable manner, and are fine beyond expression. In this operation, all the beauty and convenience lies in the internal part: There is no external appearance of anything but a little sand, which confounds the apartment of the lion-pismire with the earth, which lies round about him. By this artificial covering he lies conceal'd in safety from the injuries and insults of ill-designing birds. There he dwells in

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[1] I find that Pluche, in a late French edition of his "Spectacle", had corrected this observation on the sweating of the ant-lion. He noticed that the sand-grains forming the cocoon are spun together by the larva about to pupate.

obscurity, and lives in perfect peace and tranquillity; whereas he would be inevitably ruin'd and destroy'd, was the outside of his mansion embellish'd with any decorations that might attract the eyes of his enemies upon him.

"In this manner does he live attracted from the world, for six weeks or two months together, and sometimes more; and then resigns his eyes, his horns, his paws and his skin, which sink to the bottom of the ball, like a bundle of rags: There is nothing of him now remaining but a nymph, or embryo, with other eyes and paws, with other wings and entrails, all pack'd up and enclosed in a new skin, and conceal'd in a nutrimental fluid, in which the new animal gathers strength by slow degrees. As soon as the limbs of the new creature have acquir'd their due tone, and their necessary vigour, he pulls down the tapestry hangings with which his mansion is adorn'd, and forces his way through the walls that obstruct his passage by making use of his two teeth, which bear a near resemblance to those of a grasshopper. Now he uses his utmost efforts, enlarges the aperture, squeezes half his body through, and, at last, totally abandons his solitary apartment. His long form, which turns and twists like a *volute,* and takes up the space only of three-twelfths of an inch, begins to open and expand itself, and, in a moment, measures between fifteen and sixteen lines in length. His four wings, which were folded up, and took up no more space in the film that sheathed them, than two-twelfths of an inch, begin to expand themselves, and in less than two minutes become longer than his whole body. In short, the miscreant lion-pismire is transformed into a large and beautiful dragon-fly, who, after she has stood for some time motionless, and astonished at the glorious display of nature, claps her wings, and enjoys a liberty unknown before. With the tatter'd remnants of her first form, she has divested herself not only of her cumbrous weight, but likewise of her barbarous and bloody inclinations: She is quite another creature: And, in short, all gay and sprightly, noble and majestic.

"The insect that owes its being to the lion-pismire, deposits her eggs in the sand, in order that her young may be furnish'd with food as soon as it bursts its shell. For though sand is no part of its aliment; yet 'tis that by which it procures its daily subsistence. The insect at once sinks a little regular trench, and in a twinkling of an eye becomes an expert huntsman and an able geometrician."

It will be observed that Abbé Pluche extravagantly humanizes the ant-lion. He stresses its patience, artifice, deceit and abstinence; it combines the traits of an expert huntsman, an able geometrician and a miscreant with barbarous and bloody inclinations. It is, in modern terms, a schizophrenic criminal. No doubt, it was this anthropomorphic interpretation which made the study of the insect so fascinating to eighteenth-century readers. These seem to have been very numerous, if we may judge from Pluche's imitators, like de Beauvieu (1764) in France and Oliver Goldsmith (1774) in England, and the wide acquaintance with the habits of the ant-lion among people who commonly show no interest in natural history. This is suggested by the following anecdote in John Morley's 'Diderot and the Encyclopædists' (1923, p. 28): "Luckily for Diderot he was thus generous by temperament and not because he expected gratitude. In one case he had taken infinite trouble for one of these needy and importunate clients; had given him money and advice, and had devoted much time to serve him. At the end of their last interview Diderot escorts his departing friend to the head of the staircase. The grateful client then asks him whether he knows natural history. "Well, not much," Diderot replies; "I know an aloe from a lettuce, and a pigeon from a humming bird." "Do you know about the *Formica leo?* No? Well, it is a little insect that is wonderfully industrious; it hollows out in the ground a hole shaped like a funnel, it covers the surface with a light, fine sand, it attracts other insects, it takes them, it sucks them dry, and then it says of them, 'Mr. Diderot, I have the honor to wish you good day'."

The ant-lion was familiar not only to human parasites of the type described by Morley, but also to at least one of the philosophers of the early eighteenth century. That weirdest of French thinkers, Malebranche (1638-1715), in the eleventh dialogue of his 'Entretiens sur la Métaphysique, sur la Religion et sur la Mort,'[1] is not so much impressed by the behavior of the insect as by its usefulness as an example of preformation, or 'emboîtement.' Our modern biological notions of epigenesis, transformation, metamorphosis, elaboration and differentiation being quite foreign to Malebranche's theological mode of thinking, he adopts the opinion that the larval ant-lion really undergoes no transformation into the adult fly "but merely strips itself of its garb and arms; it casts its horns with the aid of which it makes holes and seizes the ants which fall therein." By this he does not mean, apparently, that only the dead cuticle is cast in the various ecdyses, as investigators have since shown, but seems actually to have believed that whole organs are discarded. He was, therefore, led to the utterly erroneous conclusion that the adult insect is simpler than the larva, and the larva in turn simpler than the egg. This is clearly asserted in the following passage: "Assuredly, Theodore, there is a greater diversity of organs in the *formica leo* than in the fly, and for the same reason in the silkworm than in the butterfly, for these worms also strip

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[1] I have been unable to consult the first edition of the 'Entretiens', which appeared in 1688, and surmise that Malebranche's account of the ant-lion, which is apparently drawn from Poupart's observations published in 1704, was first inserted in some one of the numerous editions published after that date. I find it in the final, revised edition of 1711.

themselves of many skins, because they give up a sort of head, a large number of feet, and all the other organs required for searching, devouring, directing and distributing the food adapted for grubs and butterflies. Similarly I see that there is more art in the eggs of grubs than in the grubs themselves, for, granted that the organic parts of grubs are in the egg, as you say, it is clear that the whole egg involves more art than does the grub alone, and so on *ad infinitum*." And since Malebranche accepted the Mosaic account of Creation about 4000 B.C. and believed that each female individual created at that time contained preformed the individuals of all future generations encapsulated one within the other, he bids us "admire, too, the variety of the organs of all the grubs and all the eggs which are contained in one another for all this time. Try to picture to yourself what the food could have been upon which the grubs and butterflies of today fed six thousand years ago. There is a great difference between the form of a demoiselle and that of a *formica leo,* but perhaps there is an equally great difference between the *formica leo* and the egg which contains it and so on."

Probably not mere coincidence but rather this extraordinary reputation of the ant-lion and later of the worm-lion were responsible for the fact that we owe the most important eighteenth-century contributions to our knowledge of these insects to five of the most brilliant and attractive personalities in the whole history of entomology. The coryphеus of this group and the one from whom the greatest influence radiated was Réaumur. He was, in my opinion, the most eminent naturalist of the century, but some confer this honor on Buffon. This is probably because Buffon dealt with larger animals, for the larger the organisms and the more they resemble man, the greater the glory they may be supposed to confer on him who chooses them for investigation. That Réaumur was the more gifted and independent observer hardly admits of contradiction, but Buffon's more copious rhetoric long served to conceal his defects as a naturalist and theorist from the littérateurs and nonscientific public, who, after all, have much to do with creating the posthumous fame of an author. Both Réaumur and Buffon were clever scientists and writers, or popularizers, and therefore followed subconsciously the best traditions of their country, which combined appreciation of literary form with eagerness for the new though still rudimentary science of the day. Our own age is making a similar and even more urgent demand for popularizers, but for a different reason. After a hundred and thirty years the sciences have become so vast, intricate and specialized and their vocabulary and symbolism so abstruse that the literary and general public find them incomprehensible and would naturally ignore them if the concomitant developments of technology were not a constant reminder of their abounding vitality. We witness, therefore, in all departments, the rise of scientists who no longer feel satisfied with the limited audience of their fellow investigators, but crave a wider hearing among a general public whose appetite for information is even keener than that of the nonscientific contemporaries of Réaumur and Buffon.

René-Antoine Ferchault de Réaumur was born at La Rochelle in 1683 and educated in the Jesuit College of Poitiers. He is said to have studied law. Nothing seems to be known concerning his adolescent predilections and ambitions. It is certain, however, that his interest in natural history and mathematics was aroused very early since he published two papers on mollusks and three containing original solutions of certain mathematical problems in the Mémoires of the Paris Academy of Sciences in 1708 and 1709. In the former year he was admitted to the Academy and was for nearly half a century one of its most ardent and illustrious members. Like many other eighteenth-century scientists he was remarkable for the versatility of his interests and achievements. A nobleman of ample means, he was able to devote his life to uninterrupted research at Paris or on some one of his estates. The more than one hundred articles and books which he published comprise many outstanding contributions on such very diverse subjects as the invention of a new thermometer, meteorology, new processes of making glass, porcelain, and steel, the tensile strength of fibres, the ductility of metals, the hanging of carriage-bodies and the fitting of axles, the artificial incubation of birds' eggs, the origin of turquoise, forest management, the preservation of museum specimens, the growth of the hard parts of mollusks and crustaceans, the regeneration of the appendages of the latter, the locomotion of marine invertebrates, the formation of pearls, the purple dye produced by certain snails, the silk of spiders, the luminescence of Pholas, electric phenomena in fishes, the digestion of birds, etc. But his work on the insects, largely embodied in his "Mémoires pour servir à l'histoire des insectes," originally planned as a work in ten beautifully illustrated quarto volumes, of which six were published from 1734 to 1742, was his most enduring achievement and has never ceased to arouse admiration. Unpublished fragments of the seventh volume were bequeathed on his death to the Academy. In 1926 I published the manuscript of one of these fragments on the ants and others are soon to be issued by French naturalists. Réaumur, as he advanced in years, became increasingly interested in the applications of physics, chemistry and biology. The insects seem to have attracted this great engineer because of their wonderful constructive activities. He called these activities 'industries,' and the biologist of the present day is merely using a different word when he speaks of them as 'behavior.' Réaumur died in 1757 as the result of a fall. For a more detailed account of his

FIG. 1. CHARLES BONNET
(*From a pastel portrait in the Public Library of Geneva.*)
(*After Claparède.*)

life and work I refer the reader to my volume of 1926.

Poupart's and Abbé Pluche's accounts of the ant-lion could hardly fail to arouse Réaumur's interest. He undoubtedly began to observe the insect long before 1740. His monograph far surpasses Poupart's in the detailed and accurate description of the larva, its behavior and its transformations. Indeed, the work was so comprehensive that all subsequent studies of the insect are largely amplifications, corrections and more careful analyses, with the aid of optical instruments and a histological technique unknown in Réaumur's time, of the morphological and behavioristic data which he accumulated. The memoir, illustrated by three admirable plates, also contains some observations obtained from correspondence with another eminent naturalist, Charles Bonnet, who had been observing the insect since 1737. We possess much more information in regard to Bonnet than to most of his distinguished contemporaries. Like Réaumur and several other versatile savants of the time, he left indelible marks of his genius on more than one department of knowledge. Early accounts of his life were written by H. B. de Saussure (1793), Trembley (1794) and de Pouilly (1794) and as late as the middle of the nineteenth century by the Duc de Caraman (1859), Sayous (1861) and others. Important studies of his work as a naturalist and philosopher were published by Lemoine (1850), Papillon (1876), Perrier (1884), Whitman (1895[a], 1895[b]) and Miall (1912), his political tenets have been critically examined by Humbert (1858) and Gaullier (1859) and his contributions to psychology by Offner (1893), Speck (1897), E. Claparède (1909), Pillsbury (1929) and others.

Charles de Bonnet was born in 1720 in Geneva of a Huguenot family that had emigrated from France soon after the massacre of St. Bartholomew. Like the sons of those other distinguished families, the de Saussures and the de Candolles, that produced so many illustrious scientists, he attended the college of his native city. His comments on the classical instruction he received are no more flattering than those of many other youthful geniuses, not to mention many dullards, who have been compelled to submit to their discipline. In his sixteenth year his interests were suddenly kindled by the reading of Abbé Pluche and Réaumur, and it was the former's account of the ant-lion, quoted above, that inspired him to become a naturalist. The episode is related by the Duc de Caraman as follows:

"The young Bonnet noticed the volume of Réaumur [probably the third volume of the Mémoires, which had just appeared in 1737] in the possession of his professor, M. de la Rive. He was able to gain a hasty notion of its contents, while it was lying open on the professor's desk during his absence; but what a difference it makes to a studious lad whether he reads thus by furtive snatches or actually possesses a book and is able to examine and study it every moment of the day and night! He therefore begged for the loan of the volume, but as he was regarded as merely a simple pupil, he was pitilessly refused. The professor did not suppose that a scarcely adolescent boy could be more than idly curious in regard to such an erudite tome. The professor replied, "Read the 'Spectacle de la Nature', which is more suitable for a youngster of your age." At the city library Bonnet made the same request and met with the same refusal. It was not till much later that the librarian, conquered by the most obstinate insistence, permitted him to carry off the precious volumes and read them at his leisure. Bonnet himself describes his experience on first reading Abbé Pluche's dialogue on the ant-lion: "I experienced on the instant a feeling which I can compare only with that experienced by Malebranche on reading Descartes' 'L'Homme.' I did not read the book, I devoured it. It seemed to me that I was developing a new sense or new faculties, and I should have announced willingly that I was just beginning to live."[1]

Before Réaumur's memoir on the ant-lion appeared, Bonnet had obtained some of the insects and had not only confirmed the observations of Poupart and Pluche, but had made some interesting discoveries of his own. The most important of these were finding a species of ant-lion (probably the larva of *Formicaleo tetragrammicus*), which walks forward instead of backward and does not make a funnel, and his famous 'Sisyphus experiment' on the common ant-lion. I translate Bonnet's lucid description of this experiment, which to my knowledge has been repeated only by McCook (1882, 1907) and Turner (1915) (see p. 136). "When an ant-lion that is busy excavating its funnel encounters a body that cannot be conveniently tossed out, he undertakes to transport it. It is well known that he is always hidden in the sand while he is working. At such times only his mandibles and head are exposed; but when he finds it necessary to transport some heavy body, such as a small pebble, out of his funnel, he leaves the sand and is no longer afraid to expose his whole body. Then he advances backward slightly, places the hind tip of his abdomen under the pebble and backs yet a little further. While he is performing these movements, his segments make corresponding movements which tend to guide the pebble towards the middle of his back and there retain it in equilibrium. But the great difficulty now is to keep it balanced while it is being carried backward up the steep incline of the funnel. At any moment the burden is liable to fall off, either to the right or to the left, or even to roll down over the back of

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[1] It is interesting to compare this statement with those of Fabre on first reading Dufour's article on Cerceris and of Forel on reading Pierre Huber's book on ants, in my volume on Réaumur (1926). Somewhat similar inspirations of young physicists and chemists are recorded by Oswald in his 'Die grossen Männer.' All these cases are decidedly suggestive of the well-known phenomena of religious conversion.

the insect. It is only by suitably raising or lowering certain parts of his segments that he succeeds in keeping the pebble poised on his back. Yet notwithstanding all his strength and notwithstanding all his dexterity as a juggler, the pebble sometimes escapes and rolls to the bottom of the pit. But the ant-lion is not discouraged; he returns to the task, again shoulders the pebble, redoubles his deftness and his efforts and finally succeeds in reaching the edge of the precipice with his burden. He does not leave the pebble exactly on the rim, because it might too readily fall back to the bottom of the precipice, but pushes it farther away. Then he at once turns about, retreats backward into the funnel and resumes his excavations. It will be readily seen that the shape of the pebble contributes no less than its volume and its weight to render its transport difficult. A pebble or any small body more or less spherical in shape is much more difficult to transport than a mass of the same volume and weight but of a flattened shape. I am unable to describe the interest of the observer while he watches an ant-lion engaged in this exacting performance. Our excitement grows apace and we are unable to lift our eyes from the insect for an instant as from moment to moment and most unexpectedly our solicitude for the tiny Sisyphus increases. His patient endurance of such strenuous labor is no less admirable than his skill. I have seen ant-lions shoulder their burdens five or six times in succession, either because the pebble had rolled down as many times or because I had substituted another pebble for the one that was being transported. One day I observed an ant-lion that was pushing for the second time a rather large pebble towards the rim of his funnel constantly follow on his upward journey the furrow he had traced in his descent. One would have said that he perceived the real advantage furnished by the borders of the funnel, since it is easy to see that they might serve somewhat to steady the pebble, or to prevent it from inclining too much toward one side or the other. Naturalists have extolled the strength of the ant when it carries or drags burdens, often for long distances and over a more or less uneven path, and it is true that the strength of this insect is amazing, but I am not sure that the strength of the ant-lion may not be even more wonderful. He is himself a rather small insect, weighing scarcely more than four grains when full grown, and yet I have seen an ant-lion of medium size pushing towards the rim of his funnel a pebble weighing two penny-weight, or forty grains."

In April, 1738, Bonnet set himself to observe the processionary caterpillars, previously studied by Réaumur, and was able to show that he had overlooked the silken threads which these social larvæ lay down as they move along in their devious paths and use as guides in finding their way back to their nest. This induced him to tell Réaumur about his discovery in a letter dated July 22, 1738. It was the beginning of a long correspondence, and though the two investigators never met, of an intimate friendship which ended only with Réaumur's death (1757).

The reply of Réaumur, then a celebrity of 55, to the callow investigator of 18, is worth quoting: "Had you not informed me that you are still a student in philosophy, I should not have believed it. You seem to me to be already a master in the observation of insects. The skill you display, and the pleasure you take in these observations convince me that your future efforts will enable you to discover many curious and hitherto unknown facts in the lives of these small animals. Your observations on the processionaries are of such a character that, had I known of them, I should not have failed to mention them when I discussed these caterpillars, and they are reported in a style which seems to me most apt, most lucid, precise and charming. I knew not that the processionaries belonged among the caterpillars that carpet their pathway with silk. The method you employed in disconcerting them, so that they failed to recognize their trail, is very ingenious. I am also greatly pleased with your other remarks, and since you really wish to call yourself my disciple, you are a disciple whom it will always be my glory to acknowledge. Your reasoning powers must quite exceed those we ordinarily find in youths of your age, since you prefer the pleasures of the mind to those many pleasures with which you cannot be reproached and which are of a nature to add nothing to our knowledge. It is therefore with great esteem that I have the honor to remain, etc."

Bonnet eventually pursued a course in law to satisfy his father, but it gave him little pleasure. At the age of 20, in 1740, he completed his important observations on the parthenogenesis of plant-lice. The paper was presented by Réaumur to the French Academy and Bonnet was appointed one of its correspondents. The works of his distinguished kinsman, Abraham Trembley (1710-1784) inspired him to investigate the phenomena of regeneration in Annelids. In 1744 he collected his various papers on insects and worms and published them as a volume entitled 'Insectologie.' Then poor health and failing eyesight, due partly to intensive use of the poor optical instruments of the time, set in and closed his brief and brilliant career as a naturalist, except for a late St. Martin's summer of research between 1770 and 1780, when he contributed several papers on the honey-bee, the fertilization of plants, the tapeworm and regeneration in snails and salamanders.[1] After 1744 he turned to psychology and philosophy and published several volumes entitled 'Essai de Psychologie' (1754), 'Essai analytique sur les Facultés de l'Ame' (1760), 'Considéra-

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[1] The peculiar infirmity with which Bonnet suffered during his later life consisted of visual hallucinations coexisting with a perfectly lucid appreciation of their character. This subject has been studied by the Genevese psychologist Flournoy (1901).

tions sur les Corps Organisés' (1762), 'Contemplation de la Nature' (1764) and 'Palingénésie Philosophique' (1769). They contain, among much speculation, now of purely historical interest, a number of brilliant passages, which, as Claparède has shown, foreshadow some of our most recent psychological and behavioristic conceptions.

During his long and placid life Bonnet seems never to have left Geneva. He died in 1793. On the occasion of his marriage in 1756 to Marie de la Rive, a lady of noble Genevese family, he received the following quaintly charming letter from his old bachelor friend Réaumur. "This news, Monsieur, which you thought would greatly surprise me and which, I confess, I did not expect, pleased me exceedingly. It is an inexpressible satisfaction to feel that the companion you did not choose till you had convinced yourself of the beauty of her soul and all the excellent qualities of her heart and mind, will bring you an increase of happiness that will endure as long as your days and hers. The feelings you entertain for each other rest on a foundation which the years cannot attack. The delight and sweetness which those years will shed on your companionship must therefore remain undiminished. It only remains for me to wish each of you a very long life and one whose termination will be the same for both. I flatter myself, Monsieur, that you will not permit Madame your wife to remain ignorant of how much you love me, and that she, far from being jealous, will be inclined to share in some measure in your feelings for me, especially if you will have the kindness to assure her that I am full of the greatest respect for her and that I shall be devoted to her, unreservedly and all my days, as I shall be yours, as long as life lasts, with the most perfect and tenderest affection, etc. Réaumur."

Though Bonnet's interests, after his short youthful period of biological research, were mainly philosophical, he nevertheless exerted a powerful influence on the younger

Swiss scientists of his time, especially on his wife's nephew, H. B. de Saussure (1740-1799) who was one of the earliest explorers of Mont Blanc, and who invented the hygrometer and accomplished work in physical geography and meteorology, and on the blind François Huber (1750-1831), one of the greatest pioneers in the study of the honey-bee. And it was the latter's son Pierre and the French entomologist Latreille who laid the foundations of myrmecology.[1] Since Pierre Huber (1777-1840) in turn greatly influenced Auguste Forel, we may trace the inspiration of Réaumur through Bonnet and an illustrious line of Swiss naturalists down to the present day. Similarly in France the inspiration of the great eighteenth-century naturalist passes through Latreille, Dufour and Fabre to Paul Marchal and many entomologists now living.

Réaumur had, undoubtedly, admirers and followers also in Germany, and one of these, Rösel von Rosenhof, was the next eighteenth-century naturalist to take up the study of the ant-lion. Born in 1705 in Nürnberg, he developed unusual talent as an observer and as a painter of miniatures. Unfortunately, his intense but rather brief activities were still further shortened by a right-sided hemiplegia from which he suffered during the seven years preceding his untimely death in 1759. Yet he produced many very careful studies of insects, fresh-water invertebrates, Infusoria, Amphibia and lizards and published them at intervals from 1741 to 1759 under the title 'Insekten-Belustigungen'. The accompanying plates are exquisitely beautiful. All the parts bound together constitute four volumes, to which a fifth was added by Kleemann, Rösel's son-in-law, from materials left after his death. Some of his herpetological observations were brought to light by Leydig

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[1] Claparède says: "The works of F. Huber, moreover, inspired those of his son Pierre, who did for the ants what his father had done for the bees. Pierre Huber was also largely influenced by Bonnet."

in 1878. Apart from Kleemann's brief biography in the fourth volume of the Belustigungen, the sources for a life of Rösel seem to be very meager. The best English account of this admirable investigator is that of Miall (1912). In the third volume of Rösel's work, issued in 1755, there is a fine article on the ant-lion, covering much the same ground as Réaumur's memoir, to which he repeatedly refers.

Most of the accounts of the ant-lion published during the latter half of the eighteenth century add little or nothing to the observations of Poupart, Réaumur, Bonnet and Rösel. This is particularly true of the writings of de Beauvieu (1764), Ledermüller (1762) and Reimarus (1798). Others (Geoffroy, 1761, and Barbut, 1781) are merely brief notices. An article by Sulzer (1776) is more important, because it calls attention to the Myrmeleontid larvæ that walk forward like other insects and do not make funnels and thus confirms the earlier observations of Bonnet and Réaumur on similar forms. The only reference I have been able to find to exotic ant-lions is Hughes (1750), who described the habits of the 'ground-ass', or 'lion-pismire', of Barbados as being essentially like those of the European species, and some observations made in Egypt by Hasselquist in 1762 and cited by Goeze (1773) in his German translation of Bonnet's 'Insectologie'. This confused account certainly does not refer to ant-lions, but probably to some species of termite (Hodotermes?).

The earliest publication on the worm-lion (Vermileo) is the following note written by an anonymous observer and hidden away in the Histoire de l'Acad. Royale des Sciences of 1706 (1731). "M. Poupart has given the history of the Formica-Leo in his memoirs of 1704, and we presuppose a knowledge of his work for the understanding of what follows. A friend of M. Carré, searching for these insects in the country, found a number of the pits which they make so adroitly, but most of them were without Formica-Leo, so

Fig. 2. QUEEN ULRICA LOUISA OF SWEDEN
(*Portrait from Arnheim.*)

that he was led to believe that they had become the prey of animals more leonine than themselves. He was soon undeceived when he noticed at the bottom of the funnels small worms about 6 lines long and half a line in diameter. He took some of them and placed them in sand, where he saw them make their pits in the same manner as the Formica-Leo. He threw into their pits ants, which the Formica-Leo is so fond of, and they seized them greedily by enveloping them with the anterior half of the body, for the other half remained embedded in the sand. Since their strength is not as great as that of the Formica-Leo, the prey often escapes, and in order to seize it again, they employ the same ruse: they steepen the walls of their pit, thus causing the animal to fall to the bottom. When these worms are fed to the Formica-Leo, it devours them, but this is not surprising because the Formica-Leo will devour individuals of its own species. These worms metamorphose into an insect very similar to a gnat, except that it is longer and stouter. The observer names them Formica-vulpes ["ant foxes"] to distinguish them from the Formica-Leo and to call attention to their *finesse*."

Réaumur informs us that the specimens described in the foregoing note were collected in the environs of Lyon. He also remarks that after seeking the insect in vain for many years, a curate by the name of Rebory sent him a number of specimens from Palud, in the Provence. For what seems to me to be an inadequate reason, Réaumur rejected the name 'ant-fox' suggested by the anonymous writer and substituted 'worm-lion', which was subsequently Latinized by Linnaeus as 'Vermileo'. The considerable number of specimens received from the Provence, enabled Réaumur to make a very interesting study of the insect's structure, metamorphosis and behavior. His paper published in 1753 in the Mémoires of the French Academy of Sciences is the last of his important contributions to entomology, and though written in his seventieth year reveals no impairment of his unusual powers of observation. I have devoted one of the Appendices of this volume to a translation of the work.

One of Réaumur's worm-lions was destined to fall into the hands of another great eighteenth-century entomologist, Charles Degeer,[1] and to become the subject of a second interesting memoir. To understand how this came about we must recall that the three 'enlightened' sovereigns of Prussia, Sweden and Russia, namely, Frederick the Great, Queen Ulrica and Catherine the Great, were keenly interested in the extraordinary cultural achievements of France and that their relations and correspondence with such thinkers as Voltaire, D'Alembert, Diderot, LaMettrie, Grimm, Madam Geoffrin, Maupertius, etc., are among the most interesting evidences of the intense intellectual awakening of the century. That Réaumur is to be included among these correspondents is clear from the following passage in his Vermileo paper: "I have since learned by experience that worm-lions can endure much longer journeys, even by post, than that from the Provence to Paris. There is every reason to suppose that they are not found in northern regions, or at any rate, they are unknown there, since Monsieur Linnaeus makes no mention of them in his 'System of Nature.' In Sweden reigns a queen whose most agreeable relaxation is the observation and admiration of the works of nature. Her taste has led her to assemble all kinds of such objects in cabinets, which she herself arranges and to which she resorts in such moments as she can spare from the arduous occupations of state. The worm-lions seemed to me worthy to engage the attention of one, who, I was sure, would not

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[1] In the zoological literature the name appears in various forms—De Geer, Degeer, de Geer, von Geer and Geer. Dr. Bequaert, while aiding me in correcting the proof of this book, calls my attention to a paper (Zool. Anzeig. 35, 1910, p. 521) in which E. Clément shows that the entomologist expressly wished his name to be written 'Degeer', because the 'De' is not the French 'de' or German 'von', but a part of the surname.

despise them on account of their insignificant dimensions, and one who beholds in the minutest of animated beings the limitless power and supreme intelligence of the Creator of the Universe. I was, therefore, emboldened to send twelve of the worms to this enlightened queen. Owing to circumstances which might have been avoided, only a single specimen reached the palace in Stockholm alive. It was graciously welcomed by the Sovereign who turned it over to M. De Geer to care for and observe. For either purpose it could not have been entrusted to a more competent person. Obedient to these enlightened instructions he was able to publish in the 'Memoirs of the Swedish Academy' his curious observations on that worm."

Ulrica Louisa (1720-1782), the queen to whom Réaumur sent the worm-lions, was the very gifted daughter of Frederick William I of Prussia and sister of Frederick the Great. Since not the least of her services to biological science was handing one of the French naturalist's specimens to Degeer, we may pause to describe her accomplishments in somewhat greater detail. Frederick William I and his queen Sophia Dorothea had ten children, five of whom became so celebrated that Woods (1906) in his 'Mental and Moral Heredity in Royalty' singles them out for special consideration and grades their intellectual and moral qualities on a scale of 10. Thus Frederick the Great is assigned 10 for intellect and only 4 for morality. The corresponding estimates of his brother and sisters are: Henry 9 — 9, Ulrica 10 — 10, Amelia 9 — 8, and Charlotte 8 — . Ulrica therefore not only had a perfect score, according to Woods, but her contemporaries would probably have given her another 10 for beauty, vivacity and personal charm. Even old Voltaire fell in love with her while he was at Frederick's court, and celebrated her unusual endowments in several poems. She in turn had the greatest admiration for his wit and intellect. Like him she was a deist and despised and ridiculed the Christian dogmas as mere superstitions. Stavenoe (1908) says that "in lieu of the positive doctrines of the church she adopted a purely rationalistic belief in a Supreme Being, and in lieu of a belief in immortality an abstract system of ethics. Among her intimates she criticized the intolerance and lust for power of the state church." She was courted by many notables but eventually married the crown-prince of Sweden, Adolph Frederick (1710-1771), and with her husband ascended the throne of that country in 1751. Voltaire called her the "Pallas Athene of the North", in contradistinction to Catherine of Russia who was styled the "Semiramis of the North." Soon after the beginning of her reign, Ulrica and the king became involved in the complicated struggles and intrigues between the Swedish francophile and russophile political factions, known as the "hats" and "caps" respectively. As the king was neither gifted nor energetic, Ulrica naturally became the center of the conflict, which lasted for many years and greatly embittered her life. Like her Hohenzollern kin, she had always been passionate, irascible, intriguing and inordinately ambitious, and the political situation in her adopted country seemed only to aggravate these qualities. Her memoirs, which cover the period from 1744 to 1762 and hence the most turbulent period of her reign, were not published till 1867-'72. They were critically examined by the historian Fritz Arnheim (1888) and found to be very misleading and mendacious. It would seem, therefore, that Wood's appraisal of her ethical qualities should be somewhat reduced. At this distance, however, we should not judge her too harshly, especially when we reflect that though sorely tried both as a sovereign and as a mother, she nevertheless found time and energy to correspond with the French savants of her time, to study history, mathematics, the natural sciences and the arts, to found (in 1753) the Swedish Royal Academy of Fine Arts and other institutions and to give personal encouragement to such men as Linnaeus, Degeer and Menanderjelm. The traits of her character which really interest us are best revealed in her letters, written during the beginning of her reign, to her mother, Sophia Dorothea. I quote portions of two among several from the collection made by Arnheim (1909-1910):

"Drottningholm, 6 Aug., 1751........I am well content here and enjoy the greatest quiet. I try to busy myself with agreeable and useful occupations, especially with my collection of medals, which is one of the largest. Beside that, I have been able to purchase in Holland two of the most beautiful collections of natural curiosities, one of which belonged to a man by the name of Skot, the other to Thenkaten (probably Lambert Ten Katen [1674-1731]). The collection of butterflies and insects from the Indies is extremely beautiful, and that of the shells is very complete. I amuse myself in classifying them with the aid of a professor from Upsala (Karl Linnaeus, 1707-1778, professor at Upsala; knighted as von Linné in 1762). He is a very amusing man, who possesses the *esprit* of society without its manners, and amuses me infinitely for both of these reasons. In the evenings he is required to walk with the King, and not a day passes that he does not find occasion to put everybody in good humor."

"Drottningholm, 5 Sept., 1752........During the entire week we have had the most terrible storms, so that I have had to deprive myself of my walks. I have passed the time in arranging my insect cabinet, and Linnaeus, professor at Upsala, is the one charged with this commission. He is a very amusing and intelligent man, but one has to overlook his manners which are somewhat boorish (*rustres*). I propose to have the whole collection engraved, not only the insects but also the shells, corals, petrifactions, minerals and marbles. This cabinet is very extensive and perhaps one of the largest in Europe. The examination of the infinite

Fig. 3. CARL DEGEER
(*Portrait from the seventh volume of his* "Mémoires pour servir à l'Histoire des Insectes".)

varieties that are found in Nature and each of which has its own utility, is a most delightful occupation." . . . .

I fail to find any mention of Charles Degeer (1720-1778) in Ulrica's letters, although he was Baron of Leutsta, Marshal of her court, Knight of the Polar Star and Commander of the Order of Wasa, and therefore could have lacked neither the *esprit* nor the manners of the very best society. We know from other sources that he was the great-grandson of Louis Degeer, who was called from Holland in 1632 by Gustavus Adolphus and greatly assisted him in establishing copper and iron smelters, gun-factories, a mint, schools and hospitals and in furthering commerce, industry and the arts in general. He was ennobled after acquiring great wealth and influence. Charles was born in Stockholm but was sent to Utrecht for the first years of his schooling. His interest in entomology is said to have been aroused by observing the habits of water-spiders when he was sixteen. Later he returned to Sweden and studied the natural sciences at the University of Upsala under Linnaeus, Celsius and Klengenstiern. On the death of an uncle he inherited the great iron mines at Dannemora and became one of the wealthiest men in the country. He expended large portions of his income, however, improving methods of mining, on works of philanthropy, such as repairing churches, founding schools and hospitals and bettering the conditions of the laboring class. At the same time he pursued his entomological investigations with great ardor and patience and eventually published them in seven quarto volumes. The first of these appeared in 1752, the last posthumously in 1778. Like Bonnet, Degeer kept up a long correspondence with Réaumur, for whom his admiration was so great that he chose for his work the same title "Mémoires pour servir à l'Histoire des Insectes." This masterly work, which was dedicated to Queen Ulrica, is illustrated with 238 plates and contains descriptions of more than 1,500 species of insects. Duncan's estimate of it and his comparison of Degeer and Réaumur, though published as long ago as 1840 and evidently drawn in part from an earlier biographical sketch of the Swedish entomologist by Catteau-Calleville and Walckenaer (1816), may still be accepted as adequate: "All naturalists competent to form an enlightened opinion on the subject, unite in admitting that these memoirs [of Degeer] are entitled to the very highest praise to which work of this description can lay claim. Both nature and fortune conspired to fit De Geer for successfully prosecuting the study to which he was so ardently attached. The natural endowments of his mind were of no ordinary kind, and the best education which the times could afford had the usual effect of strengthening and improving them, and adapting them to observe and discriminate with readiness and accuracy. His time was at his own disposal, and his ample fortune gave him the immediate command of everything that could facilitate his investigations. Such a concurrence of favourable circumstances does not often happen, and it is not often, therefore, that we can expect to be favoured with works of such value. They were combined, however, in the case of a contemporary of De Geer, the celebrated Réaumur, and, as it was the works of the latter which had the greatest influence in stimulating the zeal of the Swedish naturalist for the study, it is natural to institute some comparison between them. As a result of this comparison, it may be briefly affirmed, that Réaumur shows greater skill in making his observations, more felicity in planning experiments and a readier power of exciting interest in the narrative of them; but De Geer is less prolix in detailing the facts, more precise and infinitely more methodical. The absence of the latter quality in the French philosopher has rendered it impossible, in many instances, to determine the objects to which his observations refer. As a disciple of Linnaeus, De Geer could not fail to be early impressed with the value of system." Degeer's classification of insects is, however, in certain respects inferior to that of Linnaeus, though in others it represents an improvement, especially in his isolation of the Orthoptera, which Linnaeus confused with the Hemiptera.

Degeer's description of the single worm-lion which, as he informs us, he "received on April 8th (1751) from the hands of the queen, with the order to observe and describe it," was published in Swedish in 1752 in the Handlingar of the Swedish Academy of Sciences. A German translation was issued by A. G. Kästner in 1755. Finally, in 1776, Degeer rewrote the article in French, included references to Réaumur's observations and published it in the sixth volume of his "Mémoires", devoted to the Diptera. I present an English translation of the original article of 1752 in Appendix A of the present volume. Although the accounts of the worm-lion by Réaumur and Degeer are admirable, they are necessarily very fragmentary, owing to the fact that the larva of this insect, unlike that of the ant-lion, is of the Orthorrhaph Dipteran type and could not be adequately investigated with the rudimentary microscopic technique of the day. Hence, both Réaumur and Degeer not only overlooked certain significant morphological features but, as we shall see in a later chapter, actually mistook the ventral for the dorsal surface of the larva!

After these publications no further observations were made on the worm-lion during the eighteenth century, although brief résumés of Réaumur's account appeared in the writings of Bonnet, Rösel von Rosenhof and Herbst (1784).

CHAPTER II

THE FAUNA OF THE SANDS

ONE OF the most impressive characteristics of living organisms is the expansive, irrepressible, reproductive urge which impels them to invade, preëmpt and exploit the most diverse environments and to transcend almost incredible æons of geologic time. As J. Arthur Thomson (1920) says: "Living creatures press up against all barriers; they fill every possible niche all the world over; they show that Nature abhors a vacuum. We find animals among the snows on Monte Rosa at a height of over 10,000 feet; we dredge them from the floor of the sea, from those great 'deeps' of over six miles where Mount Everest would be more than engulfed. It is hard to say what difficulties living creatures may not conquer or circumvent. . . . When we consider the filling of every niche, the finding of homes in extraordinary places, the mastery of difficult conditions, the plasticity that adjusts to out-of-the-way exigencies, the circumvention of space (as in migration), and the conquest of time (as in hibernation), we begin to get an impression of the insurgence of life. We see life persistent and intrusive — spreading everywhere, insinuating itself, adapting itself, resisting everything, defying everything, surviving everything."

If the casual observer is less impressed than the professional biologist by this astonishing aspect of living organisms, it is, perhaps, because his acquaintance is confined to the more conspicuous animals and plants of his own environment and these have ceased to inspire any but a practical or esthetic interest. But his wonder is apt to be aroused when he encounters organisms that can manage to survive and multiply in environments so unusual as dark caverns, the intimate recesses of the soil, the abysses of the ocean, in concentrated brine and even crystallized salt, crude petroleum, hot springs, desiccated wood, horn, wool and meal, in the hot, dry shifting sands of deserts and the hostile and unstable social medium of fierce ant, wasp and termite communities. And more intimate acquaintance with the organisms most exquisitely adapted to living under such difficult conditions is sure to arouse a peculiar feeling of the sinister, malignant, weird or supernatural, or what Goethe called the 'demoniac'. These terms are all fine examples of the besetting vice of verbalism, of the tacit assumption that there must be an actual objective existent corresponding to a mental process or state, because we can coin a name for it. If this be borne in mind, there is no reason why we may not designate as demons animal organisms that exhibit disconcerting or even monstrous forms and behavior as a result of their structural and functional adaptation to extreme environmental conditions.[1]

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[1] The 'demons' of this volume are the inhabitants of extreme desertic environments, sand and dust. It is scarcely necessary to state that the word 'demon' is here used metaphorically and in the modern sense of a 'malevolent being'. The term has suffered many changes of meaning. To Homer and Hesiod it meant a benevolent supernatural being, or god, and when Socrates spoke of his δαιμων he obviously meant a benevolent spirit like the guardian angel of the devout Catholic. "In truth", as Clemenceau says, "gods and demons are all one — since good and evil (that we turn into active personalities) are nothing but our own subjective states. All gods, benevolent or malevolent, result from the same failure to analyze the facts. A good god was not obliged to create evil spirits any more than he was obliged to create the evil they perpetuated in the name of his divine

This volume deals mainly with two unrelated groups of insect demons which have acquired a very similar type of behavior as the result of living in dry dust or sand which, as Buxton (1923) says, "is in many ways the most hostile of all environments," for as he remarks later in his fine treatise, "sand probably presents more difficulties to the desert flora and fauna which attempt to colonize it than does any other type of desert. It is not, therefore, to be wondered at that the fauna of sandy areas, and particularly of areas in which the sand is loose, is a small one, and that it consists largely of animals which in overcoming the difficulties of life in sand have become unfitted for life in any other environment." It seems advisable, therefore, to devote a chapter to a general description of sand as an ecologic environment as it exists in deserts, dunes, sea-beaches and river washes, and to a hasty review of its inhabitants, the *psammophiles*. Since the sand is essentially a desert environment, even when it occurs in small stretches, it is impossible to draw a hard and fast line between the psammophiles and the xerophiles, or desert organisms in general. Sandy deserts, as we have seen, are really deserts of the extreme type. The total area of deep sand on our planet is difficult to estimate but it must comprise hundreds of thousands of square miles. Most of it is in the temperate zones and much of it is included in the Great Palæarctic Desert, stretching from Morocco to India and Central China, in the deserts of Texas, Arizona, California and Mexico and in those of Central Australia, Southwestern Africa and Western Argentina, but there are, of

charity." It seems that when one religion is supplanted by another, its gods are degraded to the rank of evil demons, or devils. In this matter Christianity has been only too willing to follow the usual practice. But long before recent religions adopted this course, there seem to have been certain kinds of Egyptian and Sumerian demons that were not debased gods of other religions. The patron-demon of the creatures considered in this book is the ancient prototype of Satan, Set, whom the Egyptians, according to G. Elliott Smith ('The Evolution of the Dragon,' 1919, p. 132), believed to be personified in all desert animals.

course, many detached dunes, sandy beaches and river washes in all parts of the world and often adjacent to or surrounded by moister (mesophytic) areas.

Though the number of psammophiles in any one region may be small, their total number in all the continents is considerable, though our present knowledge of their ecology is still fragmentary. Many of the known forms, however, are so interesting that I trust my calling them demons will not deter my readers from seeking their acquaintance. The demons and devils of the religious of all times are mere illusions and word-symbols, though they have been converted into objects of fear and hatred, and of propitiatory and exorcistic rites without number. We can adopt a saner attitude towards the demons of the dust, because they are real things that can be carefully investigated and understood and hence forgiven, admired or perhaps even loved.

Unlike other types of soil, the deep sand of dunes and deserts represents a unique environment on account of its physical and chemical peculiarities and the way it is affected by moisture and insolation, *i.e.,* exposure to the sun's heat and light.[1] Its particles are not only very readily displaced by the wind but afford a very easily penetrated, though when dry a too friable, medium for burrowing animals. Water percolates very rapidly through it, so that in deserts, where rains are very infrequent, it may dry out to considerable depths, though in our northern dunes and beaches, which receive more copious showers, it usually remains moist to within three or four inches of the surface (Hart and Gleason, 1907). Since common sand is largely silica it forms a poor soil for plant growth and is rendered even more unfavorable by the leaching action of the rain on any salts that might serve as plant foods. Hence the sparse, bunched and

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[1] For succinct statements on sand as an ecologic environment *see* Walsh (1925). King (1914) may be consulted for comparative data on sand as compared with other kinds of soil.

stunted growth of the vegetation in sandy regions. Its greater luxuriance on some of our northern dunes is due to the above-mentioned retention of moisture and dissolved salts near the surface. According to Hart and Gleason, this "water supply in the sand-dunes (of Illinois) is reasonably constant, and the plants owe their xerophytic habit to the rapid loss of water by transpiration, and not to a deficient soil content." For the fauna, however, the problem of the water supply is more serious. The plants can extend their roots to a considerable depth or store quantities of water in their tissues, but the psammophilous animals can obtain it only in the fugitive form of dew or raindrops or from the tissues of their animal or plant food.[1]

Even more important is the effect of the singular daily and annual fluctuations of humidity and temperature in the sand environment. These fluctuations have been measured by Williams (1923) and Buxton in the Egyptian Desert, by Chapman and his collaborators (1926) in the sand dunes

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[1] In this connection Buxton's observations (1924) on the absorption of nocturnal moisture by the dry vegetation in the Great Palæarctic Desert are of unusual interest. He found "that there is a great range in relative humidity between day (dry) and night (damp), and that the night air is often nearly or quite saturated with moisture, even though by day the humidity may drop to 20 per cent. Now it appears that the desiccated fragments of the annual vegetation are hygroscopic; that they take up a considerable proportion of water from the damp or saturated air at night, and hold it for several hours after the sun has risen. It seems to me that this property of the dried pieces of grass and herbage is probably one of the foundations which support all animal life in deserts during the summer. The pieces of straw, with the moisture absorbed the previous night, are eaten by grasshoppers, harvesting ants, etc. They in turn become a source, not only of food, but also of water for the birds, lizards, predaceous ants, mantids, Carabid beetles (Anthia, etc.) and other carnivorous creatures." Buxton determined experimentally "(1) That the hygroscopic property of the fragments was active at 80 per cent and all higher humidities; therefore, this source of water may be available even if no dew falls for months on end, provided that humidity at night rises to at least 80 per cent. (2) That when these fragments are saturated with moisture they hold as much as 50–60 per cent of their own dry weight.... (3) That fragments collected at 2 P.M. on a summer's day at the bottom of a hot deep valley still contained 60 per cent of water; therefore several hours of sunshine are not sufficient to dry the material."

of Asoka County, Minnesota, and by Kashkarov and Kurbatov (1930) in the Central Kara-kum Desert of Western Turkestan, with remarkably similar results. Everybody is familiar with the fact that sand exposed to the sun rapidly acquires a high temperature and cools off rapidly at night. It is not so generally known that the high diurnal temperature is confined to the surface layer of the sand and that the air above and the lower layers of sand show a rapid diminution in temperature away from the surface in both directions. This is well illustrated by the following table from Chapman's paper.

DISTANCE INCHES	TEMPERATURE			
	Raining	Clear	Clear	Clear
24 above surface.....	16°C.	25°C.	31°C.	31°C.
12 above surface.....	18	27	31	31
6 above surface......	18	31	—	—
3 above surface.....	19	32	34	33
1 above surface......	19	43	41	40
Sand Surface........	22	51	47	50
1 below surface......	23	42	40	45
2 below surface......	23	40	38	43
6 below surface......	23	38	38	40
12 below surface......	22	39	38	40

It will be noticed that on clear days the temperature of the air only one inch above the sand may be actually as much as 10°C. cooler than the surface and that there may be a difference of 10°C. or even more between points at the surface and at a depth of two inches. The following table from the same authors shows that the air temperatures three to six inches above the surface may remain stationary during the hours from 5.50 A.M. to 9.15 A.M. on a warm day, while the surface temperature is rising from 16°C. to 37°C. During the same period the temperature 12 inches beneath the surface rose from 16°C. to 27°C.

DISTANCE INCHES	TIME						
	5.50 A.M.	6.15 A.M.	6.45 A.M.	7.30 A.M.	8.15 A.M.	8.45 A.M.	9.15 A.M.
24 above...	23	23	24	24	23	23	23
12 above...	24	24	24	24	24	24	24
6 above...	24	24	24	24	24	24	24
3 above...	23	24	24	24	24	24	24
1 above...	18	19	20	23	25	25	27
Sand Surface	16	18	22	25	30	25	37
1 below...	16	18	22	25	28	28	31
2 below...	16	18	23	24	27	28	30
8 below...	16	17	23	24	26	26	28

Of the temperature measurements made by Kashkarov and Kurbatov in the Kara-kum Desert I cite only those given for April 28. They found the temperature of the air at noon 2 m. above the surface to be 29°C., at 5 cm. above the surface 33°, at the surface 52.5°, at a depth of 10 cm., 27.8°; at 20 cm., 21.60°; at 40 cm., 21.4°; and at 90 cm., 18°. They also took temperature and humidity measurements on and above the surface of the sand, both on the summits and slopes of the dunes and on the "takyrs" (perfectly flat clayish areas in the sand desert) with the results shown in the following table:

TEMPERATURES, IN DEGREES C., AND HUMIDITIES, ABSOLUTE AND RELATIVE, ON SAND DUNES AND "TAKYRS"

APRIL 28	SUMMIT	SLOPE	"TAKYR"
7 A.M.			
Temp. 2 m. above surface..	18	19	19
Hum. 2m. above surface...	7.5/49%	12.1/74%	9.4/58%
Temp. 5 cm. above surface	19	20	20
Hum. 5 cm. above surface..	8.2/50%	14.4/83%	9.5/55%
Temp. at surface.........	22	24	20
1 P.M.			
Temp. 2 m. above surface..	31	30	30.5
Hum. 2 m. above surface..	5.4/16%	10.1/32%	9.2/33%
Temp. 5 cm. above surface	35.6	36.5	35
Hum. 5 cm. above surface..	6.9/16%	12.7/29%	6.9/16%
Temp. at surface.........	55	58.5	41
9 P.M.			
Temp. 2 m. above surface..	24	23	24
Hum. 2 cm. above surface..	5.7/26%	10.1/48%	5.7/26%
Temp. 5 cm. above surface	23.2	23	23.5
Hum. 5 cm. above surface..	6.2/30%	14.4/69%	6.2/30%
Temp. at surface.........	23	22	21

It will be seen that there are considerable differences in both temperature and humidity between the dunes and takyrs, between the summits and slopes of the dunes and between the hours of the day. The humidity differences are greatest at midday.

The annual range of the surface temperature may be very great even in our northern sand dunes. Chapman gives the extremes for the region which he investigated as —40.56°C. in winter and 74°C. on July 23. Even higher temperatures are cited by Buxton, according to whom "the highest readings which have so far been taken of the surface of the soil were taken on bare sand; *e.g.*, readings of 183°F. (84°C.) on the Loango Coast, close to the Equator, and Augiera's record of 172°F. (78°C.) on a sand dune in the Sahara. The surface soil reaches such a high temperature by day that it does not cool completely during the ensuing night: as a result the minimum temperature reached by the surface of unshaded soil at night may be several degrees above the minimum temperature of the air (C. B. Williams). It is only the superficial layer of the soil which is liable to these great fluctuations of temperature."

The effect on the insect fauna of this surface layer, which is the seat of such rapid and extreme fluctuations in temperature has been studied by Chapman and his colleagues. They find that it is responsible for the existence of two quite distinct faunas, one of which is active only at night and burrows into the sand before it becomes heated in the morning, and one that is diurnal and has either acquired a considerable tolerance of high temperatures or has resorted to peculiar behavior suited to their avoidance. One of the most characteristic nocturnal forms is the tawny Carabid beetle, *Geopinus incrassatus,* which ceases all its other activities and promptly digs into the sand about sunrise. The solitary wasps which provision their larvæ in burrows with dead or paralyzed insects, are enabled to dig through the hot surface layer by repeatedly flying up into the air and cooling off. Other diurnal insects save themselves from the heat by climbing the vegetation. "In the normal course of the day all insects leave the surface of the sand when its temperature nears 50°C. (122°F.)." Chapman and his colleagues observed that all the diurnal psammophiles with which they experimented by confining them to the surface by clipping their wings, etc., died when this temperature was reached or slightly exceeded. This thermal death point agrees very closely with Brues' observations (1927, 1928) on the lethal temperatures of hot springs, with the observations of Graham (1921, 1923, 1924) on insects living under the bark of logs lying in the sun and the experimental temperatures applied by several observers to insects of various orders. Barber (1928) has recently shown that all corn-borer larvæ are killed in 15 minutes when subjected to a temperature of 54°C. and in only 5 minutes at a temperature of 68°-70°C. Similar results were also obtained by J. R. Parker (1930), who found that the eggs of two species of grasshoppers, *Melanoplus mexicanus* and *Camnula pellucida,* are killed after two hours' exposure to 50°C., and that the nymphs show the first signs of heat rigor at 49°-52°C. and complete heat rigor at 53°-54°C. In adults the latter condition sets in generally at 56° to 58°C. Although the eggs of these insects are laid near the surface, the highest temperature to which they would be subjected in Montana at a depth of 2 inches in the soil is 37.2°C., which is far from being lethal.

Buxton (1924) found insects active in the deserts of Palestine at midday in summer when the soil temperature usually reaches 60°-62°C. The Tenebrionid beetle *Zophosis punctata* is common at all times of the day when the soil has this temperature, and *Messor barbarus* and some other ants may walk in the sun when the soil is 50°-55°C. By inserting a very delicate thermometer into the bodies of some of the larger insects such as grasshoppers and the Tenebrionid Ademsia he was able to demonstrate that their body temperature was always some degrees below that of the soil and conjectured that this might be due to evaporation of water in respiration.

Owing to the pronounced fluctuations of temperature at the surface of sandy areas, the supernatant atmosphere is kept in constant movement. The heated air streams upward, producing vortices and violent winds. The dryness of the air, moreover, and its movement bring about rapid evaporation and favor the transmission of the heat, light and ultra-violet rays, for, as Buxton says, "all these rays, but particularly the ultra-violet rays, pass more readily through dry than through damp air; their effect on plants and animals is, therefore, much more potent in summer than in winter, for in summer the days are longest, the sun most nearly vertical at midday, clouds are absent, and the amount of water-vapour in the air at its lowest." Some of the psammophiles seem to possess structures or pigments that shield them from the ultra-violet rays, and V. E. Shelford (1910) has reported experiments indicating an adaptation of certain species to the high evaporation in their sand environment. He finds that "forest (low evaporation) animals turn away from air of high evaporating power, and show a preference for air of low evaporating power. Thus *the type of reaction is definitely related to the usual habitat of the animals.*" Actual morphological modifications for preventing evaporation of the body-fluids seem to occur in the large black Tenebrionid beetles which are so common and conspicuous, both in the Great Palæarctic and our Southwestern Deserts. Blaisdell (1925) maintains that "the species inhabiting some of these hot, dry regions (the Maricopa and Colorado Deserts) exhibit a wonderful adjustment to their environment. The teguments are adapted to meet the demands against evaporation and conserve the body fluids. This is secured by the manner in which the large mentum makes it possible to close the buccal aperture, and the interlocking of the last ventral segments and the lower margin of the epipleura at the elytral apex, especially in the Eurymetopini, practically sealing up the body against the drying effect of the desert."

Desert and dune, when not the scene of unusual atmospheric disturbances, seem to be the most stable and reposeful of environments, because the temperature, humidity and evaporation fluctuations, though incessant, are invisible. The landscape seems to owe the little vitality it possesses to the diurnal cycle of its illumination. In extremely arid regions even the sparse vegetation is rigid and motionless, as if congealed or fossilized, and of a dull terre-verte, drab or dun color, like the soil into which it seems to merge. In many of the plants the leaves are small, thick or covered with gray or white hairs (tomentum) as a protection against excessive transpiration, in others the stems or roots are enormously enlarged for the storage of water, in still others the foliar structures are replaced by horrid spines. All this spininess, water-storing obesity and monumental rigidity and repose are most extreme in the cacti of our American deserts, but the same peculiarities are conspicuous in the desert plants of other continents. The fauna, which is even sparser than the vegetation, seems to imitate some of its anomalies. Very many of the desert lizards are roughly scaly and spiny and like the birds and mammals affect the pallid gray or tawny hues of the soil. Quite a number of the exposed diurnal insects are clothed with white hairs not unlike the tomentum of the desert plants. To one familiar with the desert biota the dependence of all these characters on the peculiarities of the surroundings is so obvious that he fails to understand the modern laboratory and closet biologists who minimize or even ignore the effects of environment and its phylogenetic significance.

We infer from the taxonomic, or natural affinities of the animals and plants of any desert or considerable sand area that we are dealing with species or the descendants of species which once inhabited the neighboring more humid regions. In other words, the xerophiles and psammophiles are derived from mesophiles, or more moisture-loving forms that have immigrated from time to time into arid environments and have gradually become adapted to them during long periods of geologic time. It would seem that we might be able to determine the approximate sojourn of each species in such unfavorable conditions if we could measure the degree of its adaptation, but a moment's reflection shows this to be an unreliable criterion, not only because species vary so greatly in their innate, or constitutional adaptability, or plasticity, but also because a particular adaptation may be functional rather than structural. Thus in avoiding the very unfavorable conditions of its arid environment one species may rely more on behavior, another on the peculiarities of its anatomical structure. Most insects, as we have seen, avoid the hot surface layer of the soil by foraging only at night or by rapid burrowing, others by rising from time to time on their wings into the air, others by climbing the plants, while the large flightless beetles and grasshoppers and the lizards simply raise themselves on their long legs and thus avoid the overheating of their body-fluids. In all these cases the adaptations, or adjustments are purely behavioristic, but, as will be shown in the sequel, there are also many morphological devices for meeting the peculiarities of the sandy habitat. It is clear that certain species of plants and animals even in moist, or mesophytic regions are more resistant than others to droughts, and it is precisely these drought-resistant forms that seem to be able to colonize the arid tracts. Such forms would be described by some biologists as 'preädapted' to life in deserts or sand dunes, but the concept of 'preädaptation', like 'predestination' and 'potentiality', savors of the metaphysical or mystical and should be avoided.

Since the animals of the sands have been less studied than the plants of the same environment, I here introduce a general survey of the psammophile fauna, which the general reader may be inclined to omit. He may find it interesting, however, if he will fearlessly turn on his superiority complex, treat my array of generic and specific names disdainfully as so many repulsive but necessary symbols, and fix his attention on the red thread of unusual adaptations that runs through the whole account.

The lower Invertebrate animals are represented only by certain Protozoa and Mollusca. According to Buxton, "the Protozoa of the sand in the neighborhood of Cairo have been investigated by Thomson and Thomson. These microscopic animals exist in the dry sand in a resistant envelope or 'cyst' from which they only emerge when the sand is moist, and as it dries they again envelop themselves in 'cysts.' In the climate of Cairo their period of activity is reduced to a few days a year, and their period of dormancy is extremely protracted. They are exposed to light and heat and drought in the sand, and yet the investigators were able to recover about fifty species from the sand after eight months of drought. Most of them belonged to forms known elsewhere from fresh water; that they were dependent on occasional moistening is shown by their great rarity in the sand of Luxor in Upper Egypt, in an area which is without rain in the average year." I have seen no accounts of the desert snails, but in a sandy desert between Marrakech and Mogador in Morocco, I encountered numerous shells of a large species of Helix, in many of which small desert bees of the genus Osmia had made their nests. Of course, the living snail is able to tide over the hot, dry season by withdrawing into the innermost whorls of the shell after secreting a thick lid, or epiphragm over its orifice. In another locality, near Agadir, I saw enormous numbers of a small Helix, all snugly aestivating and attached by means of their epiphragms to the stems of the desert shrubs.

Nearly the whole psammophile fauna belongs to two phyla, the Arthropoda and the Vertebrata, and, of course, the majority of the Arthropod psammophiles are insects. There are, however, several Myriopods and Arachnids, *i.e.*, centipedes, spiders, scorpions and Solpugids that live in the sand. Several of the insect orders contain whole groups of species or even genera which are arenicolous. The psammophile Coleoptera, or beetles, belong mostly to four families, the Cicindelidæ, Carabidæ, Tenebrionidæ and Meloidæ. Most Cicindelidæ, or tiger-beetles, frequent dry, open soil, but some of our North American species, especially *Cicindela lepida, generosa, repanda, lecontei* and *cuprascens* are very active and conspicuous diurnal hunters of other insects on dry sand. Other species, such as *C. hirticollis,* prefer the damp sand of lake beaches. The Cicindela larva, which is as predatory as the adult, inhabits a long tubular burrow in the sand and near the surface lies in wait to capture small passing insects. According to V. E. Shelford (1908) the burrows of *C. lepida* and *generosa,* two of the most pronounced psammophiles in the genus, differ in a peculiar manner. The burrow of the former "is of such a type that the sand closes it and the larva is unable to feed much of the time," but the larva of the latter is always found in sand that is slightly shifting. "The great size of the hole would cause it to fill up with the sand moved about by the wind and thus make the animal a great amount of labour. Each larva cements the sandgrains with saliva. Accordingly its hole and pit near the opening are quite firm and the wind does not ordinarily disturb them. . . . This type of burrow possesses advantages in securing prey; the pit acts as a pitfall for small animals."

The Carabidæ of the sands are also predatory and comprise, besides the previously mentioned *Geopinus incrassatus* and several species of Harpalus and Anisodactylus of similar yellowish brown coloration and nocturnal habits, certain small forms of the genus Bembidium, which hunt on the surface of the sand during the day. The Tenebrionidæ, unlike the preceding, feed on vegetable detritus and are represented by two common species, *Opatrinus notus* and *Blapstinus interruptus* in the Illinois sand dunes (Hart and Gleason, 1907), but the family attains its most remarkable development in the deserts of both hemispheres. There are representatives of at least twelve different subfamilies, and of numerous genera in the Great Palæarctic Desert and the deserts of South Africa and Australia. Three other subfamilies are represented in the deserts of Arizona, California and Mexico. These beetles are very conspicuous on account of their large size and black color. They are not only apterous but, according to Blaisdell, have the wing-cases fused in the mid-dorsal line and enveloping the abdomen in such a manner as to protect the body from undue evaporation. Buxton (1923, 1924) gives an interesting account of some of the Palæarctic species. He was able by means of a small thermocouple inserted in the abdomen of one of the forms, *Ademsia ulcerosa,* to demonstrate that its body temperature was actually lower (36°-39.5°C.) than that of the substratum on which it rested (38°-44°C.)

I believe that the two species of the singular Meloid genus Cysteodemus, which occur in our southwestern deserts, must be regarded as true psammophiles. They resemble the desert Tenebrionids (subfam. Eleodinæ) in being wingless and in having the elytra inflated, soldered together and encasing nearly the whole abdomen. I have found *C. armatus* (FIG. 4) common near Palm Springs, California, in late April, running over the hot sands of the Mojave Desert. According to E. C. Van Dyke (1928), it may also be found on the grease-wood bushes (*Larrea tridentata* var. *glutinosa*). The female lays her very numerous, minute, white eggs in the sand, near the base of a grease-wood bush. Probably as in other Meloidæ the minute triungulin larvæ parasitize the larvæ of other desert insects, but whether the hosts are bees, wasps, or grasshoppers is still unknown.

Among the Isoptera, the termite *Reticulitermes tibialis,* hitherto regarded as a western species, has been recently found by Park (1929) to be very abundant in the upper beach and dune sands of Lake Michigan in Illinois and Indiana. Among Orthoptera several psammophile grasshoppers (Acridiidæ), which feed on the dune or sea-beach vegetation, are cited by Morse (1904): "On the drifting sands of the beach at Cape Henry, between the shore and the dunes, may be found *Trimerotropis maritima,* the maritime or sea-side locust, occurring coastwise from Southwestern Maine at least as far as North Carolina, and also along the Great Lakes. This species is unknown from inland localities, save as noted. Its congener, *T. citrina,* however, is found throughout the larger part of the central zones of the Southeastern States wherever the physical condition of

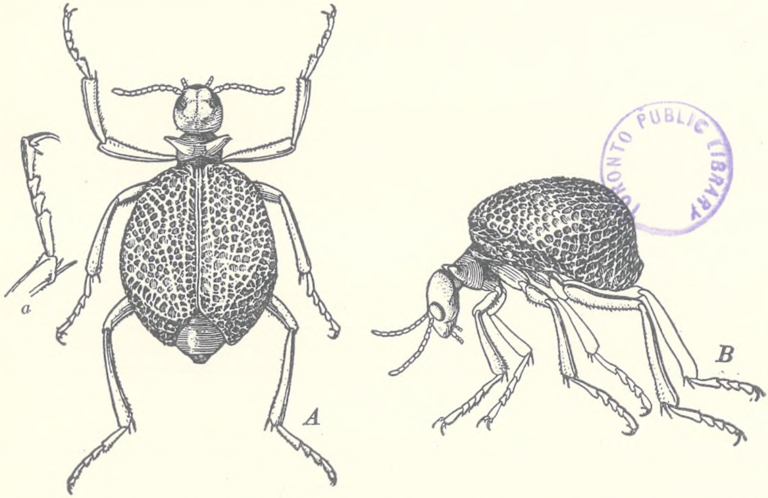

FIG. 4. *Cysteodemus armatus* Lec., a psammophilous Meloid beetle from the Mojave Desert; A, dorsal; B, lateral view; *a,* posterior tarsus. (After E. C. Van Dyke.)

the soil presents a suitable environment, being just as much at home on dusty roadsides, sun-beaten waste lands and the sandy river washes of the interior as under the nodding sea oats (*Uniola paniculata*) of the Virginia Cape, the palms of Tybee, or on the snow-white strand of Fort Barrancas. On and near the coast *Psinidia fenestralis* and *Scirtetica picta* are frequently associated with it." Hart gives a long list of grasshoppers from the sandy areas in Illinois, including the above mentioned *T. citrina* and *Ps. fenestralis,* and Chapman mentions the dune grasshoppers, *Spharagemon æquale* and *Caloptenus flavidus,* as peculiar to the dry blow-sand of the Anoka County dunes of Minnesota. He noticed that the former insect "would rise up on its feet, thus lifting its body off from the hot sand when its temperature reached 50°." Several of these grasshoppers are characterized by a very pronounced 'protective coloration', like the sand on which they rest. Hart cites as conspicuous examples *T. citrina* and *Spharagemon wyominganum.* In a recent paper, Grassé (1929) records some 16 species of Acridiidæ and Locustidæ as inhabiting the sand dunes of Languedoc in Southern France. Several crickets (Gryllidæ) also live by preference in the sands of dunes and beaches.

Hart also gives a long list of Heteroptera and Homoptera collected on the sparse vegetation of the Illinois dunes. The most conspicuous Homopteran family, the Cicadidæ, is known to include several xerophiles and psammophiles. Osborn and Metcalf (1920) and Metcalf and Osborn (1920) have published interesting notes on *Tibicen viridifasciata,* which inhabits the littoral dunes of North Carolina. The larvæ live in the sand, even where it may be reached by high tide, and feed on the roots of the sea oats (*Uniola paniculata*). According to Myers (1929), another cicada, *Melampsalta leptomera,* inhabits the sand dunes at Wellington, New Zealand, and in the larval stage feeds on the roots of marram grass (*Psamma arenaria*). The genus

Melampsalta, as this investigator has shown, comprises a confusing wealth of species, many of which occur in the xerophytic plains of Australia, though several have become adapted to rain-forest conditions in New Zealand.

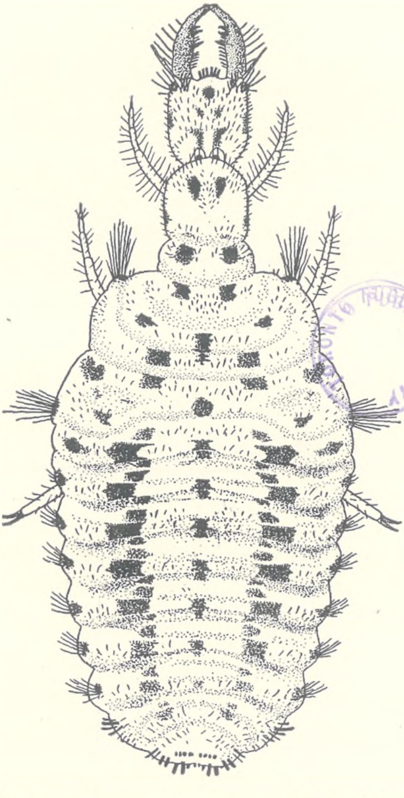

FIG. 5. Larva of an ant-lion (*Hesperoleon intermedius*) from the sands of the Mojave Desert.

Among the Neuroptera the outstanding psammophiles are the ant-lions of the family Myrmeleontidæ, the larvæ of many species of which nest by preference in sand or dust. Thus the larvæ of the little ant-lion, *Cryptoleon signatus* inhabits the sand dunes of Ipswich, Massachusetts, and the pits of another very pale larva, *Hesperoleon intermedius* (Fig. 5), are extremely abundant in the sands of the Mojave Desert of California.

The Diptera are represented by members of several families, notably the Rhagionidæ (Leptidæ) of the genera Vermileo and Lampromyia, to be discussed in detail in later chapters, the Asilidæ, Therevidæ, Dolichopodidæ, Bombyliidæ, all members of the suborder Orthorrhapha and the family Ephydridæ of the great suborder Cyclorrhapha to which our common houseflies, blowflies, etc., belong. The Asilids, or robber flies, comprise several sand-loving species, especially *Neopogon argenteus* and *Laphystia 6-fasciata* in the United States, and *Lasiopogon cinctus* and *Philonicus albiceps* in Europe. According to Melin (1923), the latter two species are almost exclusively confined to dunes or sandy lake and sea beaches. Both oviposit in the sand, and Melin describes the Philonicus female as first slowly sweeping away the sand with the apex of her ovipositor, then thrusting more than half of her abdomen into the sand and, after the eggs are laid, vigorously sweeping it over the hole with her ovipositor. The Therevidæ are similarly arenicolous but are predaceous only in their larval stages, which are passed in the soil. "Many species occur not far from running streams, but others occur in arid regions and on sand dunes where there is little or no vegetation" (Cole, 1923). In the Yosemite I have taken the peculiar long, snake-like larvæ of a Therevid in the same situations as Vermileo larvæ, that is, in the dry dust under overhanging rocks. Many of the very hairy flies of the family Bombyliidæ frequent dry, sandy spots in all parts of the world. Their larvæ prey on the young of a great variety of insects (grasshoppers, bees, wasps, etc.). Shelford (1913) has described *Spogostylum anale* as a parasite of Cicindelid larvæ, and Hart cites *S. albofasciatum* as belonging to the sand dune fauna. More striking on account of their larger size and the conspicuous black markings on their wings are the species of Anthrax, Exoprosopa, etc. At least three other families of Diptera contain species that regularly inhabit the sands of sea beaches and adjacent dunes, and all of them are conspicuously whitish pollinose or pruinose like the Asilid *Neopogon argenteus* above mentioned. The Ephydridæ are represented by *Lipochæta slossonæ* and *Scatophila mesogramma,* both widely distributed on the beaches of our Atlantic States. In similar situations in the Southern States occur the Dolichopodids *Thinophilus neglectus, bimaculatus* and *prasinus* and *Hypocharassus pruinosus* and *gladiator.* Among the Empididæ, a family partial as a whole to mesophytic regions, Melander (1927) cites the species of Coloboneura, Chersodromia and Thinodromia as psammophiles. He remarks that "the species of Chersodromia frequent mainly the sandy seashore, but some may occur on the shores of fresh water. The darker species seem to prefer the wet sand near the water's edge; the gray species occur higher up on the sand or even run up and down the beach grass." Of Thinodromia "the two known species are inhabitants of sandy beaches on the Pacific coast of North America. They are utterly unable to fly, but run nimbly over the sand and driftwood."

Few of the Lepidoptera can be regarded as true xerophiles or psammophiles, probably owing to the peculiarities of their larvæ, which are mostly soft-bodied, exposed vegetable feeders. We may mention in this connection, however, a small moth, *Prionopteryx nebulifera,* studied by Daecke (1905) in the sandy pine-barrens of New Jersey and another moth, doubtfully referred by Hart to *Olethreutes dimidiana* from the sand dunes of Illinois. The larvæ of both of these insects construct and inhabit long tubes of sand, which are attached to the stems of plants or even extend for some distance over the surface of the sand. There seems to be nothing unusual about the butterflies of our American deserts, but in the Old World Buxton has observed in several species an extraordinary ability to confine flight within small spaces protected from the wind. "Certain small Blue Butterflies (Lycænidæ) which inhabit the Great Palæarctic Desert possess the power of flight within one small bush, from the shelter of which they seldom issue. Butterflies of the genus Tarucus may be observed flitting up and down continuously inside a bush of Zizyphus, without leaving the middle of the bush, and sometimes continuing in flight for many minutes. The minute *Chilades galba,* another member of the same family, is able to limit its flight within a plant of Ononis ('Rest Harrow'), which is only a foot in circumference, and to remain on the wing in this little bush, when such a wind is raging outside as to prevent the flight of all other butterflies."

No other insect order comprises so many xerophiles and psammophiles as the Hymenoptera. In fact, it has long been noticed that the stinging forms, *i.e.,* the wasps, ants and bees which constitute the great suborder Aculeata, have a pronounced predilection for dry, hot environments. This is very striking in whole families of solitary wasps, such as the Mutillidæ, Methocidæ, Myrmosidæ, Apterogynidæ, Plumariidæ and Scoliidæ. These insects lay their eggs on the subterranean larvæ or pupæ of other Hymenoptera or of beetles. Many of the higher solitary wasps also, especially the Sphecidæ, Larridæ, Bembicidæ and Psammocharidæ are true psammophiles. The Bembicidæ capture living Diptera or collect miscellaneous dead insects and feed them to their larvæ in burrows in the sand, while the Sphecidæ (Sphex, Chlorion, etc.) and the Larridæ provide their larvæ in similar burrows with paralyzed grasshoppers, crickets or caterpillars. The Psammocharidæ have similar habits, but prey on spiders. All these wasps are exclusively diurnal insects, hunting and storing their prey only on warm, sunny days.

Chapman and his collaborators (1926) describe how the Bembicids, and probably many other solitary wasps, manage to avoid lethal temperatures at the surface of the sand: "Observations have shown that the penetration of the hot surface layer is accomplished by a juggling of time and space during which the wasps alternately dig furiously at the surface for a short period of time and fly about six to twelve inches above the surface of the sand. As the burrow deepens these flights become less frequent until the wasps are well within the uniformly lower temperature of the deeper sand. At a time when these wasps with their wings clipped were dying on the sand surface within the area where experiments were being carried on, others were alternately digging and flying, even within the same area. At times the bembicids (Microbembex) swooped down on our experiment and stole the insects which had just died at temperatures considerably above those which the bembicids themselves could endure if confined on the surface of the sand. Thus, while the bembicids, with their narrow temperature zones of activity, may not seem to be well adapted to the sand dunes, the dunes seem to be a suitable place for them to live in. The dunes furnish a substratum in which burrows may be dug easily, and present a range of temperature from which they can choose their optimum."

The Mutillid *Dasymutilla bioculata,* which Mickel (1928), one of Chapman's collaborators, found parasitizing the brood of the Bembicids (*Bembix pruinosa* and *Microbembex monodonta*), is able to endure unusually high temperatures. Experiment showed that the normal activity of the males began at 22°C. and that of the females at 24°C. The first heat paralysis occurred at 51°C. in males, at 52°C. in females, and all males were killed at 53°C., all females at 55°C. Since the females are wingless and therefore "unable to leave the surface of the sand except by entering burrows or climbing the sparse vegetation, their success on the dunes seems to be due to the high temperature which they can endure. Thus their limitation in space seems to be compensated by their increased endurance of high temperatures." This unusual resistance to heat is also seen in the large and often brilliantly colored species of Dasymutilla in the deserts of Arizona and California. On August 2, 1917, I found running about on a stretch of pure white sand at Tempe, Arizona, a large number of females of *D. gloriosa* (FIG. 6), which is red, with a dense investment of long, snow-white hairs. The air temperature must have been fully 39°C. and that of the sand surface considerably higher. In this insect the white pilosity must be highly serviceable, but even the dense carmine, yellow or

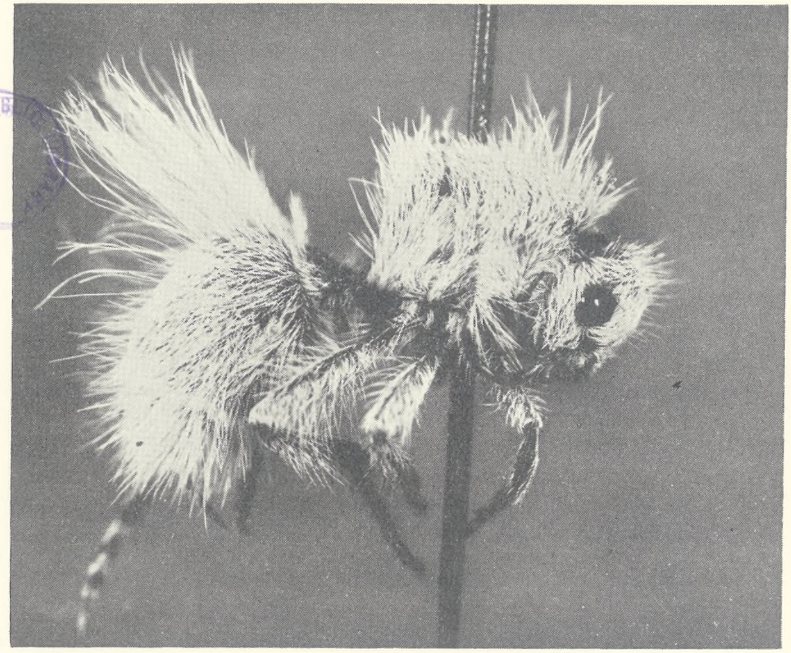

FIG. 6. *Dasymutilla gloriosa* Sauss., a Mutillid psammophile from the sandy river washes of Arizona. (Photograph by Dr. F. M. Carpenter.)

black pilosity so characteristic of other Mutillids would seem to have a similar protective function.

There is one entire subfamily of the true wasps (Vespidæ), the Masaridinæ, which is xerophilous. This is evident from their peculiar geographical distribution as has recently been pointed out by Bequaert (1929). They not only themselves feed on the nectar and pollen of flowers, but like the bees and unlike other wasps, store these substances as food for their larvæ. Some of these wasps may be included among the psammophiles, because they forage only on plants that grow in dry sand, as is the case with *Pseudomasaris wheeleri* and *edwardsi,* which I found visiting the flowers of Hydrophyllacieæ (*Eriodictyon tomentosum* and a species of *Phacelia*) in the Mojave Desert.

The psammophile bee fauna has been little studied though it must be considerable. Höppner (1901) found six characteristic local species of bees nesting in the sand dunes of the Weser Valley in Germany, and Hart gives a list of bees from the Illinois dunes, comprising several species of Colletes and Melissodes. I found the nests of one large species of Melissodes in the sand of the Mojave Desert. Graenicher (1930) describes three species of bees, *Megachile townsendiana, Osmia subfasciata* and *Halictus marinus* as being confined to the dune vegetation near Miami, Florida.

The most numerous xerophilous and psammophilous insects, both specifically and individually, are the ants (Formicidæ), but it is quite as difficult to draw a sharp line between their deserticolous and purely arenicolous forms as in the other groups we have been considering. Deep sand is in certain respects a very favorable medium for ants, because they are soil-inhabiting insects *par excellence* and the sand enables them to excavate their galleries and chambers easily and to considerable depths below the surface. Unlike other Hymenoptera, moreover, they have learned to move their eggs, larvæ and pupæ about freely and this enables them to adapt the situation of their subterranean nurseries and stores, as well as their activities on the surface of the soil to its diurnal and annual fluctuations of temperature and humidity. In deserts, therefore, many of the species become crepuscular or even nocturnal during the hot summer months. Thus Buxton (1924[b]) has noticed that the harvesting ant *Messor barbarus,* during the summer in Jerusalem, is never fully active on the surface of the soil between 9 A.M. and 3 P.M., and quite inactive when the humidity is below 45%. After 3 P.M. the activity increases till midnight and then slackens till 5-9 A.M. He has shown that several factors are involved in this periodicity, mainly temperature, insolation, humidity and, perhaps, in the slackening after midnight, fatigue. Kusnezow-Ugamsky's observations (1927, 1929) in the deserts of Turkestan show that certain ants also select seasons of atmospheric calm for their marriage flights and thus avoid the violent winds so frequent in very arid regions.[1]

The xerophile and psammophile ant fauna is made up very largely of species belonging to the genera listed on p. 65 in the first column. These forms have evidently been evolved from the mesophilic genera cited in the second column and still have numerous species in adjacent more humid environments. Thus the two xerophilous subgenera of Aphænogaster, and the genera from Novomessor to Goniomma are very probably derived from mesophilic forms of Aphænogaster like those now included in the circumpolar subgenus Attomyrma; the American Pogonomyrmex and the African Cratomyrmex are probably descendants of the genus Myr-

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[1] This is interesting in connection with Buxton's description above quoted of the flight of desert butterflies in small bushes and his remarks on the frequent reduction of wings in the desert Orthoptera and Coleoptera, an adaptation to strong winds, like the aptery of many insects on small oceanic islands. On the other hand, the winds may be utilized for dispersal as in the case of certain hairy desert caterpillars mentioned by Buxton and the well-known tumble weed (*Amaranthus græcizans*) of our western plains.

mica; the Australian Melophorus is an offshoot of Prolasius; the North American Myrmecocystus of Lasius; Cataglyphis, so characteristic of the Great Palæarctic Desert, of Formica, etc.

PSAMMOPHILOUS FORMICIDÆ

MYRMICINÆ

	Derived from
* Pheidole (numerous species)	Pheidole
Aphænogaster (subgen. Aphænogaster and * Nystalomyrma)	
Novomessor	Aphænogaster
* Veromessor	" "
* Messor	" "
Oxyopomyrmex	" "
Goniomma	" "
Monomorium (subgen. Xeromyrmex, Parholcomyrmex and * Holcomyrmex)	Monomorium
* Pogonomyrmex	Myrmica
* Ocymyrmex	Aphænogaster
* Cratomyrmex	Myrmica

DOLICHODERINÆ

Forelius	Iridomyrmex
Dorymyrmex (subgen. * Psammomyrma)	Iridomyrmex

FORMICINÆ

* Melophorus	Prolasius
* Myrmecocystus	Lasius
* Cataglyphis	Formica
Camponotus (subgen. * Myrmopsamma and Myrmophyma)	Camponotus subgen. Tanæmyrmex

Besides the groups enumerated in the foregoing table we should also include among the true psammophiles certain sporadic species or races belonging to some of our northern mesophilic genera, especially *Formica cinerea* of Europe and *F. pilicornis* of California, which nest in sandy river washes, *Manica mutica* and *bradleyi* which live only in similar situations in Utah, Colorado and California, and *Prenolepis imparis* var. *testacea* of the New Jersey pine-barrens and similar sandy areas in the South Atlantic States. It should also be noted that certain species of Pogonomyrmex, Holcomyrmex, Messor, Cataglyphis and Myrmecocystus occur only in the pure sand of deserts. This is true of *P. californicus* and *comanche,* of several subspecies of *Myrmecocystus melliger* in our southwestern deserts, and, according to Lameere (1902) of *Messor arenarius* and *caviceps, Holcomyrmex chobauti* and *Cataglyphis lameerei* and *bombycinus* in the deserts of Algeria. He gives an interesting account of *M. arenarius,* which "is the most powerful organism of the desert". It is not only a large and enterprising ant, but forms very populous colonies, which make clusters of craters, each 50 cm. in diameter. The galleries probably extend down into the soil to a distance of several meters. Lameere found that in some localities the nest of a single colony might cover more than an acre of sand!

The xerophile and psammophile ants, as a rule, exhibit certain convergent structural and behavioristic peculiarities, which may be briefly described:

(1) The workers and females of several species have the body covered with glistening or silvery white hairs which may perhaps serve to reflect the intense heat and light rays of the sun. These hairs are very well developed in many Myrmicines, e.g., in the Mediterranean *Aphænogaster testaceopilosa* and *prædo,* the species of Novomessor (*cockerelli* and *albosetosus*), Veromessor, and Pogonomyrmex of our southwestern deserts and most conspicuously in the North African Formicine ant *Cataglyphis* (*Machæromyrma*) *bombycinus,* which resembles a little ball of quick-silver as it bounds over the desert soil. I have already

called attention to this white pilosity in *Dasymutilla gloriosa,* but it is well-developed also in several psammophilous Sphecid and Bembicid wasps, in the desert bees, etc.

(2) In many desert ants the clypeus and gula, or lower surface of the head in the worker and female are furnished with rows of very long, curved hairs arranged in such a manner as to form a *psammophore* (Wheeler, 1907, Santschi, 1909). This is really a crate or basket in which the excavating ant can transport the sand grains to the surface in a small mass or pellet, instead of wasting time and labor in carrying out single sand grains with the mandibles. The psammophore is similarly developed in several unrelated genera which are indicated by asterisks in the list on p. 65.

(3) Owing to the periodical scarcity of insect or liquid food in deserts or sandy areas various ants have specialized in one of three different kinds of behavior:

> (a) Some species have become swift-footed hunters of other insects on the sands. To this group belong the species of the genera Dorymyrmex and Myrmecocystus in the American deserts and the genus Cataglyphis in the Great Palæarctic Desert.
>
> (b) Many ants have found it advantageous to abandon insect food, at least during seasons of its greatest scarcity, and to collect and store the seeds of the sparse grasses and other herbaceous desert plants. Here belongs a long list of harvesting ants of the genera Pheidole, Veromessor, Messor, Oxyopomyrmex, Goniomma, Holcomyrmex and Pogonomyrmex.
>
> (c) Yet other species, the 'honey ants,' store the honey-dew of Aphids and Coccids, the exudations of oakgalls or the nectar of flowers in the crops of certain workers or soldiers, which thus become 'repletes'

with abnormally distended gasters. Such individuals manage to retain their liquid stores during the protracted droughts and disgorge them to their thirsty sister workers when needed. The forms which adopt this singular behavior belong to several unrelated genera, such as Pheidole, Melophorus, Myrmecocystus, Camponotus and Prenolepis, e.g., the psammophile *P. imparis* var. *testacea.*[1]

The most characteristic psammophiles among Arachnids are certain spiders and the Solpugids, or wind scorpions. Hart (1907) describes a jumping spider, *Phidippus insolens,* which closely resembles ('mimics') female Mutillids, as hunting on the blow sands of the Illinois dunes. Emerton (1912) has made a study of four psammophilous species of Lycosa (*pikei, nidifex, missouriensis* and *wrighti*). They are all colored like the sand and "their burrowing habit is so far developed that, excepting adult males during the mating season, their whole life is passed underground or within a short distance of the mouth of the burrow. As soon as the young leave their mother they make burrows of their own proportional to their size. The digging is done by covering the sand with silk enough to hold the grains together and it is then gathered into pellets of convenient size and carried in the mandibles to the mouth of the burrow, where it is thrown outward by the ends of the front feet and on open sand the pellets may be seen in

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[1] We might add a fourth adaptation, namely fungus-gardening, which is exhibited by at least one psammophilous ant, *Mœllerius versicolor,* in the Arizona and West Texan deserts, but this species is merely an exceptional derivative of the Attine ants (comprising more than 100 species) which have developed the fungus-growing habit in the rain-forests of tropical America. The species of Pheidologeton and Aneleus of the East Indies, though mesophiles, have nevertheless acquired the habit both of storing seeds and of converting their soldiers into repletes. In Australia the species of the mesophilic genera Leptomyrmex and Oligomyrmex have become honey-ants and the same is true of certain species of Plagiolepis in Africa and of our common North American *Prenolepis imparis* which lives in moist situations.

a circle of three or four inches radius round the hole. When watching for prey, they sit with the front of the body out over the edge of the hole and the legs turned under. They are sensitive to the slightest movements on the ground, and when down in their burrows will notice the walking of an insect within an inch or two of the hole and come quickly to the top." *L. nidifex* and *missouriensis,* which sometimes nest in hard soil, build low turrets of vegetable detritus around the openings of their burrows, but *wrighti* and *pikei* are more exclusively inhabitants of pure sand and make only vestigial turrets or none at all.

The Solpugids are a singular group of highly predaceous, nocturnal psammophiles, of which a number of species have been described from the Great Palæarctic Desert and the deserts of our Southwest. They have very hairy bodies, long, slender legs and powerful, vertically and alternately working jaws. Owing probably to their pinkish color and rounded abdomens, they are called "niños de tierra" (earth babies) by the Mexicans, who without reason dread them as being very venomous. When disturbed, they run with extraordinary rapidity, which may account for their being called 'wind scorpions' in our text-books. While digging up ant-colonies, I have occasionally encountered these creatures deep in the sand. Once many years ago I observed a number of individuals of a small species, each under its own dry cowchip on a sandy cattle range in Eastern Wyoming. Very little was known of the habits of the Solpugids till Hingston (1925) published his study of a large species (*Galeodes arabs*) in the sandy deserts about Bagdad. His fascinating account of its gruesome feeding habits and those of the true scorpions in that region is, unfortunately, too long for quotation.

The desert vertebrates are, of course, less numerous than the desert Arthropods, but numerous species, nevertheless, and more particularly those which frequent sandy areas, exhibit certain striking adaptations. For a comprehensive account of the lizards, birds and mammals of the Great Palæarctic Desert, the reader is referred to Buxton's 'Animal Life in Deserts' (1923). The psammophilous lizards exhibit two kinds of modifications, according as they are "sand-runners" or "sand-swimmers". The former belong to several families and genera and have the toes of the fore and hind limbs fringed with elongated scales. "It seems legitimate to conclude," Buxton says, "that the fringe widens the surface, which presses on loose sand and acts in the same way that a snow-shoe does on loose snow." Barbour (1926) calls attention to another modification which subserves the same function, namely the "duck-like web-feet" in a gecko (Palmatogecko), which lives on the sands of the Kalahari Desert of Southwest Africa. These various dilatations of the toes might also be of use in burrowing. The sand-swimmers are skinks which exhibit several profound structural adaptations to rapid burrowing in loose sand. The nose, or rostrum, is pointed and protruding and some of the forms, according to Barbour, have acquired a "remarkable modification in the form of a window in the lower eyelid. In some species this window is a single round transparent disk; in others it occupies the whole eyelid and the lid itself is permanently closed and fused with its fellow. It is the lower eyelid invariably that is modified in this way, which, of course, is a great protection from blowing sand." The body of the sand-swimmers is covered with smooth scales and the limbs may be greatly reduced or even lost, so that locomotion through the sand is accomplished entirely by wriggling the body. After observing these lizards in the great sand dunes about Mogador, Morocco, I was able to interpret the statement of a young Frenchman who informed me that he had actually "seen fish swimming in the sands of the Sahara." Buxton calls attention also to fringed scales surrounding the eyes in some sand-dwelling lizards and to the specially developed rostrum in many psammophilous snakes.

Perhaps the most interesting reptilian psammophile in the United States is the small limbless lizard *Anniella pulchra,* which inhabits the sand dunes of California, Arizona and southward. It is related to the European slow-worm, Anguis. According to Coe and Kunkel (1906), who made a careful study of its anatomical peculiarities, it is capable of rapid locomotion through the sand, but spends much of its time lying in wait, with only the fore part of its head exposed above the sand, for its prey, which consists of small beetles, larvæ, spiders, etc. When the prey reaches the lizard's immediate vicinity, "it raises its head an inch or more above the sand and crawls out of its burrow until its head is directly above the object. It then arches its neck sharply and with its jaws widely opened thrusts its head down quickly into the sand, thus holding its prey firmly pressed against the surface of the sand. The struggles of the prey to escape force it farther into the mouth of the lizard and in the course of a minute or two it is completely engulfed. It is held for some time in the lizard's mouth before being swallowed. More or less sand is swallowed at the same time, and this accounts for its presence in both the stomach and the rectum of many of the lizards under examination." In its waiting in concealment for the approach of its prey and its habit of smothering it in the sand after its capture, Anniella displays interesting resemblances to the ant-lions and worm-lions.

The adaptations to desert life on the part of birds seem to be mostly behavioristic. Buxton cites the observations of Hartert, Rothschild and others on several passerine birds in the Algerian Sahara, which "regularly make their nest against the windward side of small bushes and so avoid being smothered with sand and débris. They then fortify the outer side of the nest with a mass of pebbles, apparently in order to protect the nest from wind. This seems to be the invariable habit of Clot-bey's lark (*Rhamphocorys clot-bey*), which collects pebbles weighing as much as half an ounce." Some of the desert birds adopt special methods of protecting their eggs from the heat, and the species of sand-grouse (Pterocles), which range from Spain to Central Asia, have adopted an extraordinary method of watering their young. Though these birds nest on the desert soil they fly many miles to drink at the rivers. The young feed on seeds from the time of hatching. Meade-Waldo observed their method of obtaining water in an aviary, as shown by the following passage quoted by Buxton: "The male rubs his breast violently up and down on the ground — a motion quite distinct from dusting,— and when his feathers are awry gets into his drinking water and saturates the feathers of his underparts. When soaked he goes through the motion of flying away, nodding his head, etc.; then remembering his family is close by, he would run to the hen, make a demonstration, when the young run out, get under him, and suck the water from his breast — the appearance being that of a mammal suckling her young. The young pass the feathers through their bills, and keep changing places until the supply becomes exhausted. Until the young can fly *they take water in no other way,* and the cock gives it to the young only." This habit of wetting the breast feathers while drinking also serves to protect the unhatched eggs from the heat, "for", as Buxton remarks, "when one parent returns from watering, and relieves the other from the duty of incubation, its breast is saturated with water. Therefore, it appears that the eggs and the soil on which they are laid are wetted every day, which must tend to prevent overheating."

The larger mammals show little adaptation to desert conditions apart from their paler color and greater ability to endure thirst. Among the small rodents, however, there are certain groups that are specialized for life in the loose sand. The most singular of these are known as jerboas, zerbils, kangaroo rats and pocket mice, exclusively nocturnal forms which have adopted a more or less bipedal, saltatory mode of locomotion and show various stages in the reduction of their hind digits from five to three. They belong to some twelve genera and have evidently been independently evolved from at least four different murine families in different desert regions of the globe. And, curiously enough, there are two genera of Dasyurine Marsupials, Antechinomys and Phascogale, which have taken on similar characters in the deserts of Central Australia. This complex of small jumping mammals, whose taxonomic relationships and wide distribution are shown in the following table taken from Buxton, constitutes a very remarkable example of ‘convergent’, or ‘parallel’ evolution.

The Heteromyid forms occurring in our Southwestern deserts belong to the genera Dipodomys and Perognathus. They have been recently studied by Vorhies and Taylor (1922), Bailey (1923), Sumner (1925) and Dice (1930). Dipodomys lives on weeds and other dry vegetable substances, Perognathus also on roots and tubers. Dice found in the White Sands, near Alamogordo, New Mexico, an area of some 270 square miles of pure white gypsum sand, two species of kangaroo rats, *Dipodomys merriami* and *ordii*, the Ruidoso grasshopper mouse, *Onychomys leucogaster ruidosæ*, the Chihuahua deer mouse, *Peromyscus maniculatus blandus* and a nearly white pocket mouse, *Perognathus gypsi*, which is peculiar to the region. According to Kashkarov and Kurbatov (1930), the larger gerbille, *Rhombomys opimus*, in the Kara-kum Desert of Turkestan lives on hay. These authors state that it “stores the sedge, *Carex physodes*, in its burrows, drying it beside the openings. The animals put up the hay in the same way that man does, and, to prevent its blowing away, stick pegs two inches long, made of *Astragalus confirmans*, into the sand.

GROUPS OF SALTATORY DESERT RODENTS AND MARSUPIALS

ORDER	SECTION	FAMILY	SUB-FAMILY	GENUS	HABITAT
Rodentia	Myomorpha	Dipodidæ	Dipodinæ	Allactaga	Great Palæarctic Desert
				Dipus	
				Jaculus	
"	"	"	Zapodinæ	Zapus	America
"	"	Muridæ	Murinæ	Conilurus	Australia
				Notomys	"
"	"	"	Gerbillinæ	Gerbillus	Great Palæarctic Desert
				Meriones	
"	"	Heteromyidæ		Dipodillus	
				Dipodomys	America
				Perognathus	"
"	Hystricomorpha	Pedetidæ		Pedetes	S. Africa
Marsupialia	Polyprotodontia	Dasyuridæ	Dasyurinæ	Antechinomys	Australia
				Phascogale	"

The dried sedge collected in one place near two burrows weighed 2,566 gr., the hay near a third burrow, 637 gr. The stores of dried sedge can seldom be found in the early morning." The Marsupials mentioned in the above table are insectivorous.

The peculiar reduction of pigment, or pale sandy or tawny color, so common among desert reptiles, birds, rodents, insectivores and carnivores, is usually regarded as a form of 'protective coloration'. This may be true of the diurnal reptiles and birds, but, as Sumner contends, it must have some other meaning in the case of the mammals, which are all nocturnal. In these forms, moreover, the color cannot be attributed to the direct bleaching action of the sunlight since it is shown by experiment to be hereditary. Sumner believes that it may be due to aridity because the amphibious muskrat, *Ondatra zibethica pallida,* of desert streams shows the same peculiarity of coloration. It should be noted that the same or a similar type of coloration occurs in certain nocturnal Arthropods (Lycosid spiders, Solpugids, some Carabids) as well as on the exposed body and wing surfaces of certain diurnal insects (grasshoppers). Sumner leaves the causation of the pale coloration of desert mammals in doubt. Concerning the very similar pigmentation of desert birds, Görnitz (1923) and Rensch (1929) make more positive statements. Görnitz distinguishes two kinds of melanin pigments, the blackish brown eumelanins which are decreased, and the reddish brown phæomelanins, which are increased by aridity. The disappearance of the eumelanins and the predominance of phæomelanins in dry, hot environments are explained on the assumption that the latter are higher oxidation products of the former, since black eumelanins can be artificially converted into brown phæomelanin-like pigments by long exposure to the sun or treatment with hydrogen peroxide.

Perhaps we should also include among the xerophiles or psammophiles certain tribes of men like the Indians of the Arizona and Colorado Deserts. According to J. C. Van Dyke (1925), Father Garces more than a century ago found that "the Jamajabs (a branch of the Yumas) endure hunger and thirst for four days." The Indians of the Coahuila Valley, in the sandy Mojave Desert, seem to be equally inured to drought at the present day. "And, too, it is said that the Yumas have traveled from the Colorado to the Pacific, without any sustenance whatever. No one, not to the desert born, could do such a thing. Years of training in starvation, thirst and exposure have produced a man almost as hardy as the cactus and just as distinctly a type of the desert as the coyote." Certain writers believe that desert tribes exhibit a kind of treacherous behavior not unlike that of the desert animals to be discussed presently. Thus Lucian Romier (1929, p. 43) asserts that "the man of the plain, steppe, or desert is more inclined to deceive or betray than to attack. The quarrels of mountaineers are bloody, those of plainsmen venomous."

It will be seen that all the Arthropods above enumerated, except the Tenebrionid beetles, caterpillars, grasshoppers, certain ants, the bees and Masaridine wasps, are predators. The same is true of the vertebrates, except certain granivorous birds, the rodents and antelopes. It is this predominance of predatory forms, especially in the sandy and most forbidding desert regions, their spiny vegetation, stinging heat, duststorms and illusory mirages, that gives them such a malevolent and demoniac aspect, and close observers of the desert, especially at night, have frequently called attention to the ruthless behavior of its fauna. Van Dyke finds that it possesses "one quality more general than special since almost everything possesses it, and that is ferocity — fierceness. The strife is desperate; the supply of food and moisture is small, the animal is very hungry and thirsty. What wonder then that there is the determination of the starving in all desert life! Everything pursues or is pursued. . . . Taking them all in all, they seem like a precious pack of cutthroats, these beasts and reptiles of the desert. Perhaps there never was a life so nurtured in violence, so tutored in attack and defence as this. The warfare is continuous from the birth to the death. Everything must fight, fly, feint or use poison; and every slayer eventually becomes a victim. What a murderous brood for Nature to bring forth! And what a place she has chosen in which to breed them! Not only the struggle among themselves, but the struggle with the land, the elements — the eternal fighting with heat, drought and famine. What else but fierceness and savagery could come out of such conditions?" And Hingston voices a similar and even more vivid impression of insect savagery in the deserts of Mesopotamia: "There is a vicious facies about this desert fauna. Poison and sting and herculean strength are the weapons that engage in the battle of the night. At times I have caught a glimpse of it with the aid of a lamp, and more often I observe a contest by day. One time it is a centipede fastened on a beetle, and another time a scorpion with a cricket in its pincers, still again a solifugid munching at diptera or raking a locust into its mill. Spiders have their snares in the dusty thorn and seize on the victims that fall into their nets, others live under broken clods, others at the bottom of cylindrical burrows and come forth at night to join in the chase. By day the ants cause tremendous destruction. We see a cricket, a beetle, a locust, a larva carried successively through the gate of the nest; on the sand we see them grip the unwary diptera or drag the terrestrial molluscs to their store. The robber-flies are watching on points of vantage, the dragonflies are decimating clouds of chironomids, the ant-lions are waiting in their funnel-shaped pits. Solitary wasps are chasing cockroaches and spiders, others are seeking out flies and caterpillars, others hauling crickets over the sand. How vast, how deep is this complex scheme of the interdependence of living beings! Each creature is in arms against its fellow. The tangled skein of desert life oscillates in every thread. Yet the whole is fixed with perfect balance, guided, no doubt, by as unswerving laws as those which move the planets in their paths."

Sumner is inclined to regard the above-quoted passage from Van Dyke as an exaggeration due to ignoring the law of Malthus, and asks: "Why should the struggle for existence be necessarily more keen when the food and water supply is small than when it is great? A larger supply would fill more mouths, but would there not be more mouths to fill?" He admits, nevertheless, that so far as the plant-eating animals are concerned, spininess of the vegetation "would seem to indicate an extraordinary intensity in the pressure of population upon subsistence in the desert." It seems to me that Van Dyke and Hingston are impressed not so much by the internecine struggle of the desert biota as a whole as by that of the various faunal components. While this struggle is undoubtedly more noticeable in the great open spaces of deserts and dunes than in more humid environments with denser vegetation and many more species and individuals, it is clear, nevertheless, that the ratio of predaceous to plant-eating species, both among Arthropods and vertebrates, with the exception of the mammals, which are mostly rodents, is much higher in desert regions. Hence the struggle between the various individuals is absolutely greater and more impressive than in mesophytic regions. In the latter the more luxuriant vegetation nourishes vast numbers of plant-eating forms, and their enemies are most frequently parasites whose slow and subtle exterminative activity fails to obtrude itself on the observer. It must not be forgotten, moreover, that the prey of the predatory xerophiles is also their main and, in many cases, their only source of water as well as food, and even when the vegetable food-source, on which in last analysis all animal life depends, is almost eliminated or at any rate very difficult to determine, as in the case of the cave animals, the latter may manage to maintain themselves in a vicious and precarious circle by feeding on one another's tissues and excreta. The cave faunas and those of the great ocean depths certainly resemble the desert faunas in being predominantly predatory though the extreme physical conditions under which they manage to survive are so different, the caves and ocean depths being cool, dark and humid whereas the deserts are hot, luminous and arid.

CHAPTER III

POST-EIGHTEENTH-CENTURY OBSERVATIONS ON THE ANT-LIONS

THE abundant ant-lion literature published since 1800 is of two kinds — original articles, which have increasingly contributed to our knowledge; and general accounts in entomological text-books and natural history journals. I shall not consider the latter, which even at present are often little more than summaries of the observations of Poupart, Pluche, Réaumur and Rösel. Few really scientific accounts were published during the first three decades of the nineteenth century, but a rather sudden revival of interest in the insect set in between 1830 and 1840 and has continued, so that there has been no dearth of new and valuable observations during the past hundred years. This revival and persistence of interest was doubtless due to the ant-lion being an easily procured and very favorable laboratory animal, partly to the constant improvement in biological technique, which could not fail to suggest reinvestigation of the facts recorded by the early observers, and partly to the increasing differentiation of the biological sciences, which encouraged investigators to make a more intensive study of particular aspects of the insect's anatomy, physiology and behavior. It will be expedient, therefore, to abandon the chronological procedure of the introductory chapter and to consider the contributions since 1800 according to the predominant interests of their authors.

Before the behavior of a particular organism is investigated by any entomologist convinced of the great importance of evolution, it is advisable to view it against the background furnished by its collective allies, both living and extinct. This procedure should yield a preliminary phylogenetic appreciation, which, though vague and suppos-ititious to a degree, has nevertheless a considerable heuristic value that cannot be ignored without unduly narrowing and over-simplifying such interpretations as may be reached from more precise observation and experiment. We therefore turn first to the most recent opinions of systematists and paleontologists concerning the status of the ant-lions among their living and fossil congeners. And in order that our background may not lack depth of perspective we shall consider even some of the more remote relatives in the natural family and order to which the ant-lions belong.

Some recent systematists regard the order Neuroptera as including two suborders, the Planipennia and the Megaloptera, but others, whom I shall follow, regard these as independent, though closely related, orders and retain the old Linnaean name Neuroptera for the Planipennia. Of the two this group is obviously the more highly specialized, as shown by the mouthparts of the larvæ, since their mandibles and maxillæ are developed as peculiar piercing and sucking organs. The maxilla is enclosed in a ventral groove of the mandible in which it moves like a piston. Since the mouth opening is closed throughout larval life, the juices of the prey, which consists nearly always of other insects, are drawn through the groove or canal into the gullet, partly by the pumping action of the maxilla and partly by the dilatation of the muscular walls of the pharynx. Another peculiarity of the Neuropteran larva is the temporary modification of the excretory organs, or Malpighian tubules, as silk-secreting glands for spinning the spherical or subspherical cocoon in which it pupates.

The ant-lions belong to the Myrmeleontidæ, one of the four families forming a natural group or superfamily, the Myrmeleontoidea, which are regarded as the highest and most specialized of Neuroptera. Although much attention has been devoted of late to the classification of the Myrmeleontidæ our knowledge of the species and their distribution is still very rudimentary. Neither the structural nor the behavioristic peculiarities of the larvæ have been utilized in the classification, because very few of the species have been reared, except those belonging to the meager European fauna. Petersen (1918) and Withycombe (1925) divide the family into two sections, the primitive Archæmyrmeleontida, with the single genus Palpares, and the more specialized Neomyrmeleontida, comprising all the remaining genera. Most of these are based on such feeble characters that they might more properly be regarded as subgenera. The family has a world-wide distribution, though it is, of course, represented by the greatest number of species in tropical and subtropical countries. A few forms extend their range as far north as British Columbia and Ontario in North America and Finland in Europe, but none occurs in Sweden or Great Britain. All the New World forms belong to the Neomyrmeleontida. According to Banks (1927), our Nearctic fauna is a northward extension of the Neotropical, the genera Brachynemurus, Hesperoleon, Austroleon, Glenurus and Psammoleon being common to both American continents, but absent from the Old World. The genus Dendroleon, though well represented in Eurasia and Australia, does not occur in the United States. The genus Myrmeleon, which comprises the true ant-lions, with the European *M. formicarius L.* as the type, is cosmopolitan. In the recent monograph of the North American Myrmeleontidæ from which these facts are taken, Banks enumerates 70 species, belonging to 19 genera. Of these Hesperoleon contains 26 and Myrmeleon seven species; each of the 17 remaining genera has less than six and the average in a genus is only 2.1 species. It would seem, therefore, that there has been undue multiplication of taxonomic categories in the family.

Although so few species have been studied in the larval stage it is apparent, nevertheless, from the following data that there is considerable diversity of habit within the family Myrmeleontidæ:

(1) So far as known the larvæ of all species of Myrmeleon *sens. str.* have very similar habits. They all make funnel-shaped pits in sand or loose earth and walk only backward. Some other genera, however, exhibit the same behavior, e.g., Neseurus, as I have observed in the Canary Islands, and Callistoleon of Australia (Tillyard 1926).

(2) The species of most Myrmeleontid genera do not make pits, but merely conceal themselves under sand or detritus and are able to walk both forward and backward. This is certainly true of the European Palpares, Acanthaclisis, Formicaleo, Dendroleon and the Australian Alloformicaleon. Tillyard (1926) has described "a delicate and almost ghost-like" Australian species, *Xantholeon helmsi,* whose larva merely hides in the sand on the floors of sandstone caves in the vicinity of Sydney. Indeed, according to this author, of the 36 genera of Myrmeleontidæ known from Australia, only the species of Myrmeleon and Callistoleon make pits.

(3) There are species that live a more exposed life than any of the preceding. Gravely and Maulik (1911) find that the larvæ of the Indian *Macronemurus contractus* (erroneously cited as a Myrmeleon), which hunt their prey on tree trunks, do not "hide under stones or rubbish, or cover themselves with a cloak of foreign matter as do the

larvæ of some other genera. They only attach a little dust in a thin layer to the dorsal surface of the head and thorax, the abdomen being apparently always bare in spite of its pale color." The direction of locomotion is not mentioned, probably because it is forward as in most insects.

(4) According to Redtenbacher, the European *Myrmocælurus trigrammicus* makes a funnel by walking backward like Myrmeleon, but is also able to walk forward.

(5) The larva of an undetermined species observed by Biró (1897) in New Guinea makes a double pitfall, i.e., a large funnel, like the ordinary Myrmeleon, and a smaller secondary funnel at its lower end. This larva, like that of Myrmocælurus, walks backward while excavating its pit, but runs forward rapidly. It not only resorts to the device of throwing sand at its prey but if unsuccessful promptly leaves the pit and pursues it over the sand. Biró often saw several individuals chasing the same insect.

(6) Another larva, *Hesperoleon intermedius* (FIG. 5), which I have observed in great numbers in the Mojave Desert, not only excavates a steep-sided pit but prolongs its center downward as a narrow tube. Since the pitfalls are made in the open desert, the tubular deepening may be an arrangement for enabling the larva to lie in wait for its prey as far as possible from the hot surface layer of the sand. Like Myrmeleon, this species is unable to walk forward.

These data suggest that intensive investigation of tropical and subtropical Myrmeleontids may reveal a great number of behavioristic patterns. Meager as they are, however, they represent what we may regard as at least four different phylogenetic stages of behavioristic development within the family. The most primitive stage seems to be that of the Macronemurus larva, which leads a free, active, predatory life, though it masks its head and thorax with a thin layer of dust, apparently a reminiscence of the greater accumulation of detritus observed in the larvæ of the primitive Neuropteran family Hemerobiidæ. The second stage is represented by the more lethargic forms that bury themselves in sand and detritus (Palpares, etc.), the third by Myrmocælurus and Biró's larva, which make pitfalls though they still retain the ambigradient gait of the preceding stage. Myrmeleon, finally, representing the culminating stage, has become more sedentary and exclusively retrogradient. On the basis of venational and other characters, recent taxonomists (Petersen 1918, Withycombe 1925, Banks 1927 and others) agree that this is the most highly specialized genus in the family, a conclusion which is also indicated by a comparative study of the three other groups of the superfamily Myrmeleontoidea, namely the Nymphidæ, Ascalaphidæ and Nemopteridæ.

The lowest family, the Nymphidæ, sheds considerable light on the antiquity and phylogeny of the true ant-lions. It comprises only one living species, the Australian *Nymphes myrmeleonides* which closely resembles a Myrmeleon. The larva was first described by Froggatt (1902-'03) from specimens taken in late November at Armidale, New South Wales. They were "hiding among rubbish or clinging to overturned logs, so well coated with bits of dirt that only the front of the head and mandibles were exposed; until disturbed they remained perfectly motionless, but moved quickly when touched. In captivity they took no food and after remaining three weeks in a jar, three of them pupated, forming typical, rounded, parchment-like pupal cases. From the situation in which they were found, they would probably feed on wood ants." *N. myrmeleonides* is closely related to three species of Nymphites, which were described from the Lithographic Shales of Solenhofen (Malm) and a species of Sialium from the Lower Purbeck (Malm) of England, and were regarded by Handlirsch (1908) as connecting the Protohemerobiids with Nymphes, which in turn leads up to the Myrmeleontids. Recently Carpenter (1928) has described, from the Solenhofen Shales, another genus, Mesonymphes, which has an extraordinarily modern aspect. "If a Neuropteran with the venational characteristics of Mesonymphes were found in the tropics at the present time, it would probably not arouse much comment. The only feature of this insect which is more primitive than that of Nymphes is the small number of cross-veins." All this confirms the opinion of Tillyard (1917) who says, after a close study of Myrmeleontid wing-venation: "There has been a general agreement in looking upon the Nymphidæ, a small family confined to Australia, as representing the probable type from which the Myrmeleonidæ have been developed. But this agreement is not, so far as I can ascertain, based on any definite evidence, but merely on a general impression of the Myrmeleonid-like appearance of the well-known *Nymphes myrmeleonides* Leach. We now have definite venational evidence to go upon, and we may say at once that it fully establishes the claim of the Nymphidæ to be regarded as the remains of the ancestral group from which the Myrmeleonidæ have sprung, the course of evolution being marked by a gradual reduction in the general density of venation, in the size and prominence of the pterostigma and in the length of the antennæ (which become stouter and clavate), and by a change from a wandering (probably nocturnal), carnivorous larva, with omnivorous tastes, to a sedentary, pit-dwelling, ant-feeding form."

If the foregoing considerations are correct the Nymphid ancestors of the Myrmeleontids go back at least to the Jurassic. There are, however, no known fossil remains of true Myrmeleontids antedating the Tertiary. Berendt (1830) determined a specimen in the Baltic amber (Lower Oligocene) as a Myrmeleon and Burmeister recorded a "Myrmecoleon" from the same formation. Charpentier described a *Myrmeleon reticulatum* (?) from the Miocene shales of Radoboj, and Schlotheim (1823) found what he took to be a Myrmeleon larva from the Flötzmuschelkalk (Tertiary). Not only, therefore, had the family Nymphidæ and its derivative, the Myrmeleontidæ, been differentiated by the beginning of the Tertiary but the same is true of the other two families to be discussed below, the Ascalaphidæ and Nemopteridæ. At any rate, a couple of species of the former family, an Ascalaphus and a Suhpalacsa, have been described by Oustalet (1870) and Hagen (1858) respectively from the Upper Oligocene of France and Germany, and Cockerell (1907) discovered in the Miocene beds of Florissant a very typical Nemopterid, *Marquettia americana,* which is barely distinguishable from the existing genus Halter.

The family Ascalaphidæ, according to Van der Weele's monograph (1908), embraces 201 known species distributed among 54 genera. They are closely related to the Myrmeleontidæ but more narrowly confined to tropical and subtropical regions, and are, both as larvæ and adults, larger and more robust insects. At first sight the adults resemble dragon-flies but may be at once distinguished by their long clubbed antennæ, and in some species at least by their strong musk-like odor. The larvæ (FIGS. 7, 8*A*) resemble those of the ant-lions in having the hind tibia and tarsus fused to form a single joint, the only other forms in which this occurs among the Neuroptera being, as Withycombe (1925) has shown, the larvæ of the Ithoniids, and in these the fusion occurs in all three pairs of legs. The head of the Ascalaphid larva is much broader and less mobile than that of Myrmeleontids and distinctly cordate posteriorly. The abdomen is broad and flattened, with laterally produced segments. The setæ on the body are also very different, being mostly short, stubby and longitudinally fluted, and therefore of the type called "dolichaster" by Withycombe, whereas they are "macrotrichia", i.e., long and slender bristles in the ant-lions. The fact that typical dolichasters occur on the anterior dorsal margin of the head in all first stage Myrmeleontid larvæ indicates that the Ascalaphid larva is more archaic. This is also suggested by the exposed method of oviposition, the habits of the larvæ and the construction of the cocoon. Accounts of these stages in a number of genera have been published by Guilding (1827-Ascalaphus), Percheron (1833-Ascalaphus), Le-

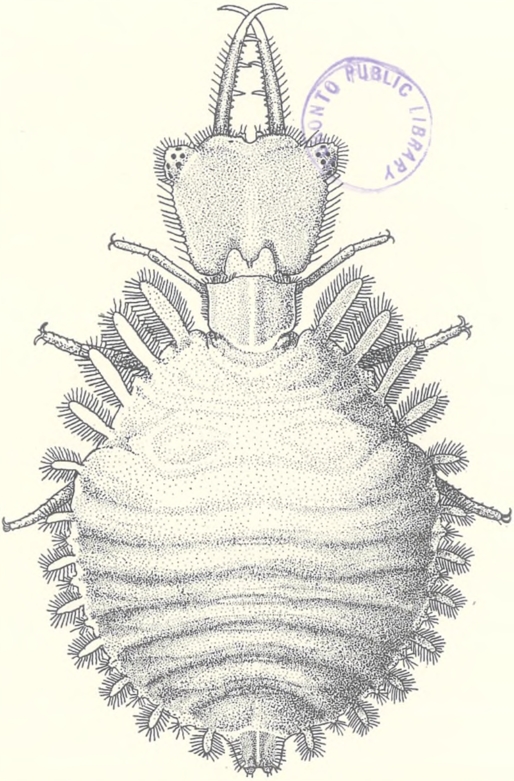

Fig. 7. A green, leaf-inhabiting Ascalaphid larva from Panama.

febure (1842-Ascalaphus), Guérin-Méneville (1846-Ascalaphus), Brauer (1854-Ascalaphus), Westwood (1888-Ascalaphus), McClendon (1902-Ululodes), Gravely and Maulik (1911-Pseudoptynx), Ghosh (1913-Helicomitus), Zaki (1917), Withycombe (1924-Ascalaphus, Ameropterus, Helicomitus, (?) Tmesibasis), van Someren (1924), Tillyard (1926-Suhpalacsa, Acmotus, Stilbopteryx) and Rabaud (1927-Ascalaphus). Some species lay their eggs in very regular rows on plants, either at the tips of stems or along the midribs of leaves (Zaki). In the former cases (American species), as observed by Guilding, Westwood and McClendon, certain structures (repagula), which are really abortive eggs, as McClendon has shown, are placed as series of stockades around the stem below the serially arranged eggs and have therefore been regarded as a protective device. Tillyard (1926) describes the just-hatched larvæ of some Australian species as "sitting close together on the egg shells, all combining to capture an unwary insect; but as soon as one of them reaches the second instar it becomes a cannibal, and many of its brothers fall victims to it." The larvæ of Ascalaphids are lethargic, lying in wait for their prey and normally walking forward, though they are also able to walk backward. Some of the species live on the ground or on the bark of trees (Pseudoptynx, Ameropterus and some Ascalaphus). An undetermined species (FIG. 7) which I have occasionally seen near the laboratory on Barro Colorado Island, Panama, awaits its prey with open jaws and its body flattened down along the midrib on the upper surfaces of leaves. Some of the plant-inhabiting species, like the one just mentioned, have no tendency to cover their bodies with detritus, but this habit is more or less pronounced in others, especially in the terrestrial species (Ululodes). Of Ameropterus of Trinidad Withycombe says: "The larvæ may rest on their empty eggshells for days and are very sluggish.

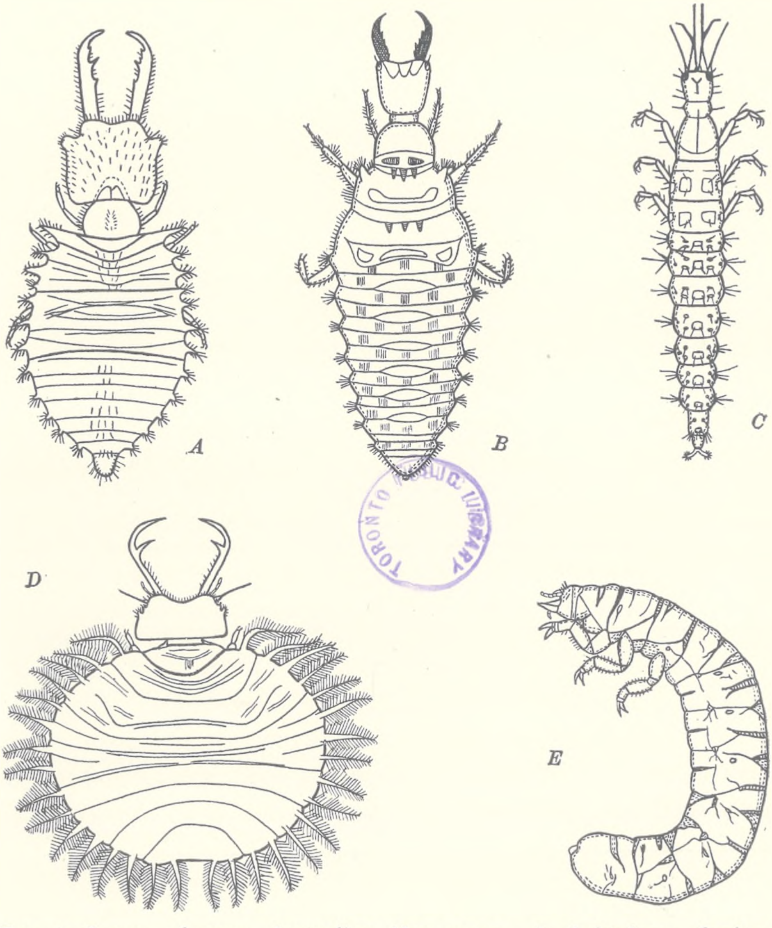

FIG. 8. Larvæ of some Australian Neuroptera. *A, Suhpalacsa flavipes* Leach; *B, Acanthaclisis fundata* Walk.; *C, Euosmylus stellæ* McL.; *D, Osmylops pallidus* Banks; *E, Ithone fusca* Newm. (After Tillyard.)

When they do leave the empty eggs, a very curious performance may be witnessed. If the larva is provided with fine sand, it will proceed to place sand grains upon its back. Ghosh, writing of *Helicomitus dicax,* says that the particles are placed on the back by means of the jaws. I have also observed this with Ascalaphus when hard material such as a brick, has been provided, but when loose sand is given, the larva places the fine grains singly upon its back by means of its fore legs. The action is quite unique and human-like. Each grain is taken between the two tarsal claws and the fore leg is lifted and bent backwards onto the dorsum of the prothorax. The fore legs are generally used alternately and in succession. It is an exceedingly peculiar operation, and one which I should have hardly thought possible, but I have observed it repeatedly." This masking of the body seems to be quite unnecessary in some of the plant inhabiting species, owing to their protective coloration. Gravely and Maulik describe the larva of the Indian Pseudoptynx as living on bark and as flattening itself down and remaining motionless, so that it is almost indistinguishable from its environment. Withycombe (1925) says that a beautiful African form (Tmesibasis?) "is clearly cryptically colored and would be almost invisible upon a tree-trunk. The pattern on the brownish body is produced by patches of black and white. . . . The lateral lobes of this specimen are much produced and flattened. They spread out as a considerable fringe round the insect, and would be closely applied to the tree-trunk." Van Someren (1924) has also described lichen-colored East African Ascalaphid larvæ that harmonized remarkably with the bark of trees and the green paint on a gate post on which they were resting. The Panamanian species above mentioned is green and almost indistinguishable from the leaf on which it rests. Here, too, the fringed lateral lobes of the abdomen are closely applied to the substratum and the jaws, as in the bark-inhabiting *Ameropterus selysi,* observed by Withycombe in Trinidad, are so widely opened ("to about 280°") that they are directed backward and completely hidden under the sides of the mesothorax. When full-grown the Ascalaphid larva, like that of the ant-lion, spins a spherical cocoon, but it is more or less covered with bits of leaves, twigs and other detritus and hidden in crevices of the bark or of the soil, if this happens to be the normal environment of the species. The adults are crepuscular like the ant-lions. Two very primitive genera, Stilbopteryx, represented by a

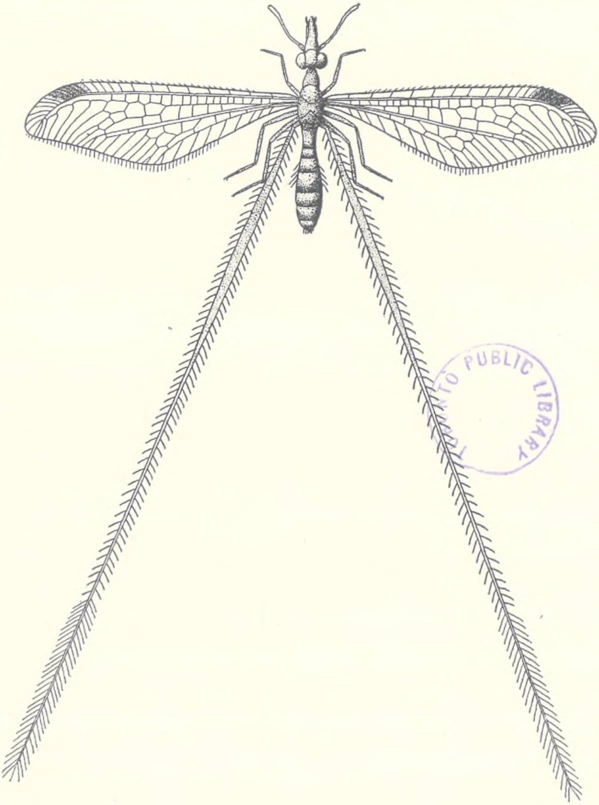

FIG. 9. *Croce filipennis,* an Indian Nemopterid.

couple of species in Australia and Albaridia with a single species in Brazil, have sometimes been regarded as constituting a distinct family, the Stilbopterygidæ, but Van der Weele (1908) gives them only subfamily rank (Protascalaphinæ). Tillyard (1926) describes the Australian species as closely resembling true Ascalaphids but as having shorter antennæ. The larvæ are "huge, black, rugose creatures with round, somewhat flattened bodies, spiny lateral processes, large head and immense jaws; they live in débris on the ground. Imagines fly at dusk with great speed, high up in the air in clearings in the bush. They have no power to dodge in flight and are easily caught by interposing the net in their path."

The remaining family of Myrmeleontoids, the Nemopteridæ, is usually regarded, on the basis of its venational and other structural peculiarities, as less closely related to the ant-lions. The imagines are beautiful insects, with broad, often mottled or banded fore wings and the hind wings reduced to long, narrow, ribbon-like appendages. The not very numerous species are now confined to the subtropical and tropical portions of the Old World, but that the family was once cosmopolitan is shown by the occurrence, mentioned on p. 87, of *Marquettia americana* in the Miocene shales of Colorado. The larvæ, which are veritable dust demons, are peculiar in having a neck-like constriction between the head and thorax, though in the typical genus Nemoptera (*N. bipennis*), described by Withycombe (1924), this constriction is not exaggerated. The larval habits of this species are unknown but it probably lives concealed in the sand or dust of dry open plains like some ant-lion larvæ that do not make pitfalls. The subfamily Crocinæ, however, comprising small, mothlike species (Fig. 9) with a prominent front, short antennæ and extremely tenuous hind wings, are really cavernicolous insects, whose singular larvæ inhabit the dust on the floors of caves, tombs and neglected human dwellings. The most extraordinary larva in the group (FIG. 11), with an inordinately long and slender neck was discovered by Roux in

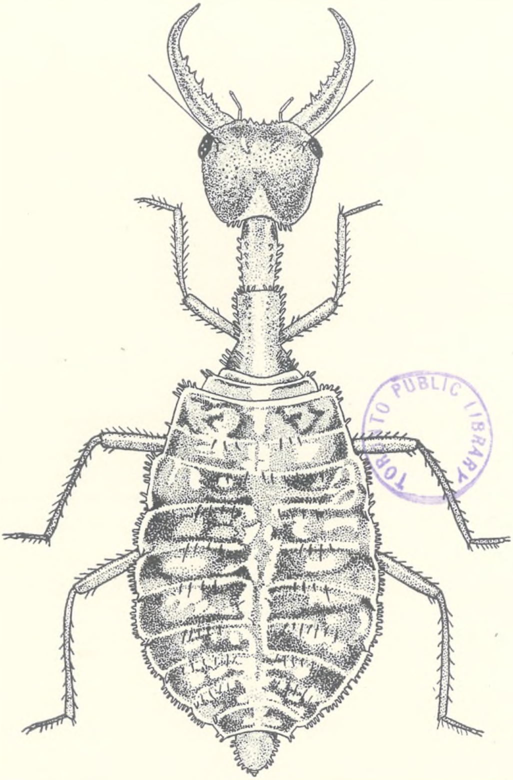

FIG. 10. Larva of *Croce filipennis* Westw. of India. (After Imms.)

the dust of ancient Egyptian rock-tombs as long ago as 1833 and named *Necrophylus arenarius*. It was redescribed by Schaum in 1857, and remained an unsolved taxonomic enigma till it was rediscovered in 1923 in caves and under rocky ledges along the Nile and the imago reared by Storey and E. B. Williams. Eltringham (1923) and Withycombe

(1923[a], 1923[b], 1924) published excellent accounts of the insect. The latter author regarded it as a new species and named it *Pterocroce storyi,* but I have shown (1930) that it is, in all probability, identical with *Necrophylus arenarius.* Aharoni (Blair 1920-21) had previously reared the imago of an allied Crocine, *Nina joppana,* from a very similar larva, though with a slightly shorter neck, found in the dust of caves in Syria in company with gray ticks "called in Arabic 'Delm'." The only other Crocine that has been reared is *Croce filipennis* (FIG. 9). Its larva (FIG. 10), as Maxwell-Lefroy (1909, 1910), Ghosh (1910) and Imms (1911) have shown, inhabits the dust on the floors of bungalows, outhouses, etc., in India. In this form the neck though more elongate than in Nemoptera, is much shorter and stouter than in Necrophylus or Nina. The imago is crepuscular, or flies only in the dark corners of rooms, unlike that of Nemoptera, which flies about in broad daylight. Imms has investigated the whole life-cycle of the insect, beginning with the eggs which were laid freely by the female in beakers containing dust. The larvæ were fed on book-lice (Psocids) and young larvæ of larder beetles (Dermestes). The former are probably the usual food, since they abound in its natural habitat. The larva conceals itself under a covering of sand or dust. According to Imms, the spheroidal pupa is "notable on account of its method of accommodating the long hind wings. These are many times coiled after the manner of watch-springs: they cross each other near their bases, so that the right wing lies on the left side and *vice versa.* The pupa is enclosed in a cocoon composed of sand and débris bound together by silk." That other species of the subfamily Crocinæ are likewise crepuscular and cavernicolous is suggested by the fact that Navás (1910) captured imagines of the Spanish *Josandreva sazi* flying about at dusk within the cavities of old walls, especially those containing sand or dust.

The larval habits of the four Myrmeleontoid families briefly considered in the preceding paragraphs are very largely terrestrial, the exceptions being certain Ascalaphids, which are arboreal or at any rate live an exposed life on plants. Is this to be regarded as a comparatively recent development from terrestrial propensities or is it a persistence or reminiscence of a more ancient preterrestrial

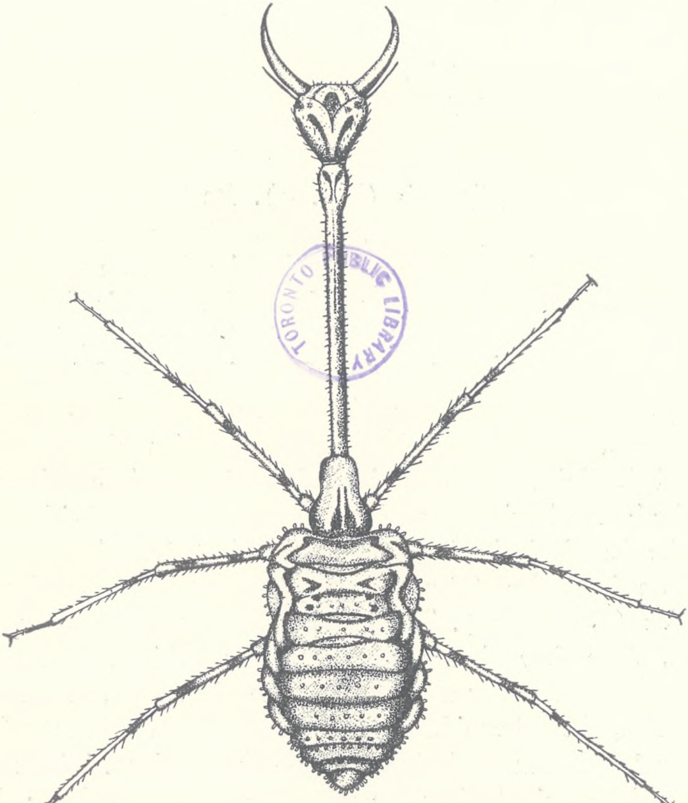

FIG. 11. Larva of *Necrophylus arenarius* Roux of Egypt. (After Eltringham.)

connection with plants? This question is not easily answered because the more primitive superfamilies of Neuroptera do not enable us to determine which of these conditions is really the more ancient. On the one hand the Hemerobioids and the Osmyloids, which in all probability gave rise to the Myrmeleontoids through the Nymphids, are largely phytophilous, and on the other, the larvæ of those most primitive of all Neuroptera, the small superfamily Ithonioidea of Australia (FIG. 8*E*), burrow in the ground and resemble the chaffer larvæ on which they feed.

These Ithonioids, indeed, are supposed to connect the Neuroptera with the Megaloptera, which they resemble in the greater number of larval instars and the venational and other characters of the imago (Tillyard, 1922, and Withycombe, 1924). The Osmyloids are of particular interest on account of the diverse specialization of the larva particularly in the families Mantispidæ, Osmylidæ, Sisyridæ and Myiodactylidæ. The first stage larva of Mantispa is free-living and carabiform like most other Neuropteran larvæ, but after it has become parasitic on the eggs of spiders, it becomes maggot-like, with very short and useless appendages. The same is true of the larva of *Symphrasis varia,* known to parasitize the brood of wasps (Polybia) in Brazil (Brauer, 1887). In the Osmylidæ, represented by the genus Osmylus (FIG. 12*A*), the larva has long slender, straight jaws and is almost amphibious, living in damp localities under stones along the borders of streams but not actually in the water. The larva of Sisyra (FIG. 12 *B, C*), however, is definitely aquatic and lives as a parasite in fresh-water sponges (Westwood, 1842, Anthony, 1902, Withycombe, 1923[b]), using its long needle-like mandibles for piercing and sucking the juices out of its host's tissues. Very different are the larvæ of the Australian and Papuan Myiodactylididæ (Myiodactylus and Osmylops), which have very broad, flat and transversely elliptical bodies and slender mandibles abruptly bent inward at their tips (Fig. 8*D*). According to Tillyard (1926), they are green and hide on the undersides of leaves of Eucalyptus and other plants with their mandibles held open at an angle of more than 180°, ready to snap any insect that comes within reach. The resemblance of this behavior to that of the green Panamanian Ascalaphid larva mentioned on p. 89 is obvious.

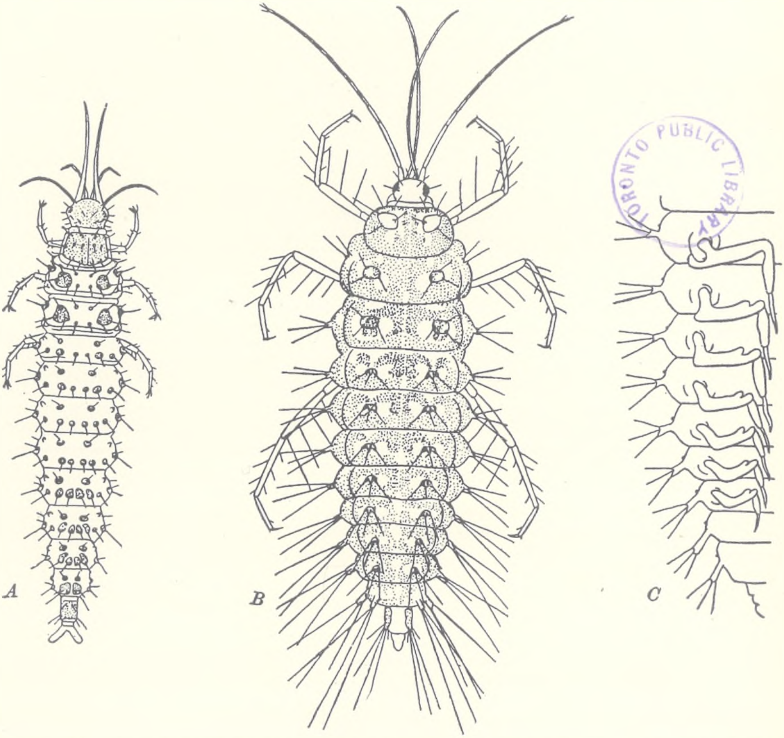

Fig. 12. *A,* Larva of *Osmylus chrysops* L. of Europe; *B,* Larva of *Sisyra fuscata* Fabr. of Europe; *C,* half of ventral surface of abdomen of same, showing the jointed gills. (After E. Rousseau.)

I have dwelt on the various Neuropteran larvæ and have figured a number of the more striking types, because

Rabaud (1927), after presenting a much smaller series—the larva of an ant-lion, an Ascalaphus, an Osmylus and a Chrysopa—has advanced certain generalizations which seem to me to be decidedly inapt. He contends that while all these larvæ differ greatly in behavior, their structural resemblances are very close, that their adaptation to their environment is a matter of their nervous reactions and that these are by no means necessarily accompanied by morpho-

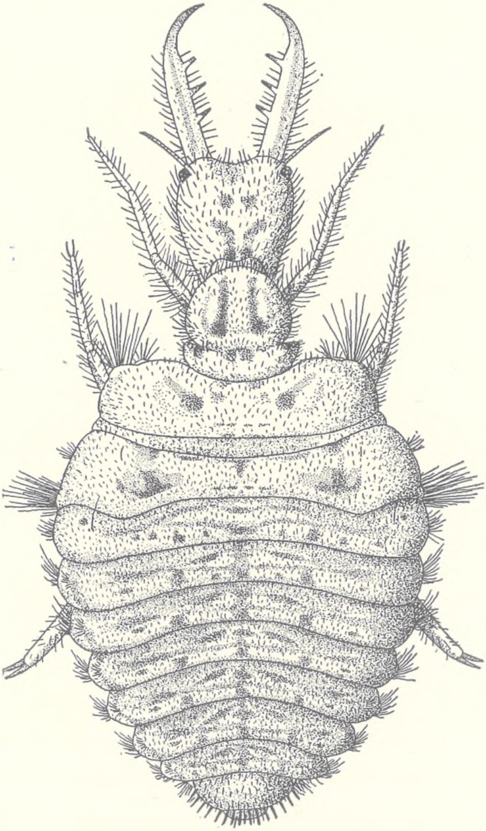

FIG. 13. Full-grown larva of the common North American ant-lion, *Myrmeleon immaculatus.*

logical or functional adaptation in the details of their structure. He believes, therefore, if I understand him correctly, that there is "an independence of conformation and of sensory physiology as opposed to the ethology" of the various species. I am unable to adopt this point of view, for any close study of the Neuropteran larva, such as has been undertaken by Doflein (1916) in the case of the antlion, or by Withycombe (1924) in a number of other forms, cannot fail to reveal a host of very subtle morphological and functional adaptations to the specific environment and especially to the prey. The whole body of the Myrmeleontid larva, as Withycombe (1924) says, "is modified for its manner of living, even the setæ being employed for the seizure of prey"— and he might have added, also for tossing sand —"by an upward and backward movement. The hind legs and the apex of the abdomen are modified for digging backward." And Doflein (1916) is equally emphatic when he remarks that "we have in the ant-lions an example of the most extreme adaptation of structure to the conditions of existence. The structure of the organs and their concomitantly inherited mode of functioning enable the animal to maintain its singular and apparently so precarious manner of living. At the same time it is no longer able to adapt itself to unusual conditions and hence, when these change, very easily succumbs. We therefore discern in its activities, one of the main types of animal behavior, the *rigidly adapted type,* in which the animal is endowed at birth with the structure and ability to respond to the most delicate modulations of its normal environment. We have called this one-sided adaptation: we may also speak of the ant-lion as a *life-specialist.*" The same considerations apply to other Neuropteran larvæ. Are we to suppose that the gills and the needle-like mandibles of the sponge-sucking Sisyra (FIG. 12 *B, C*) are merely "quelconques", to use Rabaud's expression, because its general structure is Neuropteran? We have only to glance at the very different mandibles in the accompanying figures of Ascalaphus, Myrmeleon, Osmylus and Sisyra to realize that these parts have undergone far-reaching structural and functional adaptations during their long phylogenetic history. Withycombe (1924) has shown that there are really two different types of mandibles among Neuropteran larvæ, the straight, which are present in forms (Sisyra, Osmylus, Chrysopa, etc.) that feed on creatures that cannot readily escape and the caliper-like, which characterize forms (Myrmeleon, Ascalaphus, Osmylops, etc.) that seize struggling or easily escaping prey. These types are evidently divergent developments of the intermediate and feebly curved jaws of the Megaloptera and of the most generalized of all Neuropteran larvæ, Polystœchotes (Welch, 1914).

We may conclude from this long and, I fear, rather wearisome survey, that the evolution of the Neuroptera culminated, even as early as the Oligocene, in the highly specialized genus Myrmeleon. Its cosmopolitan distribution and abundance wherever conditions are favorable, also show that it is, with the possible exception of the aphis-lions, or Chrysopids, the dominant group of the order. This seems to contradict the usual assumption, expressed by Doflein and more emphatically by Rabaud, that the ant-lions lead a very precarious existence in their arid environment, but it must be remembered that the usual interpretation of their frequent long periods of immobility without feeding, may be unduly anthropomorphic. These periods are very probably not spells of actual starvation but of 'asitosis', a frequent phenomenon in insects, larval, pupal and imaginal. So many Neuropteran larvæ exhibit a similar immobility and refrain from actively seeking their food that we may suppose the condition to be both ancient, or of long standing and less deleterious than we might be inclined to assume. The immobility undoubtedly retards metabolism, but

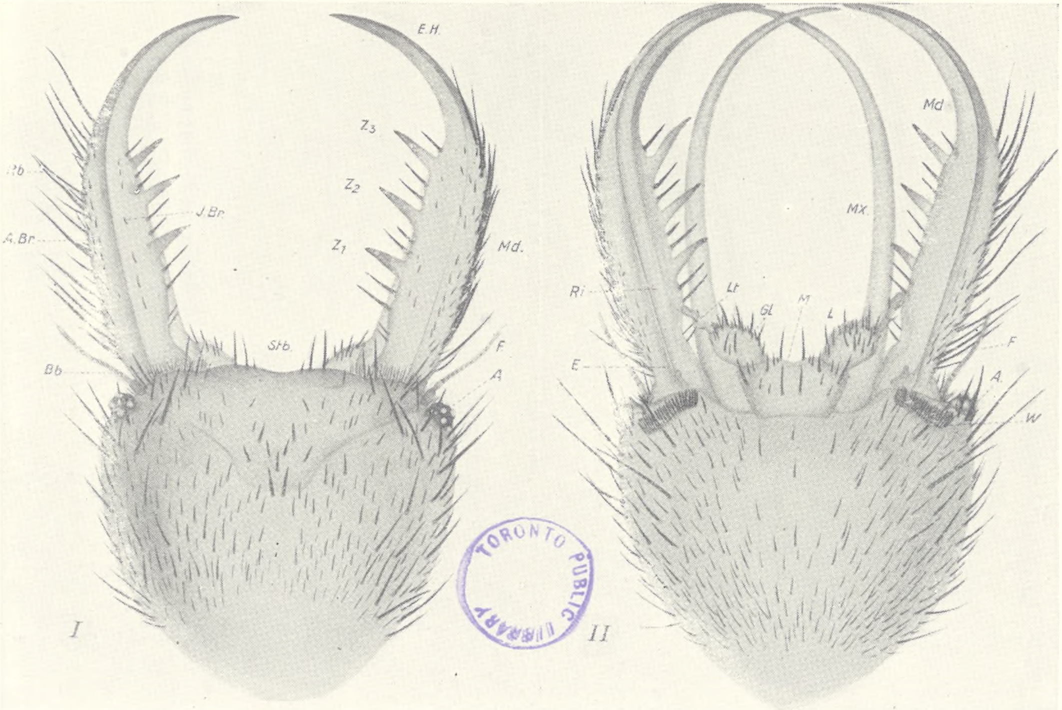

FIG. 14. I, Head of ant-lion from above (x 30), A, eyes; F, antenna; Md, mandible; E.H, its terminal hook; Rb, its marginal setæ; A.Br, outer rows of bristles; J.Br, inner row of bristles; Stb, frontal bristles; Bb, upper row of hairs on the mandibular articulation; Z_1-Z_3, inner teeth of mandible.

II, Head of ant-lion from below, with the maxillæ (Mx) drawn out of the grooves (Ri) of the mandibles (Md); F, antenna; W, comb of hairs beneath the eye; M, median piece of labium or lower lip; Gl, glossa; Lt, labial palp; L, labial bristles; E, proximal end of mandibular groove. (After F. Doflein.)

the much more voluminous fat-body in ant-lion larvæ and other lethargic species as compared with such active hunters as the larvæ of many Hemerobiids, shows that under normal conditions ant-lions do not suffer greatly from starvation. The facts that only liquid food is ingested, that the stomach does not communicate with the hindgut during larval life and that there is a very thorough assimilation of such prey as can be captured, may also be significant in this connection, as it is in the case of the similarly lethargic larvæ of many of the higher Hymenoptera. It is true that growth is retarded, but this may not be a serious disadvantage. The ant-lion's motto is "all things come to him who waits", and the inhabitant of such a sparsely inhabited medium as sand or dust is not pressed for time. There is also the further consideration that the ant-lion's asitotic and digestive idiosyncrasies may have been developed during the gradual decline of a geological age (the Early Tertiary) when the insect fauna was considerably richer in species and individuals and prey, therefore, more abundant than at the present time.

My review of the work on the ant-lions since the eighteenth century must be greatly condensed and confined to their more interesting structural, physiological and behavioristic peculiarities. Most of the literature of the early nineteenth century, though cited in the bibliography at the end of the volume, I shall pass over without comment. Much of it, indeed, consists of more or less casual observations of the creature's habits and adds little to the discoveries of the preceding century. During the seventies, eighties and nineties of the last century, however, when taxonomy was becoming more precise and morphological investigation was all the vogue, the ant-lions and their allies became favorite objects of study and a number of solid contributions were published by Hagen, Brauer, MacLachlan, Meinert, Dewitz, Nagel, Rambur and especially

Redtenbacher. The behavioristic accounts of these and other European authors refer to the two common species, *Myrmeleon formicarius* and *M. europæus,* which may be readily separated in the imaginal stage, because the former has unspotted, the latter spotted wings, but their larvæ are almost indistinguishable. Those of *formicarius* seem to be characterized only by having dark spots on the hind tibiæ and trochanters (Redtenbacher 1884b). We are not always sure, therefore, of the species to which the observations refer, unless the imago has been reared and accurately identified. This confusion also pervades some of the papers published during the present century. Rey (1895) believed that the two species differ also in the manner of making their pits and in the choice of habitat, *formicarius* living in protected and *europæus* in open places.

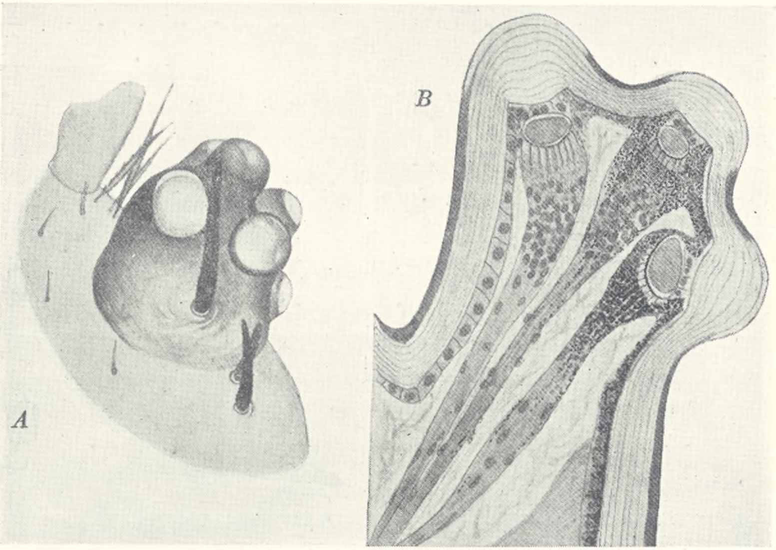

FIG. 15. *A,* Right ocular tubercle of Myrmeleon, from above, showing six of the seven eyes. *B,* Section through same, showing three of the eyes with their bulging corneas, their vitreous bodies, retinæ and optic nerves. (After Doflein.)

This may account for certain discrepancies in the literature. The continuing divergence of the interests of the taxonomists on the one hand and of the anatomists, physiologists and behaviorists on the other has been unfortunate, since the latter often make little effort to identify their material accurately and the former fail to record the behavioristic and habitudinal information which they possess.[1]

The ant-lion studies published since the beginning of the present century have not only absorbed all that was valuable in previous work but, owing to more refined observation and more frequent resort to experiment, have revived what was beginning to be a languid interest in the insect. This new literature includes a number of important contributions by Comes, Doflein, Bierens de Haan, Lozinski, Meissner, Navás, Petersen, Rabaud, Rengel, Stäger, Tillyard, Withycombe, etc. It is a reproach to our American entomologists that they have shown so little interest in the ant-lions, especially when the richness of our fauna is taken into consideration. Besides the taxonomic works of Hagen and more recently of Banks, there is only a rather meager series of observations on habits and behavior by Birge, Mrs. A. B. Comstock, Hagen, Moody, Moffat, McCook and Rau and a somewhat more ambitious experimental study by Turner (1915). Moreover, most of the observations are old and all refer to a single species, *Myrmeleon immaculatus*, which occurs throughout the

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[1] Hence such confusions as the one of which Rabaud (1927) seems to be guilty when, on p. 437, he figures and describes the larva of *Megistopus flavicornis* Rossi as a typical ant-lion and on pp. 452-463 describes the behavior of Myrmeleon, without indicating in any way that the two descriptions refer to quite different insects. Redtenbacher stated in 1884 that the habits of the Megistopus larva were unknown and I fail to find any account of them in the more recent literature. Either, therefore, Rabaud has made an interesting discovery, without knowing it, in finding that it makes pits, or he has failed to notice that the larva with which he experimented differs generically from the one he used as a paradigm of ant-lion structure. Or did he select Megistopus merely because its abdomen is narrow and more like that of the other Neuropteran larvæ which he figures?

United States and is closely related to the European *M. formicarius*. According to Hagen, the American species has a somewhat longer pupal period and its pitfalls are deeper in proportion to their width. Of the behavior of the exotic species of Myrmeleon we possess only a few general descriptions, namely of *M. leachi* in St. Vincent and Jamaica by Guilding (1833) and Gosse (1851), of *M. frontalis* in Java by Jacobson (1912, 1926), of *M. uniseriatus* in New South Wales by Tillyard (1915) and of *M. celebensis* in the Philippines by F. X. Williams (1928). Some of the early explorers, like D'Orbigny and Darwin, refer to ant-lion pits in Patagonia and Australia, but give no clue to the generic identity of the larvæ.

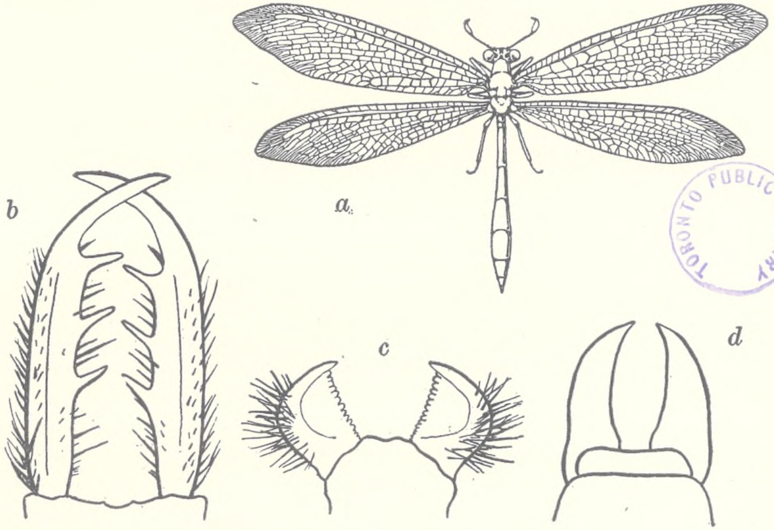

FIG. 16. *a,* Imago of ant-lion. (*Myrmeleon formicarius* L.) (After Hesse and Doflein); *b,* mandibles of larva; *c,* of pupa; *d,* of imago of same. (After Lucas.)

The imaginal Myrmeleon (FIG. 16 *a*) is a delicate, elongate insect, measuring 5 to 6 cm. and resembling a damsel-fly, except that its antennæ end in knobs and its two pairs of wings, instead of being rounded, are pointed at their tips. The eyes are large, prominent and of the usual compound type, the mandibles short, broad and edentate (FIG. 16 *d*). The insect appears in dry open woods or sandy localities from June to August, rarely as early as May or as late as November. It is crepuscular or nocturnal, resting during the day on the low vegetation. When disturbed its flight is fluttering and hesitating. Its life span, as determined by Meissner, is about 20 days. It feeds, according to Redtenbacher (1884), on a variety of small insects, but Réaumur saw it eating fruit (plums). The sexes are very much alike, except in size. No careful study has been made of the mating habits or of oviposition; Réaumur, Rösel and all the early observers mistook the reddish meconial pellets—the solidified remains of the larval food, which are discharged by the imago soon after emergence—for eggs. These, however, were first seen by Brischke (1879), who describes them as small, white and elliptical. They are deposited in a row, adhering to one another, in the sand. He gives their number as five only, but Meissner (1917) states that they number about a dozen. For oviposition the female prefers situations with southern or southwestern exposure. The eggs hatch before winter and the youngest larvæ, though at first paler, have the same form and structure as the oldest. Réaumur and later Girard (1866) and Giard (1893) noticed that the imago, and especially the male, when pressed between the fingers, emits a pleasant odor of roses and that this clings also to the boxes in which the insect emerged. Girard called attention to the emission of a similar odor in several other arenicolous insects and Giard remarks that "it would be more exact to say that it is peculiar to several insects whose larvæ are myrmecophagous, e.g., the Cicindelidæ [tiger-beetles]. It is due, without doubt, to some formate with an organic base. In fact, it is known that ethers thus formed some-

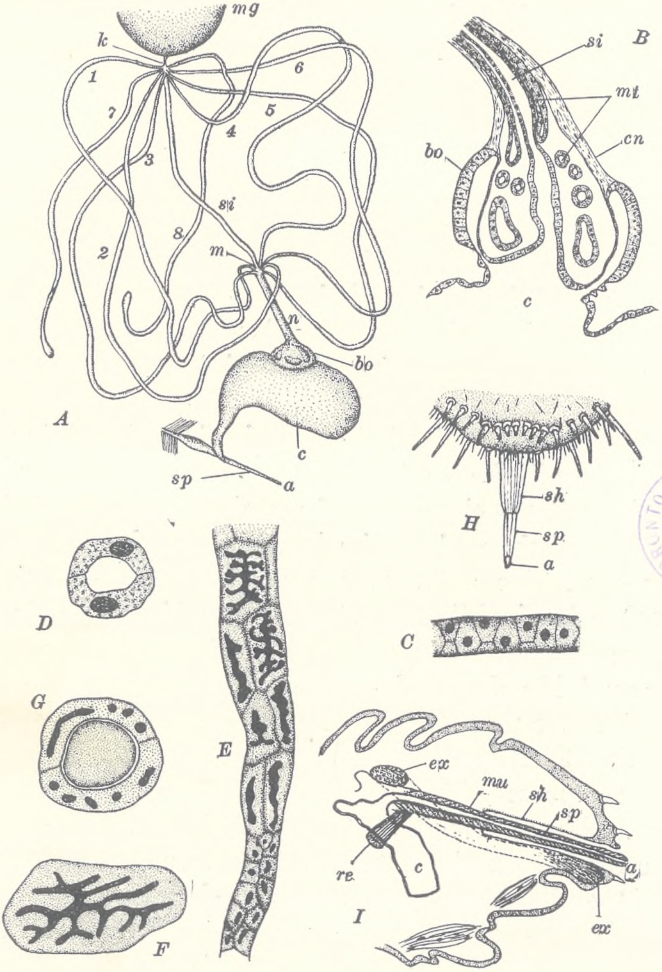

FIG. 17. Structure of hindgut of *Myrmeleon formicarius* and its modification as a spinning organ (after Lozinski). *A,* hindgut and its appendages *in toto; mg,* posterior end of stomach, or midgut; *k,* anterior contracted end of small intestine (*si*); 1-8, the eight Malpighian tubules arising from the small intestine near *k; m,* point at which the Malpighian tubules 1-6 apply themselves to the posterior portion of the small intestine, run back and terminate with expanded tips in the button-shaped organ (*bo*); *c,* large intestine, or cæcum; *sp,* spinneret; *a,* opening (anus) at tip of spinneret; *B,* longitudinal section through button-shaped organ; *si,* small in-

times have agreeable odors. Ethyl formate is even employed in the manufacture of artificial rums." More recently Eltringham (1926) seems to have discovered the source of the odor in peculiar glands enclosed in small knob-shaped organs at the bases of the hind wings of the male. The scent seems to be diffused by a tuft of hairs on the surface of the knobs. He detected similar organs also in the males of several other Myrmeleontid genera.

The whole life cycle of the ant-lion is longer than that of most insects, owing to the intermittent and quantitatively extremely variable food supply of the larva. In any locality, therefore, there are apt to be great differences in the size of individuals presumably hatched at very nearly the same time. Even in the laboratory, where food may be provided in greater abundance than in the field, the larvæ often fast or become asitotic for long periods. Meissner (1908), after long observation, concludes that the normal life cycle covers two whole years. Thus larvæ hatched from eggs in the summer of 1905, failed to produce imagines till the summer of 1907. There were three periods of active feeding, during three consecutive summers, separated by two periods of prolonged hibernation of about 240 days each. Since these larvæ were well fed in the laboratory, it is not improbable that in the field some individuals may have a triennial or even more prolonged larval period. Meissner

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testine; *mt,* Malpighian tubules, *cn,* connective tissue sheath enclosing Malpighian tubules 1-6; *bo,* button-shaped organ. *C,* piece of Malpighian tubule in excretory phase; *D,* cross-section of same; *E,* portion of Malpighian tubule beginning to secrete silk, showing transformation of excretory cells with simpler round nuclei into large sericiparous cells with ramified nuclei. *F,* a single sericiparous cell, more enlarged; *G,* cross-section through sericiparous portion of *E,* showing the liquid silk in the lumen; *H,* hind end of abdomen of larva with extruded spinneret; *sh,* sheath of spinneret; *sp,* spinneret, *a,* anal opening. *I,* median sagittal section of tip of body with retracted spinneret; *c,* cæcum, continued as the fine lumen of the spinneret (sp) to the anal opening (a), *sh,* sheath of spinneret; *mu,* muscles in walls of spinneret; *ex,* extensor muscle which everts the organ; *re,* retractor muscle which withdraws it into the body.

(1906) found that the larva moults its skin at long intervals, but the exact number of ecdyses was not determined. He was convinced that there are four or five and that the larva, after passing its second winter, pupates without another ecdysis except, of course, the one immediately preceding pupation and following the spinning of the cocoon.

Compared with the slender, elegant imago, the larval Myrmeleon (FIG. 13) is a rough, squat creature scarcely more than 10 to 12 mm. long when full grown. Its head (FIG. 14), is rather small and subtrapezoidal, narrowed behind and feebly rounded on the sides, with long, flattened mandibles (*Md*), straight at the base and rather strongly bent inwards at their falcate, pointed tips. Along their internal borders there are three stout teeth (*Z1*—*Z3*) and several stiff bristles, or setæ. Each mandible is hollow, or rather channelled on the ventral side with a deep groove (*Ri*) in which lies the smooth maxilla (*Mx*), shaped somewhat like the mandible but more slender and cylindrical, and with its acute tip microscopically serrated on both sides. The serrations are directed towards the tip along the inner and towards the head on the outer side. Detailed studies of the mouthparts have been made by Dewitz (1881, 1882), Meinert (1879, 1889), Lozinski (1908), Doflein (1916) and others. Though a mouth opening is present, as Meinert demonstrated, it remains tightly closed throughout larval life, and the juices of the prey are conducted to the mouth cavity along the mandibular grooves in which the maxillæ may be moved forward and backward like pistons. According to Lozinski, there is at the base of the maxilla a gland that pours its secretion into the mandibular canal. The labium (FIG. 14 *II*), or lower lip is small and consists of a broad basal piece (FIG. 14 *II M*), with short, separated glossæ (*Gl*), each bearing a small 4-jointed palp (*Lt*). The 11- to 13-jointed antennæ (*F*) are very small, slender and naked. The eyes (FIG. 15), which were first carefully studied by Hesse (1901) are 14 in number, seven on each side. They stand out as separate convexities on a rounded protuberance situated at the anterolateral corner of the head and directed outward. Hesse found each eye to consist of a well-developed lens and vitreous body and a retina made up of 40 to 50 slender retinulæ, or sense-cells, terminating distally in distinct visual rods. One of the seven eyes on each protuberance is directed downward, another almost horizontally and forward, two are turned laterally and one posterolaterally; the two on the upper surface are directed upward and slightly anterolaterally. The seven lenses are therefore directed towards all sides, except backward. The structure and arrangement of the eyes show that they are by no means poorly developed or vestigial, though they are of a primitive type and, as Hesse suggests, represent a transitional stage between ocelli and compound eyes. There is also experimental evidence to show that the ant-lion perceives the direction of the light and to some degree the position of its prey. Authors like Comes (1909), who claim that the insect is blind, are certainly in error. Rabaud (1927), too, has probably underestimated its visual powers in his endeavor to show that it is a purely tactile creature.

Beneath each eye there is a peculiar comb of short bristles (FIG. 14 *W*), which may serve to keep the sand out of the maxillary articulation. The ant-lion's neck is long, narrow and so mobile that it permits the bending of the head, not only downward and vertically upward, but also to a lesser extent, laterally. The three thoracic segments are distinct; the prothorax is small, semicircular and nearly as narrow as the head; the mesothorax is broader, and the metathorax is the broadest segment in the body. The abdomen, which gradually tapers posteriorly from its base, consists of nine visible segments, traversed on both the dorsal and ventral sides by a pair of longitudinal furrows.

The abdominal, as well as the meso- and metathoracic segments, each have a welt-like swelling on each side. Furthermore, each of these segments, except the last abdominal, has on each side a tubercle furnished with a tuft of long setæ. These are best developed on the thoracic segments. The last segment bears on its broadly rounded tip two rows of very short, stout, blunt, backwardly directed setæ. There are ten pairs of spiracles. The first and largest pair is on the shoulders of the mesothorax. The stigmal orifice is two-lipped and the lips are provided with teeth which, when the orifice is closed, fit into one another like those of a steel trap, an arrangement that would seem to be admirably adapted to keeping the dust out of the tracheæ. There are two much smaller spiracles on the sides of the metathorax and each of the abdominal segments has a still smaller pair. Besides their toothed borders all these spiracles are protected by clusters of peculiar bifurcate hairs, which probably act as dust-breaks.

The legs are peculiar in structure, and in having long coxæ which are widely separated. All are so arranged that the terminal joints can be turned either anteriorly or laterally, a significant peculiarity in connection with the retrogradient gait of the insect. The fore and middle legs are weak and very slender, the fore pair usually directed straight forward along the sides of the head, the middle pair laterally and at right angles to the median longitudinal axis of the body. The hind legs are short and stout and have the tibia and tarsus fused to form a single joint. These legs are always strongly flexed. All the legs possess pairs of stout claws, which in the hind pair, as Doflein has shown, are worked by an interesting mechanism.

Though on the whole rather feebly chitinized, the antlion's integument is tough, of a sordid yellowish brown or yellowish gray color on the dorsal surface, with the ventral surface and legs paler and the mandibles reddish. The head and thorax are symmetrically spotted or clouded with dark brown and there are several rows of spots of the same color on the dorsal and ventral surfaces of the abdomen. The general coloration may be described as cryptic, or protective, since it is very much like that of the medium in which the insect lives, and the resemblance is increased by the dust or sand particles adhering more or less firmly to the bristly surface of the body. The structure and arrangement of the setæ, which are the ant-lion's most important sense-organs, have been carefully studied by Lozinski (1910) and Doflein (1916). Some of them, especially on the tip of the abdomen, the anterior border of the hind legs and other parts concerned in locomotion, are designated as staying bristles ('Stemmhaare'). They are stout setæ with very mobile articulation to the integument and are often covered with longitudinal rows of serrations. Both Lozinski and Doflein describe large gland cells in connection with their bases. These setæ pass over into those of a longer and more pointed type, the macrotrichia ('Langborsten'). Others of a shorter type ('Kurzborsten'), usually in clusters and occurring on the more exposed surfaces of the body, especially on the dorsum and venter of the abdomen, are directed forward and have somewhat recurved tips. These three types are the first to receive all the stimuli of pressure and touch that assail the insect and are, therefore, important because they function both mechanically and as sense-organs. Setæ of two other smaller and more delicate types are distributed among the preceding, namely, the plumose setæ, which are long and tapering and beset with 8 to 10 rows of very fine outstanding hairs, corresponding to the fine serrations on the staying bristles. They are found on the body but not on the mandibles nor, in their typical form, on the legs. The last type comprises the furcate hairs ('Gabelhaare'), which have a short base and two long tapering prongs diverging at right angles from the base and therefore almost parallel with the insect's integument. They are covered with a delicate plumosity and are more or less flexuous. Most of the aforementioned types of setæ are connected by intermediate forms confined to particular parts of the body. Some of them on or near the bases of the mandibles and the articulations of the legs are designated as postural hairs ('Stellungshaare'), because they inform the insect of the relative position of its joints and segments. They would seem to be important, because, so far as known, Arthropods have nothing corresponding to sensory innervations of the muscles and therefore lack a complete equivalent of the vertebrate 'muscle-sense'.

Much has been written on the food preferences of the ant-lion and on the organs concerned with securing the prey and digesting its tissues. And though all authors agree that the ant-lion will readily seize almost any small living insect, crustacean, spider or Myriopod, not to mention another individual of its own species, that comes within reach of its mandibles, there has been considerable difference of opinion in regard to its predilection for ants. Comes (1909), for example, claims that after long observation of the ant-lions on the slopes of Mt. Etna he failed to see them capture a single ant, and Meissner (1917), who has had these insects under observation for years, declares that they do not as a rule prey on ants. On the other hand, the majority of authors, including Doflein (1916), are convinced that ants are the most important prey, at least of the older larvæ. Stäger (1925) has shown that in some Swiss localities where ant-lions abound, ants or their nests may be difficult to find, while in others where ants are abundant, ant-lions may actually make their pitfalls in the fine detritus near or even on the nest mounds. From observation of our American Myrmeleons, I should say that in most localities ants constitute a considerable part of their dietary. This is probably due to the fact that worker ants, on account of their small size and lack of wings, are more easily caught in the pitfalls than many other insects and are, indeed, much more frequently caught simply because they happen to be the most active and numerous insects on the soil throughout the spring and summer months even in the dry sandy spots preferred by the ant-lions.

Of the internal organs of the larval ant-lion, I shall consider only the alimentary canal, because of its unusual interest in connection with the treatment of the food, and the singular, transient specialization of the Malpighian tubules as spinning organs. Réaumur was the first to be impressed by these remarkable conditions, and their study has been continued down to the present time by a series of investigators — Ramdohr (1811), Dutrochet (1818), Dufour (1834), Burmeister (1839), Brauer (1854), Leydig (1855), Gerstäcker (1874), Meinert (1879, 1880, 1889), Dewitz (1881, 1882), Adlerz (1890), Rengel (1908), Lozinski (1908, 1910, 1911, 1921 a-c), Doflein (1916) and Stäger (1925). I have already described the structure of the mouthparts. They show that the ant-lion can utilize only liquid food already digested outside the body as in larval water beetles (Dytiscidæ) and fire-flies (Lampyridæ), which have similar mouthparts. The living prey is seized with the mandibles and the finely serrate tips of the stylet-like maxillæ are thrust forward along the mandibular canals through its integument. This permits the entrance of a poisonous liquid which is a secretion either of the maxillary glands described by Lozinski or of the salivary glands. That the secretion is extremely virulent has been demonstrated by Stäger, who found that it will kill an ordinary ant (Formica) in an average time of 3.3 minutes, a medium-sized spider in from one to three, and an earwig (Forficula) in seven minutes. Probably the poison is a toxalbumin like that of certain spiders, as Stäger suggests. Since all the soft tissues of the victim are soon completely liquefied, so that they can be sucked back through the very tenuous capillary spaces between the mandibles and maxillæ into the long, slender gullet and stomach, we must assume either that the poison has a proteolytic as well as a paralyzing and lethal action, or that a second secretion, derived from the stomach itself, is simultaneously, as claimed by Bugnion (1926) for fire-fly larvæ or, as has been shown in the larval water beetle Dytiscus (Portier 1909), subsequently injected. Even in some adult beetles like the Carabids the stomach yields a proteolytic secretion which is poured on the food (Jordan 1910, 1913), and something very similar occurs in blow-fly larvæ, as Fabre observed in 1907. Further discussion of this matter will be reserved for Chapter V, where I shall show that a very similar extraintestinal digestion occurs in the Vermileo larva.

The alimentary tract of the ant-lion is so complicated that, notwithstanding all the skill and patience of the long series of able investigators above cited, certain details, such as the source of the poison and proteolytic secretions injected into the prey, still remain obscure. The general anatomy of the tract, however, is clearly like that of many other insects. It consists of the three primitive regions, the foregut, midgut and hindgut, each of which, except the midgut, has undergone further subdivision and differentiation. The foregut yields the mouth-cavity, pharynx, gullet (œsophagus), crop (ingluvies) and gizzard (proventriculus), the midgut the stomach (ventriculus) only, the hindgut the small intestine (ileum) with the Malpighian tubules, the large intestine (colon, or what Lozinski calls the cæcum), and the rectum, which is peculiarly modified to form the spinneret. Behind, the mouth-cavity, which, as we have seen, has no external opening during larval life, except the mandibular channels in which the maxillæ move, is followed by the pharynx, a short region with muscular walls, important in the act of imbibing the juices of the prey. A pair of small salivary glands enters the pharynx before it passes over into the œsophagus, a long, slender tube which serves to conduct the liquid food to the crop. Like the œsophagus, this is a thin-walled, chitin-lined structure with muscular walls, but is much more voluminous. It seems to function merely as a temporary receptacle for the food, which is gradually passed back into the stomach through a short valve-like constriction, the greatly simplified homologue of the complicated proventriculus of many other insects. The stomach is a broad, curved, tubular organ, 8-10 mm. long, and very feebly constricted in the middle. It has been known since Réaumur's and Rösel's time that its lumen, or cavity, is closed at the posterior end throughout the life of the larva. Hence there can be no evacuation of the unassimilated portions of the food through the remaining sections of the alimentary canal, known collectively as the hindgut. Renzel (1908), has devoted a special paper to his own and previous investigations of this peculiar occlusion of the stomach. Now since this organ is closed off from the more posterior portion of the alimentary tract, it must be the seat of all absorption of food and of at least such secretions as are not produced by the maxillary and salivary glands.

Our interest therefore centers in the stomach lining, which consists of large columnar epithelial cells with their apices next to the lumen and their bases next to the muscular walls of the organ. We possess two interesting studies of the stomachal epithelium of the ant-lion, one by Adlerz (1890) and one by Lozinski (1922^c), but while their illustrations are alike, their interpretations are contradictory, for what Adlerz regards as the secretory activities of the cells are described by Lozinski as absorptive. Though the latter is a very competent investigator I believe, nevertheless, that this detail in his fine studies of ant-lion anatomy is erroneous. The stomachal epithelium obviously exhibits changes very similar to those observed by many other authors in a number of insects of all orders and will be again discussed in Chapter V in connection with the Vermileo larva. According to the latest researches on insects in general, so thoroughly reviewed by Jordan (1913), all the cells of the stomachal epithelium are alike (homomorphic) and each of them passes through alternating absorptive and secretive phases. What is usually called the 'resting stage' is absorptive. The apical surface of the cell as seen in sections is then sharply marked off by a peculiar striated border, the rhabdorium, formerly supposed to be cilia, before it was learned that these structures do not occur in Arthropods though common in various organs of all other animals, except the thread-worms (Nematodes). After functioning for a time in absorption the cell passes over into the secreting phase by accumulating in its cytoplasm a clear liquid. The rhabdorium disappears and the secretion causes the apical end of the cell to swell and eventually to break off as one or more droplets which fall into the lumen and diffuse among the food. Thereupon the cell shortens, reacquires the rhabdorium and enters on another absorptive phase. After repeating this cycle a number of times the cell is worn out, is pushed into the stomach cavity to be itself digested and its place is taken by a younger cell, one of the germinal, or substitution cells ('Ersatzzellen'), that are present in small, compact clusters here and there between the bases of the adult epithelial cells. Not only the cytoplasm but also the nucleus of the functional epithelial cell in its various phases undergoes interesting changes, but these are too intricate for consideration in this place. After passing through the secreting phase and before reacquiring the rhabdorium, the epithelium in part or as a whole gives off, as Lozinski has shown, a delicate, continuous, chitinous 'peritrophic' membrane, which surrounds the undigested remnants of the food after each feeding, so that in all sections of the whole stomach, its cavity is seen to be occupied by a solid mass of refuse, interspersed with concentric membranous envelopes like the skins of an onion. It is this mass, including urates apparently excreted at certain times by the stomachal epithelium, that is retained in the midgut even during the pupal stage and is finally discharged as the meconial pellet after the lumen of the stomach has in the imago become continuous with that of the hindgut.

For the purpose of elucidating the peculiar differentiation of the hindgut, I have borrowed the illustrations (FIG. 17) from the first of three valuable papers by Lozinski (1911, 1922*a,* 1922*b*). The small intestine (*A si*), though surprisingly tenuous, nevertheless possesses a lumen, but as previously stated it is closed off at its junction with the stomach. As shown in the figure, there arise from the intestine a short distance behind the stomach eight Malpighian tubules (FIG. 17 1-8), each of which is nearly as thick as the intestine. Two of the tubules (7 and 8) end freely in the body cavity with enlarged tips, whereas the other six loop backward and at the point *n* seem to reunite with the intestine, which continues for some distance as a somewhat thicker structure and then suddenly expands to form what Lozinski has called the button-shaped organ (*bo*). He has shown in section, however, that the six tubules instead of actually uniting with the intestine, merely apply themselves to its surface and continue backward for some distance enclosed in a sheath of connective tissue (thus causing the apparent thickening of the intestine) and terminate with their enlarged blind tips in the button-shaped organ. The latter therefore consists of the somewhat enlarged end of the intestine surrounded by the tips of the six Malpighian tubules and enclosed in a short sac produced by the forward folding of the next section of the hindgut, the thin-walled large intestine, or cæcum (*c*). This is abruptly narrowed posteriorly and continued as the rectum, which ends in the telescoped, tubular spinneret (*sp*). The minute opening at the tip of this peculiar eversible organ is therefore morphologically the anal orifice (*a*).

The Malpighian tubules, of course, function as excretory organs, or kidneys, and have the same structure as in other insects as shown in FIG. 17 *C,* being slender tubes with walls consisting of a single layer of cells with flattened, ellipsoidal nuclei. In cross-section (FIG. 17 *D*) the small lumen is seen to be enclosed by only two or three cells. Now when the adult larva is about to pupate, these cells show first, a heightening of their excretory function and a sloughing of some of their cytoplasm into the lumen, and then rather suddenly undergo an extraordinary transformation into sericiparous, or silk-producing cells. This occurs throughout all the tubules, except in short portions at the junctions of all of them with the intestine and the blind, enlarged tips of the six enclosed within the button-shaped organ. Both the cells of the Malpighian tubules and their lumen increase in size and the nuclei of the former become greatly ramified (FIG. 17 *E, F, G*), and begin to secrete the glairy liquid silk into the lumen. This substance pours from each of the tubules into the small intestine which conducts it to the cæcum where it is stored. During the spinning of the cocoon the liquid passes through the rectum and the protrusible, mobile spinneret as a fine sticky thread which on hardening in contact with the air acquires all the properties of silk. After the cocoon is spun the cells of the Malpighian vessels lose their sericiparous function, resume their original structure and again become excretory!

This direct transformation of specialized excretory cells into specialized sericiparous cells and *vice versa* is so unusual and will appear even to some biologists as so improbable that a few comments seem to be called for. The facts are indisputable. The phenomenon is not confined to the ant-lion but probably occurs in all the Neuroptera, since the same transformations of the Malpighian tubules have been described by McDonnough (1909) in the aphis-lion (Chrysopa) and since the structure of the alimentary tract and the method of cocoon-formation are very similar in all the other members of the order. The fact that these insects possess no special sericiparous organs, but merely modify their excretory organs temporarily for this purpose appears less startling, perhaps, when we reflect that in another region of the alimentary tract, the stomach, the very same epithelial cells exhibit alternate absorptive and secretory functions with concomitant morphological differentiations of their cytoplasm and nuclei. We may also note, as of unusual interest, the fact that the cells of the ant-lion's Malpighian tubules in the sericiparous phase, with their extraordinary ramified nuclei, are strikingly similar to those of the sericteries, or silk glands of larval moths and butterflies (Lepidoptera) and sawflies (Tenthredinoids). In these insects, however, the silk glands were originally salivary glands. Though they are now entirely sericiparous throughout larval life, we can readily conceive from what we have learned from the Neuroptera, that the direct transformation of salivary into sericiparous cells may have been originally an ontogenetic process. Perhaps this may still occur among some of the more primitive moths and sawflies.

When the full-grown ant-lion larva, lying in the dry sand, is ready to spin, it is confronted with the problem of enclosing itself in a spherical cocoon without at the same time enclosing any of the particles of the surrounding medium. Redtenbacher (1884) has given the following very plausible description of the creature's procedure: "At a depth of 3-10 cm. the larva begins some time in May or June to spin its singular sand and silk cocoon by extruding the slender, fusiform spinneret from the tip of its abdomen and allowing the, at first sticky and liquid but rapidly hardening, thread of silk to escape from its orifice. The act of spinning and the way in which the spherical cocoon originates, escape observation, because the larva will spin only under the sand, but from pupæ and cocoons unearthed in various stages of completion we may be reasonably sure that the process must be somewhat as follows: The larva while spinning lies on its back, with its abdomen curved ventrally and, while the sticky thread is issuing, moves the spinneret about in circular, spiral and confusedly irregular paths. Since the sand grains are thus cemented together by the sticky strands, there arises at first a confused band of sand, which is gradually consolidated to form a hemisphere open below. The subsequent procedure is altogether unknown, so that the following remarks are little more than conjecture. Even during the spinning of the above-mentioned hemisphere the larva, while still lying on its back, keeps rotating in a circle, but later it turns over completely so that its dorsal surface is again uppermost. Probably the lower hemisphere is completed in this position and attached to the upper one by similar movements of the abdomen. I often endeavored to boil cocoons that had been spun, not in sand but in sugar or salt, in order to ascertain the course of the silk thread, but was unsuccessful, because the interwoven strands were too firmly glued to one another to admit of separation in boiling water. In all probability, the walls of the silk cocoon, which at first form a thin layer, are later considerably thickened, after the two hemispheres have been united, by the spinning of several layers over the inside. On any other supposition we can scarcely understand how the walls can consist only of delicate bluish white silk without any admixture of sand grains. I regard the above-mentioned reversal of the body as probable, because the cavity of the cocoon never contains any loose sand, and this would seem to be possible only if the animal lies with its concave ventral surface uppermost, and thus raises the superjacent sand together with the already completed hemisphere to make a space free from sand beneath its body." Lozinski (1911), too, describes the outer cocoon as being spun as two separate hemispheres which are later united and then lined with layers of silk.

The completed cocoon measures 10-14 mm. in diameter and is slightly smaller in the male than in the female, owing to the fact that the sexes differ appreciably in size. The task of spinning it may not require more than a single night. After the curled-up larva has rested for seven or eight days, its skin splits down the middle of its back and is stripped off from the pupa and left to one side. The pupa is curled in a ring and is at first soft and ivory yellow but gradually deepens in color and acquires a harder integument. The parts of the imago are now clearly visible, but the mandibles (FIG. 16 *c*) are neither those of the larva nor of the imago, but are short and stout, with distinctly denticulate inner borders. Redtenbacher (1884) gives the length of the pupal period of *Myrmeleon formicarius* as 28-30, Meissner (1908) as 50 and Zàvadsky (1922) as 49 days. When ready to emerge the pupa uses its peculiar mandibles to bite a circular slit through the wall of the cocoon so that part of it can be raised as a lid. Then through the opening thus produced it pushes itself up to the surface of the sand by wriggling its abdomen, its skin ruptures along the back and the imago emerges, at first very pale and delicate, with the abdomen greatly lengthened as compared with that of the larva and pupa. In the course of a few hours the integument hardens, the limp and crumpled wings expand and the adult coloration is assumed. About half an hour after eclosion the contents of the pupal stomach are voided in the form of the hard, pinkish, cylindrical or biscuit-shaped meconial pellets which were regarded by Réaumur, Rösel, Geoffroy and others as eggs. Had they stopped to notice that the males also void these pellets they would not have fallen into this error, which persisted in popular literature till the latter part of the nineteenth century.

The numerous accounts of the behavior of Myrmeleon, published since the beginning of the eighteenth century, clearly reflect the successive changes which the interpretations of animal behavior in general have in the meantime undergone. We may, in fact, recognize four such interpretations, which for lack of better terms I shall call those of design, evolution, tropism and configuration. The earliest observers, Poupart, Réaumur, Bonnet and Rösel, naturally regarded the ant-lion as specially created and both physically and mentally designed to carry on generation after generation the ingenious art, or "industry" of making funnel-shaped pits in the sand for the purpose of surprising and capturing prey. To these investigators its behavior seemed so much like what would be exhibited by a man reduced to the same Lilliputian dimensions and constrained to live under the same peculiar conditions that only an anthropomorphic interpretation seemed probable, for we must bear in mind that the scholastic and theological notions of the Middle Ages, though dispelled from the field of physics during the preceding century, still haunted the biologists of the eighteenth and first half of the nineteenth centuries. We know that the resulting lucubrations gave rise to a vast literature of design, culminating in Paley's 'Natural Theology' and the 'Bridgewater Treatises.' The whole period, as Wilm (1925) has remarked, is "to the modern empiricist and non-theological temper, one of the dreariest and most unproductive in the whole history of philosophy."

With the promulgation and spread of evolutionism during the latter half of the nineteenth century, interpretation of animal behavior undergoes a radical change. The old notion of design is supplanted by the concepts of individual and racial development and the genetic interrelationship of all organisms. Animal behavior of the type seen in the ant-lion, now called 'instinct', is investigated by the historical and comparative methods which begin to dominate human and animal psychology as well as anatomy, embryology, paleontology and physiology. Light is sought on the meaning of the instincts by comparing the behavior patterns of allied, that is genetically closely related species. This method was also applied to the ant-lion by Redtenbacher (1884, 1884*a*) and Brauer (1853), but the results are rather meager, because so little was known at the time concerning the behavior of the Neuroptera in general and of the Myrmeleontids in particular. Among entomologists the small, archaic order Neuroptera has never been as popular as the vast, showy orders Coleoptera, Lepidoptera, Hymenoptera and Diptera. The first part of this chapter, in which I have reviewed our present knowledge of the phylogeny and paleontology of the Myrmeleontids, shows that we are still unable to give any account of the probable phylogenetic origin of the pit-making behavior of Myrmeleon.

Although comparative and historical methods, in the hands of experts, have yielded valuable insight into many developmental and evolutionary processes, it began to be recognized during the closing decades of the nineteenth and the opening decades of the present century that these methods are loose and vague, and owing to the lacunæ in the paleontological record, often of little more value than conjectures, and hence scientifically inadequate.

While many investigators still retain their faith in the usefulness of the methods employed by the great evolutionists of the last century and continue diligently to amass collections in our museums and to explore the fauna of our planet in search of more and more materials for comparative study, others, following the examples of Loeb and Verworn, repudiate all phylogenic speculation and evolutionary hypothesis and turn to purely objective and experimental methods as the only reliable sources of behavioristic and physiological knowledge. The latter, leaning heavily on chemistry and physics, believe that the analyses of behavior into such elementary responses as the tropisms and reflexes and their aggregation into chain-reflexes are adequate substitutes for the old 'instincts.' The ant-lion has been investigated from this point of view by Comes (1909), Doflein (1916) and Rabaud (1927), and, with some reservations, by Turner (1915). Comes, an ardent disciple of Loeb, found the insect to be positively stereotropic, or thigmotropic (keeping as much as possible of its body-surface in contact with the sand), positively geotropic (moving downward towards the earth, instead of away from it) and positively thermotropic (entering iron-filings gradually heated from 20° to 60° C., but then reversing its tropism, i.e., becoming negatively thermotropic and escaping). According to this author, the sand inhabited by the ant-lions in Catania on hot summer days, must have a temperature as high as 50°-55° C. He also noticed that the insect is negatively phototropic (moves away from the light). Turner in his study of our American ant-lion (*Myrmeleon immaculatus*) encountered the same tropisms, or taxes as Comes, except thermotropism. "The ant-lion may be considered positively geotactic, positively thigmotactic and negatively phototactic; with the reservation that all of its movements cannot be explained in the Loebian sense." He also investigated its peculiar 'death-feigning' reflex, or 'letisimulation.' It has long been known that the ant-lion on being roughly handled or dropped, remains motionless for several minutes. Turner summarizes his observations on this type of behavior as follows: "The length of a feint and the position of the longest feint in a series of successive feints varies in different individuals and in the same individual at different times. There is no obvious relation between the temperature, the strength of the stimulus, or fasting and the duration of a letisimulation. . . . In the ant-lion all letisimulation poses are not death attitudes. It is to be grouped with those insects in which the letisimulation pose varies with the attitude of the individual at the time when the stimulating shock is received. Although pinching a leg and, sometimes, even blowing on the body, will usually cause a letisimulating ant-lion to come out of its feint, in the majority of cases, it will submit to the clipping off of the tips of its legs and of its mandibles without responding in any visible manner. In the ant-lion letisimulation seems to be but an exaggerated prolongation of the pause made by most animals when they are startled. The total behavior of a death-feigning ant-lion supports Holmes's contention that 'the instinct of feigning death is connected with much of what is called hypnotism in the lower animals'; and endorses James, when he says: 'It is really no feigning of death at all and requires no self-command. It is simply terror paralysis which has become so useful as to become hereditary.' "

The most thorough analysis of ant-lion behavior into taxes, simple sensory responses and reflexes is that of Doflein. He, too, gives a careful description of its death-feigning but adds observations on its righting movements and phototaxis and was the first to call attention to the fact that when it is lying quietly in wait, it faces away from the source of the light and therefore towards the more strongly illuminated half of its pit. (FIG. 18.) In regaining its feet after being placed on its back, it turns away from the light. By placing the larva on blackened paper Doflein obtained permanent records of its various phototactic movements. His study of thermotaxis, which is more exhaustive than that of Comes, shows that the ant-lion is most active between 25° and 30° C. (an unusually high optimum), and is able to discriminate between different temperatures. When it moves into regions where the sand is 28° to 30° C., it remains in them as if trapped, thus resembling Jennings' Infusoria after they had chanced to swim into a weakly acid medium. Doflein shows that the responses to contact (thigmotaxis, stereotaxis, or haptotaxis) are even more powerful than those to light and temperature. On the other hand, chemical stimuli (chemotaxis, chemoreception) are very weak and seem to be mediated by the small, delicate antennæ. He finds that all the movements involved in the foregoing reactions are reflexes, the three most important of which are boring, tossing and snapping (Bohr-, Schleuder- und Schnappreflexe). The first is exhibited in the rhythmic movements made by the insect when working itself

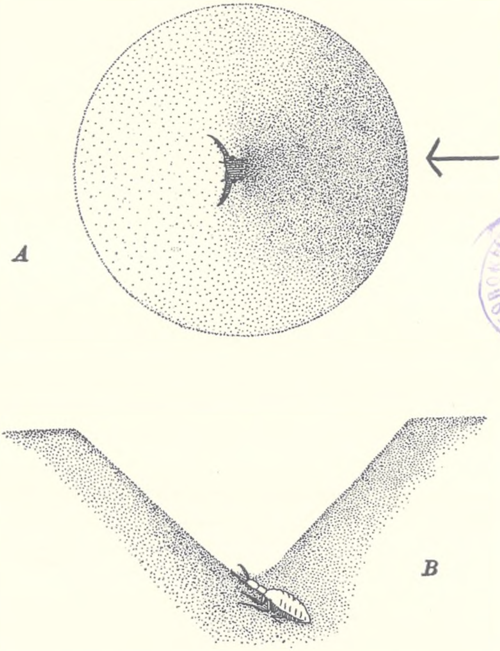

Fig. 18. *A*, Pit of Myrmeleon from above showing position of the insect facing away from the source of the light (indicated by the arrow); *B*, Position of the insect when lying in wait in the bottom of its pit. (After Doflein.)

backward into the sand by means of its hind legs and anal segments, or when moving about beneath the surface; the second, in the spasmodic tossing of sand by means of the upward and backward jerking of its head; the third, in the sudden closure of the mandibles. All of these reflexes may be released by tactile stimuli. Doflein actually designates the ant-lion as a 'pure reflex automaton', and as a fine example of the 'fixedly adapted type' of organism, like so many other insects, as contrasted with the 'regulatory type' of the higher vertebrates. Rabaud's account of ant-lion behavior adds little to those of Comes, Turner and Doflein. Even more than Doflein he stresses the tactile, or thigmotactic responses, stating that the "behavior of the larval ant-lion is an exclusively tactile behavior, at least so far as the capture of the prey is concerned." He fails to detect any chemotactic responses, says nothing about thermotaxy and nothing of importance about reactions to light.

While the literature briefly reviewed in the preceding paragraphs may have considerable value as physiology, it leaves much to be desired as an account of the behavior of the ant-lion. This was noticed by Meissner (1917), Stäger (1924, 1925) and Bierens de Haan (1925), all of whom have protested against Doflein's interpretation of the insect as a 'pure reflex automaton' and have cited numerous behavioristic peculiarities that cannot be explained either as simple tropisms and reflexes or as chain-reflexes. But even these authors do not seem to go far enough in their criticisms or adduce the most fatal objections to Doflein's simplicist interpretations. Instead of analyzing the ant-lion's activity into elements which, after they have been recognized and named, cannot be put together again to yield any intelligible meaning, it would seem preferable to start, like the configurationists ('Gestaltists'), from a consideration of the insect's behavior as an organized whole.[1] The antlion's behavior is obviously made up of three main consecutive cycles: first, the one involving the construction of the pitfall and its employment, second, the spinning of the cocoon, and third, the reproductive behavior (differing according to the sexes) of the imago. The first cycle is repeated again and again throughout the long larval life, the second and third occur only once. Each of the cycles is initiated by internal stimuli, the first by hunger, the second by the transformation of the Malpighian tubules into silk-glands, the third by chemical changes in the gonads. I shall confine myself largely to a consideration of the pitfall cycle which consists of an organized train of activities comprising the construction of the pit in a very mobile medium, the concealment of the larva in a state of immobility with widely opened jaws (not a state of letisimulation but of tension!) at the very point to which a trapped insect is automatically precipitated, the sudden seizure of the insect, the prompt withdrawal and smothering of it in the sand, its paralysis, the extraintestinal digestion and imbibing of its juices, the ejection of its exhausted carcass and the repairing of the disordered pitfall. This cycle is clearly appetitive, or a 'goal-activity', initiated and guided by a constellation

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[1] As defined by R. H. Wheeler (1929, p. 545), *Gestalt,* or configuration, is "a mental process regarded as an organized or uniform pattern of a given form, or structure, that may remain constant while the details of the pattern may vary, e.g., a *melody* played in different keys. The term emphasizes the principle that when mental processes (or motor responses) are studied as segregated phenomena many of their properties are not observed — the whole from which these properties are derived frequently escapes observation. Considered as a response, the *Gestalt* is an organized whole, while the stimulus-pattern which elicits it is an *arrangement* of stimuli. *Gestalt* also refers to organized (configurational) motor reactions of the organism (co-ordinated movements)." Compare also his remarks on page 119: "The animal's behavior is not a mechanical performance, because external and internal conditions alike are controlling it; that is to say *a total system of forces of which the organism is a member is giving direction to the activity.* As a consequence, the organism modifies its own behavior with respect to a goal, the goal being the point at which the tension is resolved."

of internal and external stimuli such as hunger, darkness, a certain temperature, the presence of a sandy medium, etc. It is at first often executed by random movements but soon becomes a more definitely organized preparation for securing the prey, culminates in the consummatory acts of its seizure and digestion and concludes with a state of satiety and quiescence. While the whole train of activities presents a definite pattern, its details are nevertheless variable and may themselves become so complicated as to have the appearance of minor or subordinate cycles. This is best seen in the making of the pitfall and the capture of the prey. As Stäger, Meissner and others have shown, the ant-lion subtly adapts its behavior to that of the trapped insect. If the latter happens to fall into its jaws in the proper position, it is instantly seized, buried, paralyzed and sucked out, but if it is at first awkwardly or inconveniently grasped, it is either repeatedly tossed into the air or against the walls of the pit till the proper hold has been secured, or if it escapes, is showered with sand till it is again brought within reach. If this fails the ant-lion may actually leave its pit and pursue the prey, though this procedure, owing to the insect's retrograde mode of locomotion, is not apt to be very successful.[1]

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[1] In this connection I cannot refrain from quoting two observations that vividly illustrate the plasticity of the ant-lion's behavior. The first is from Stäger (1925, p. 78): "In March 23, 1924, I witnessed the following performance by some very hungry ant-lions that had not been fed during the entire winter though they had made pits. There were in a cigar-box two large pits separated by a distance of 6 cm. (measured from rim to rim), which we may call pits *A* and *B*. A slater (wood-louse) which I threw into pit *A* was instantly seized by the resident "lion," but before it succumbed to the poison, I snatched it from the creature's jaws and threw it into pit *B,* where the occupant grabbed it still living. Now if the reader supposes that the cheated ant-lion of pit *A* timidly withdrew into the sand after my intervention, as indeed usually happens, he is mistaken. On the contrary, the robber, suffering the pangs of hunger, only behaved the more wildly and incessantly tossed up sand from the bottom of its pit. Since, however, the slater, which was no longer in pit *A,* failed to roll down, the ant-lion, still actively tossing sand, ascended for some distance, contrary to all rules, the wall of its pit nearest pit *B* and then, walking and continuing to throw sand, broke through the sand separating the two pits and thus quickly

The ant-lion sometimes exhibits a kind of behavior even more difficult to interpret as reflex or tropistic than the instances cited by Stäger, Meissner and Bierens de Haan, but before describing it, it will be advisable to consider the making of the pit. This has been described very differently by different observers and some seem never to have seen it. The discrepancies in the literature are in part due to the fact that the insect excavates its pit only at night, or at any rate in the dark and when quite undisturbed. The eighteenth-century naturalists, Poupart, Réaumur, Rösel and Geoffroy, all describe the performance as follows: The ant-lion begins the excavation by making a circular groove, with the diameter of its future pit, by moving backward on the surface and rhythmically tossing

succeeded in entering the pit of its neighbor, who in the meantime had been in possession of the stolen prey. As I did not wish to risk the death of both larvæ, I interrupted the experiment. That this unusual performance was a direct pursuit of the prey seems to me certain." After calling attention to the frequent turning of the ant-lion on its body-axis or in circular paths in order to reach its prey with the jets of sand, Stäger continues: "Such a wild chase as the one above described is exceptional. I can only explain it as due to the animal's intense hunger and its desire not to lose the opportunity for a satisfying meal. The case is scarcely analyzable on the theory of reflexes. Here again the drive of the whole procedure lies in the psychical sphere, the plasticity of which is clearly apparent. And here, too, the reflexes are entirely in the service of the desired goal."

The second observation is from Bierens de Haan (1925) and refers to a combat between a large ant and an ant-lion shaken up together in a vial. "The two grapple with each other in turn. The ant-lion seizes the ant with its mandibles and hurls it to the ground, the ant bites its opponent's head and the sides of its body, both insects rolling about like two fighting dogs. Now the ant-lion lies on its back and the ant is on top, now their positions are reversed and the ant is underneath. Sometimes the larva snaps at the ant when the latter is not touching it, or suddenly hurls itself at the ant when it is resting on the wall of the vial and only gently touching the ant-lion with one of its legs. The attacks of the larva on its momentarily quiescent enemy are remarkable, since they are evidently a continuation of the action without perception of the original stimulus. It is also remarkable that the larva does not kill and devour the ant, though the latter was occasionally held for some minutes in its mandibles. The withdrawal under the sand, therefore, seems to be an important link in the food-securing behavior, since without it the prey cannot be killed."

the sand from the inner border of the groove to the outside by means of its head and closed mandibles. What actually takes place is not easily seen. The early naturalists believed that the insect shovelled the sand onto its head and mandibles with its left fore foot when making the circular groove in a clockwise, or with the right when making it in a counter-clockwise direction, but since ant-lions with extirpated fore legs excavate as usual, these delicate appendages can be of little importance in the operation (Turner, 1915). The sand simply falls on the head and mandibles while the insect is moving backward. After digging the circular groove, which, of course, leaves a broad, low, truncated cone of sand in the center, the ant-lion continues in the same direction within the circle and in a gradually contracting spiral path, thus deepening the furrow and gradually cutting away the central cone till the sand has all been thrown out and the funnel-shaped pit is completed. We may call this the circuitous method of pit formation. It has also been observed by Guilding (1833) in *Myrmeleon leachi* of the Island of St. Vincent, by Redtenbacher (1884), Rey (1895), Meissner (1919), Stäger (1925), and Voigt (1925) in the common European Myrmeleons, by Biró (1897) in an unidentified Papuan species and by McCook (1882, 1907), Turner (1915) and myself in our North American *M. immaculatus*. I also vividly remember seeing Myrmeleon larvæ making their pits in this manner in the fine sand around the foundations of a large building in Ancon, Panama. Dozens of the insects feverishly commenced plowing their spiral furrows as soon as the brief tropical twilight set in and had finished their pits soon after dark.

To one who has witnessed this behavior on many occasions it is surprising to find that a number of keen observers who have kept ant-lions for long periods have never seen it and describe instead a very different method of excavating the pit. The first to doubt the occurrence of the circuitous method was the eminent English entomologist Westwood (1838). Although he saw the larva moving backward in spiral paths, he remarks, "but it does not appear to me that this retrograde motion has anything to do with the actual formation of the cell, since as soon as it has fixed upon a spot for its retreat, it commences throwing up the sand with the back of its head, jerking the sand either behind it or back — *ossaque post tergum, magnæ jactata parentis* (Ovid) — or on one or the other side. It shuts its long jaws, forming them into a shovel, the sharp edge of which it thrusts laterally into the sand on each side of the head, and thereby contrives to lodge a quantity of sand upon the head, as well as the jaws. The motion is, in fact, something like that of the head of a goat, especially when butting sideways in play. In this manner it contrives to throw away the sand, and by degrees to make a hole entirely with the head, the fore legs not affording the slightest assistance in the operation." This simple method which may be called the direct to distinguish it from the circuitous, is the only method that has been seen by Comes (1909), Navás (1913), Mrs. A. B. Comstock (1913) and Doflein (1916). Doflein even goes so far as to characterize the early naturalists' accounts of the circuitous method as "false interpretations of accidental occurrences."

It is certain, therefore, that the ant-lions have two very different methods of making pits. At first sight the confusion in the European literature would seem to be due to differences in the species of Myrmeleon observed. This was the opinion of Rey (1895), who claimed that *M. europæus* adopts the direct, *formicarius* the circuitous method. But this cannot be the source of the discrepancy, because Stäger has recently observed both methods in *europæus,* and McCook and Turner had previously found the same to be true of our American *immaculatus*. Stäger, who has made a careful study of the methods of pit-formation discovered a means of registering the precise path traversed by the excavating insect. It has been known for some time that ant-lions will live and make their pits in a variety of powdered substances, such as salt, sugar, emery powder, iron-filings, etc. All these substances, however, have a tendency to run like sand and therefore to efface the spiral path. Stäger placed his insects in dry, powdered sphagnum moss, which retains the impressions made by the insect, so that the completed pit has the form of a spiral ramp with sharp borders. I have obtained the same results with *M. immaculatus* kept in powdered sphagnum. More recently Voigt (1925) claims to have found loess to be an even better substance for preserving the spiral tracings. Stäger concludes that "the ant-lion's method of making the pit was quite correctly described by the early observers. The larva proceeds according to a definite and hereditarily fixed plan, but within this rigid plan of construction it allows itself, so to speak, certain liberties, in that sometimes one and the same individual will trace its spiral path only to the right [clockwise] in one pit, in another only to the left [counter-clockwise], and in a third by a complete reversal of the body, now to the right and now to the left." The pits occasionally formed by the direct method are small and often due to unfavorable conditions such as a too heavy medium (iron-filings) or too low a temperature, but such pits may be used for capturing prey. Turner found that the pits formed directly by our *M. immaculatus* are often enlarged subsequently by the circuitous method. Finally, it may be noted that according to Krausse (1915), *M. europæus* sometimes omits the formation of the pit altogether, simply digs itself into the sand and, remaining immobile with exposed and wide-open mandibles, captures its prey like the non-pit-making Myrmeleontids Acanthaclisis, Palpares and Dendroleon.

The foregoing condensed account of variability in the pit-making behavior of the ant-lion is, perhaps, sufficient to show that the insect cannot be regarded as a pure reflex automaton, especially as a like variability also characterizes all the remaining activities of its feeding cycle. But the behavior which lends itself least easily to a reflex, or mechanistic interpretation is that to which Bonnet called attention in his 'Sisyphus experiments'. (See p. 22.) Both Stäger and Bierens de Haan failed to mention this singular record in their criticism of Doflein, perhaps because they regarded it as apocryphal. Very similar behavior, however, has been observed by McCook (1907) and Turner (1915) in the American *M. immaculatus*. I therefore quote their accounts in full, beginning with McCook's: "In the early part of the last century a French observer told a remarkable story of the way in which a Myrmeleon larva got rid of pebbles too large to be moved from its pit by tossing with the head. The correctness of this statement was questioned, and I therefore put it to the test. Three pebbles, all larger and heavier than the larva, were dropped into the centre of a pit where they would be most inconvenient to the occupant, and likely to prompt her to remove them. The experiment succeeded perfectly. The ant-lion thrust its head beneath a pebble and tried to toss it from the pit. Having failed in this, it tried another mode. It placed the end of its abdomen against and a little beneath a pebble and began to push backward. A little time was taken to adjust the pebble so that its centre of gravity would be against the end of the body. Then the animal began to back up out of the pit, pushing the pebble before, or rather behind it, up the side, and to a point a short way beyond the margin, where it was left. A small furrow was thus made in the sand, curved from the point of departure up the wall of the pitfall. The pebble was kept perfectly balanced during the entire movement, which was quite rapid and made with the ease and assurance as well as the celerity of an expert. All of the three pebbles were thus removed; and the experiment was repeated a number of times, always with the same result. Some well-rounded bits were now dropped into the sand in order to increase the difficulty of balancing the load; but this made no difference in the larva's action. A round pebble was balanced and removed quite as readily as any other. That this task required no little acrobatic skill I satisfied myself by sundry experiments. My deftest efforts to push a pebble before the point of a pencil, *à la Myrmeleon,* were not an eminent success. It was a curious and amusing spectacle — this odd little creature backing the accurately poised load, larger and heavier than itself, up the shelving sandy wall of its domicile, and then returning to put its house in order! Thus the correctness of the early observations of M. Bonnet were confirmed."

This singular behavior is even more circumstantially described by Turner. He does not refer to McCook, but to Bingley (1805), who merely cited Bonnet's observations. "Perhaps it sounds too much like a fairy tale; yet it is comparatively easy to induce an ant-lion to behave in this manner. I frequently induced it either by placing a small stone in the center of the ring of a pit that was being constructed; or, by depositing a similar object in the bottom of a completed pit. When the stone is placed in the center of the ring, as the ant-lion burrows spirally inward, there is sure to come a time when the stone will fall into the furrow. When the ant-lion returns to that point it encounters the obstacle. Usually it burrows under the object and continues on part of the way around the circle. Then, turning, it backs through the furrow thus made until it has inserted the tip of its abdomen under the impediment. It then backs slowly up the slope with the burden poised upon the tip of its abdomen. The edges of the abdominal somites and the small bristles thereon prevent the stone from slipping forward; while the dirt on each side prevents it from falling sidewise. Throughout this entire upward journey the whole body of the ant-lion is above the ground. It is an astonishing sight to see the insect backing in almost a straight line, up the steep slope, with the burden poised on its back. When the burden has been disposed of, usually at the edge of the pit, the ant-lion turns about and returns to the bottom of the pit, usually in the furrow made by the upward struggle, and continues her digging. The furrows made before my eyes have always been straight or nearly so; but one made in my absence was quite curved. When the object was placed at the bottom of a finished pit, sometimes the object was allowed to remain; but, in most cases, sooner or later, it would be removed, in the following manner. When it had tossed up a few loads of dirt, the larva would back away from the obstacle in a straight or a curved line; then turning, it would back through the furrow thus made and proceed as described above. When the stone is too heavy for the insect to handle in the manner mentioned above, it either deepens the pit on one side of the obstacle, or buries the obstacle by mining under it or else abandons the pit. In several important respects the behavior observed by me differs from that described by Bingley; (1) never once did I see the stone fall from the insect's back and roll to the bottom of the pit, (2) obstacles encountered in constructing the pit were usually removed at once, (3) such bodies were usually deposited just beyond the rim of the pit, (4) occasionally they were left on the side of the pit."

Though the three accounts of Bonnet, McCook and Turner differ in details, some of which, like the greater skill of the American ant-lion in transporting pebbles, may be specific peculiarities, they nevertheless agree in proving that the insect is able, quickly and appropriately, to remove obstacles suddenly injected into the normal cycle of its activities. Merely tossing out a pebble with its mandibles, when it is very small, but transporting a larger pebble on its back and depositing it on the rim of the pit, or leaving a very large pebble in the pit to continue excavating in a more favorable situation, are very far indeed from being mere reflex activities. The same is true of the resumption and completion of a goal activity like that of making the pit, after its sudden interruption, as in Bonnet's and Turner's experiments. Here the importance of the internal stimulus is very clear. When a higher vertebrate behaves thus we admit that it possesses some insight, or intelligence. Must we assume that the ant-lion cannot rise to such a level?

In conclusion the enemies of the ant-lions may be briefly considered. These insects probably suffer most from the cannibalism of their own species, if we may judge from the difficulty of keeping several of them together in close quarters, but even in the field their awkward retrograde method of locomotion must occasionally bring them within reach of the mandibles of their voracious neighbors. Other enemies seem to be remarkably few. None, in fact, has been recorded from North America, but long ago two Hymenopterous parasites were briefly noticed in Europe. One of them is a small Ichneumonid, *Cryptus myrmeleonidum,* reared from *M. formicarius* larvæ and described by Boudier (1834), the other a small black Chalcidid, *Hybothorax graffi,* reared from an ant-lion by Graff and described by Ratzeburg (1844). Redtenbacher (1884), too, in the course of his observations on ant-lions, seems to have encountered these parasites and says that they "probably lay their tiny eggs in the abdomen of the ant-lion without being noticed. The latter, however, is not incommoded, but eats and digs its funnel as usual and even pupates quite regularly. In the meantime the larvæ that hatch from the parasite's eggs have nourished themselves at the expense of their host, pupate within its pupa, which therefore perishes, and eventually escape by perforating the pupal skin and cocoon." I infer from Redtenbacher's account that 20 to 30 of these small parasites may emerge from a single ant-lion. Ratzeburg conjectured that the adult female Hybothorax, when it attacks the ant-lion for the purpose of oviposition, has its abdomen protected by the pair of stout processes that extend back from the metathorax. Boudier believed that the Cryptus attacks the ant-lion while it is exposed on the surface of the sand. It is indeed improbable that either of the parasites assails its host within its pit. We know that the ant-lions are by no means sessile organisms as Rabaud (1927) would have us believe, but at night sometimes walk considerable distances over the surface of the sand. On such occasions they might be readily attacked by small Hymenoptera.

The only other ant-lion enemy that I have found mentioned in the literature is an unidentitfied Pompilus-like wasp seen by Biró (1897) preying on the Papuan Myrmeleontid cited on p. 84 as leaving its pit and pursuing its prey over the sand. I quote Biró's vivid description: "The wasp, as is her wont, skipped and flitted about with sudden pauses on the partitions between the ant-lion pits, taking great care not to fall into one of them, though her size and strength were such that she had nothing to fear beyond a disagreeable encounter. A whole troop of hungry ant-lions had left their secure pitfalls and were creeping about hither and thither under the surface of the dust without taking any particular direction, while the wasp, continually on the go, turned up now at this point, now at that, planning her attack with the insight of an expert. All of a sudden she pounced on a full-grown larva and stung it with her long, curved sting while it was under the sand. She had aimed well, and the ant-lion ceased to move. The wasp then dug it out of the sand with her fore feet and with fanning wings dragged it over the surface. Though I stood ready with my net, I refrained from capturing her because she had laid her prey aside and was searching about on the harder soil. She soon found a convenient spot and began to work diligently, biting and breaking up the particles of earth and sweeping the detritus back with her fore legs between her four out-spread hind legs. She had already dug to such a depth that she was no longer visible in the oblique burrow, when she encountered an unexpected obstacle. The work was therefore interrupted and she sought another spot and again began to dig and scrape. She had to repeat this process a third time before she finally succeeded in finding earth sufficiently soft for her purpose. Thereupon she returned to the forsaken ant-lion, dragged it into the burrow and undoubtedly deposited an egg with it. She then closed the burrow with scraped-up soil. But now my net fell over her. Only after she had finished closing the opening of the burrow, making it level with the surrounding soil, and was about to take wing, did she become aware of the fate she had so blindly encountered."

CHAPTER IV

POST-EIGHTEENTH-CENTURY STUDIES OF THE MEDITERRANEAN WORM-LION

(*Vermileo vermileo* L.)

THE wide distribution and abundance of the ant-lion in Europe, no less than its investigation by the great naturalists, of whom some account was given in the first chapter, were, of course, important factors in establishing its reputation as one of the marvels of the insect world. The worm-lion, though in certain respects even more remarkable — since its very similar behavior is conditioned by a much simpler morphological structure — has attracted fewer observers and has therefore remained comparatively unknown. The reasons for this will be apparent as we proceed, but before reviewing the post-eighteenth-century studies of its behavior I deem it expedient to insert a brief account of its family and subfamily relationships, with some general data on the geographical distribution of the various species of Vermileoninæ now recognized by entomologists.

The worm-lions belong to an interesting family of Diptera, or two-winged flies, the Rhagionidæ, or Leptidæ, as they were formerly called. Though one of the smaller groups of the order, it comprises no less than 400 species, of which 123, representing 17 genera, are known to occur in North America, north of Mexico, and is described by Verrall (1909) as including "orthorrhaphous brachycerous eremochætous flies of rather small to rather large size and of more or less elongate shape; usually thinly pilose or almost bare, and with the tibiæ (or at least the posterior pairs) always spurred; ambient vein entire and squamæ small." The three formidable words at the beginning of this sentence only mean that these flies are feebly hairy (eremochætous) and belong to the more specialized short-feelered division (Brachycera) of the most primitive suborder (Orthorrhapha) of the Diptera, or those having pupæ that split in the mid-dorsal line to permit the adult fly to emerge instead of being enclosed in the indurated, circularly splitting larval skin (puparium) common to such very highly specialized Diptera as the common housefly and its innumerable allies, the Cyclorrhapha. Authorities differ in regard to the position they assign to the Rhagionidæ among the various Brachyceran families, but most of them now agree in placing it near the beginning of the series, and Williston (1908) and Wesché (1912) assign it the lowest and most primitive rank. There is also considerable difference of opinion concerning the number and arrangement of the subfamilies of Rhagionids, owing to the fact that the genera are very heterogeneous. Verrall (1909), Bezzi (1926) and others regard the worm-lions as constituting a distinct subfamily, the Vermileoninæ, though Leonard (1930), the latest monographer of the family, places Vermileo among the Rhagioninæ. In my opinion, we are justified in regarding the Vermileoninæ as a very ancient and rather isolated group of Diptera, with unmistakable relationships to several Brachyceran families, for, as Verrall has shown, the venation of their wings is reminiscent of the Tabanidæ and Bombyliidæ, their dichoptic head is that of the primitive Rhagionid subfamily

Xylophaginæ, the male abdomen and genitalia resemble those of Leptogaster among the Asilidæ, and the long proboscis of one of the Vermileonine genera, Lampromyia, is very similar to that of certain Cyrtidæ, Bombyliidæ, Apioceridæ and Empididæ.

The subfamily Vermileoninæ consists of only two genera, Vermileo and Lampromyia, with perhaps a third to be described in Chapter VIII. Of Vermileo only three species are known, *V. vermileo* L., which I shall call the Mediterranean worm-lion, *V. comstocki* Wheeler, the Sierra worm-lion, and *V. opacus* Coquillett, of Nevada and New Mexico, which Leonard believes to differ specifically from *comstocki.*[1] Unlike the genus Vermileo, Lampromyia is confined to the Old World. It comprises seven described species, with the following peculiar distribution, which will be considered in greater detail in Chapter VII:

Lampromyia cylindrica Fabr. (=*funebris* Dufour) — Spain, North Africa and Canary Islands.

Lampromyia canariensis Macq.— Canary Islands.

Lampromyia pallida Macq. (=*miki* Marchal) — Spain, North Africa and Canary Islands.

Lampromyia sericea Westw.— South Africa.

Lampromyia appendiculata Bezzi.— South Africa.

Lampromyia argentata Bigot — South Africa.

Lampromyia brevirostris Bezzi — South Africa.

Since the close of the eighteenth century the Mediterranean worm-lion, to which the remainder of this chapter will be devoted, seems to have been of more interest to systematists than to students of insect behavior. And as usually happens in the case of insects supposed to be 'monotypic', or the sole representatives of their genera, sporadically distributed and therefore rare in collections, the worm-lion has become the center of prolonged nomenclatorial

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[1] A fourth species, *V. dowi* from Cuba, must now be added. See note at end of Chapter VIII.

discussion. All the great dipterists of the nineteenth century expressed their views on its systematic status in the generic and specific names they invented or adopted. The insect, therefore, appears in the literature under the following aliases:

Musca vermileo Linnaeus (1758), *Rhagio vermileo* Fabricius (1775), *Nemotelus vermileo* Degeer (1776), *Leptis vermileo* Fabricius (1805), *Vermileo degeeri* Macquart (1834), *Psammorycter degeeri* Blanchard (1840), *Leptis cylindraceus* O. G. Costa (1844), *Apogon dufouri* Perris (1852), *Dasypogon dufouri* Walker (1854), *Vermileo vermileo* Williston (1886), and *Psammorycter vermileo* Bezzi (1898).

After much searching among the pulverulent tomes of bygone generations of dipterists for the reasons for all this discrepancy, and after emerging as a veritable demon of the dust, I have decided to spare my readers the rehearsal of the arguments presented by the several authors for their verbal preferences. Should any future student seek to follow my example — which God forbid! — he will find the bibliography dealing with the worm-lion synonymy under the following authors in the list of literature appended to this volume: Bezzi (1898, 1900), Bigot (1879, 1881), Blanchard (1840), Brauer (1883), O. G. Costa (1894), Coucke (1893), Degeer (1776), Fabricius (1775, 1794, 1805), Griffini (1895), Kertész (1908), Linnaeus (1758), Macquart (1826, 1834), Mik (1887, 1894), Perris (1852), von Röder (1892), Schiner (1862), Verrall (1909), Walker (1854), and Williston (1886, 1908).

Clearly, the one and only correct scientific name of the insect, according to our present code of nomenclature, is *Vermileo vermileo* and all the other names are merely so much nomenclatorial slag to be thrown on the synonymic dump, but this name cannot be attributed to Degeer, as nearly all dipterists have assumed. Systematists even as recent as Kertész (1908), having failed to look up Degeer's original paper of 1752, have supposed that he mentioned the worm-lion as *Musca vermileo* and that Linnaeus adopted this name in the tenth edition of his 'Systema Naturæ.' But Degeer, in his paper of 1752, mentions the insect only as the 'sandmasken' or 'masklejonet,' which are Swedish for sandlarva and Réaumur's 'verlion,' and Linnaeus was really the first to Latinize the latter term as the name of a species of fly referable to his genus Musca. When this comprehensive genus was later being gradually resolved into several genera, Macquart (1834) converted the Linnaean specific name *vermileo* into a generic name and gave the insect a new specific appellation, *degeeri.* This procedure has been countenanced by many subsequent authors, but the established usage of modern taxonomy requires that both Linnaeus' specific and Macquart's generic name shall be retained. The repetition of the same word, which seemed reprehensible to a former generation of dipterists, and is still inadmissible according to the botanical code of nomenclature, can no longer be avoided in zoölogy. We agree with Williston (1886) that there is no more impropriety in calling the insect *Vermileo vermileo* than in calling a man Mr. Thomas Thomas. Henceforth, therefore, the Mediterranean worm-lion should be known as *Vermileo vermileo* Linnæus (*not* Degeer).[1]

The references in the literature indicate that *V. vermileo* is by no means a common insect. Nor are the locality data sufficiently numerous to permit plotting its whole geographical range. The anonymous first observer (1706) of

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[1] In ornithology we may even have trinomials in which the same name is twice repeated, as in *Cardinalis cardinalis cardinalis* for one of the subspecies of the cardinal bird. Verrall (1909, p. 258) surmised that Linnaeus instead of Degeer should be cited as the authority of *Vermileo vermileo,* but he was baffled by Degeer's and Linnaeus' references to the former's early paper. Linnaeus cites it as being in the "Act. Stockh.", Degeer as in the "Acta Acad. Suec." The citation "Vetensk. Acad. Handl." has long been available in Hagen's "Bibliotheca" (1862).

its habits cites no precise locality for his specimens, though Réaumur states that they were taken near Lyon. His specimens, as we have seen, were collected by Rebory at Palud in the Provence, but he mentions the occurrence of the insect also in the Auvergne. De Romand (1833) found the larvæ in great numbers in fine disintegrated tufa in the park of Vernon, near Tours, and Perris (1852) recorded them from the Landes. Courtiller (1867) studied some larvæ which he probably collected near Saumur, in the department of Maine-et-Loire. They have been found more recently by Falcoz (1927) at Vienne in the Dauphiné, in dry powdery soil along a wall protected by a parapet. Strobl (1906) described a new subspecies of *V. vermileo* as *nigriventris* from adult flies captured at Cercidilla (Bolívar) and Los Molinos (Mercet), Spain, and Navás (1913) claims to have found the larvæ of *V. vermileo* near Madrid and in Catalonia and Aragon. In 1925 I found them in considerable numbers on two of the Balearic Islands, as I shall relate in more detail in the sequel. According to Bezzi (1898), the insect is widely distributed in peninsular Italy. The larvæ have been taken in the botanical garden of Milan by Bezzi (1892), and at Bra, in Piedmont, by Griffini (1895), the flies at Parma by Rondani, the larvæ at Rome by Barbiellini, at Camaldoli near Naples and on the Island of Ischia by O. G. Costa (1844), and in Calabria by A. Costa (1863). The friar Gredler found many larvæ in the "Glimmersand" of the garden of the Franciscan monastery at Bozen, in Southern Tyrol. Palm (1869) records them from the same locality and also from the Trudener Thal, near Neumarkt "under overhanging cliffs." More recently Th. Becker (1921-22) has again found the larvæ at Bozen, making their pits among the paving stones of the monastery courtyard. Mik (1887) obtained specimens from the Island of Lessina in Dalmatia and they were also taken in that country by Novak. Mik calls attention to the fact that the ancient citation by Schrank (1781) of their occurrence at Linz, in Austria, is erroneous and in all probability referable to a species of Rhagio (Leptis). These records show that the fly ranges over a considerable part of Spain, Central and Southern France, the whole of Italy, Southern Tyrol, Dalmatia, and the Balearic Islands. That it may be found eventually in Greece and Asia Minor is suggested by its occurrence in Egypt, where it has been taken by Professor H. C. Efflatoun, who sends me the following note: "The larvæ of *Vermileo vermileo* have been found by me quite commonly and during the months of September to April in Wadi Digla, Wadi El-Tih and Wadi Gendali (Eastern Desert, between Cairo and the Gulf of Suez). They make funnel-shaped pits, very similar to those produced by ant-lion larvæ, beneath the sloping undersurfaces of overhanging limestone cliffs. The nature of the soil under these cliffs is calcareous and owing to weathering conditions pulverized into an extremely fine dust. The cliffs overhanging the Vermileo pits always have a northern or northwestern exposure and no Vermileonid larvæ have ever been found out in the open Wadi. On various occasions many adults have been bred from these larvæ, but the adults have never been seen in their natural habitat, though the above mentioned localities have been visited very often and during every month of the year."

The finding of *V. vermileo* in Egypt also suggests that the insect may yet turn up in Tunis, Algiers, Oran or Morocco. I failed, however, to find it in Morocco during the spring of 1925, though I scrutinized the dust at the bases of old walls and under overhanging rocks in many likely places between the Great and Middle Atlas. Brauer (1883) claims that there were larvæ from the Canaries in the Vienna Museum, but these were most probably the larvæ of one of the three species of Lampromyia known to occur in those islands. I believe, therefore, that I have cor-

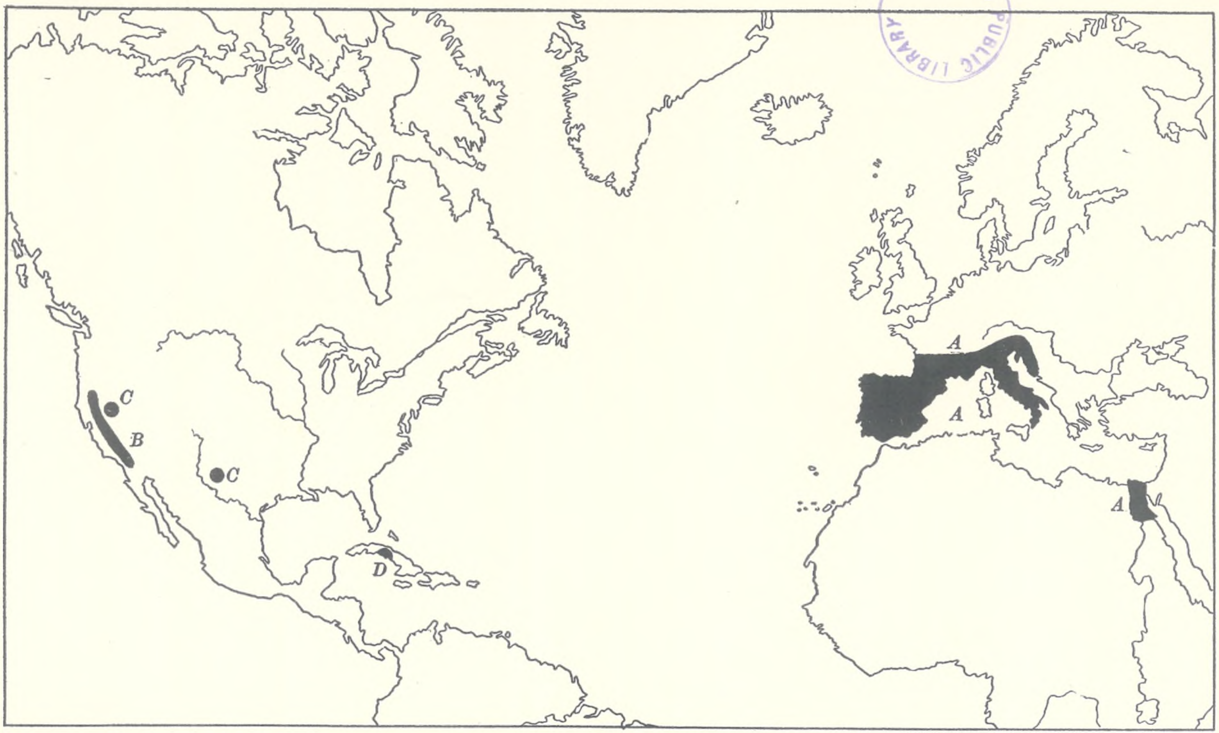

Fig. 19. Map showing known distribution of the four species of Vermileo. *A,V.vermileo, A′,V.vermileo* var. *balearicus* var. nov.; *B,V.comstocki; C,V.opacus; D,V.dowi* sp. nov.

rectly indicated the known geographical range of the insect on the accompanying map (FIG. 19), though future collectors may succeed in finding it not only in Sicily and Sardinia but also in certain parts of the Mediterranean littoral of Asia and North Africa.

Most of the post-eighteenth-century accounts of the structure and behavior of the *V. vermileo* are either brief summaries of Degeer's and Réaumur's papers or, when based on actual observations, contain little that these investigators failed to see. In fact, only a few authors, namely de Romand, von Siebold, Brauer, and Falcoz, have contributed new observations on the behavior and structure of the larva, and the paper of one author, Courtiller (1867) contains some rather startling blunders. De Romand (1833), in a paper which is largely a confirmation of the earlier observations, was the first to notice the larva's ability to fast for long periods. He says: "This larva may live a long time without feeding. Year after year I have left a great number of them in a box for six whole months without giving them any food and without their being able to obtain any. Yet when I again began to feed them, they were ready to eat and, after repeatedly changing their skin, attained their first transformation and eventually the stage of the perfect insect." He fails to mention the time of year of this protracted fast, but it was probably the six months of normal hibernation, and his larvæ seem to have pupated in the spring after feeding had been for some time resumed. This seems to follow from von Siebold's and Falcoz's observations mentioned below.

In 1861 the talented German zoölogist von Siebold published an interesting account of some worm-lions which he obtained from the Franciscan friar Gredler of Bozen. These larvæ preferred soft-skinned Formicine to hard-shelled Myrmicine ants but also readily accepted plant-lice, delicate flies, small caterpillars and young spiders. They declined small bug-like insects and small hard-shelled beetles, the former probably on account of their disagreeable odor, the latter because of their hard chitinous integument. According to Gredler, their natural food in Bozen consisted of the ants *Aphænogaster subterranea* and *Lasius brunneus* and small slaters (Oniscids). Von Siebold describes in detail the making of the pit and capture of the prey. With respect to the latter he noticed the following singular plasticity of behavior: "If the captured prey is suitable and the larvæ have seized it correctly they hold it fast in their embrace, but instantly set it free if it proves to be unsuitable or seems too large or vigorous. They then withdraw into the sand and do not reappear, leaving the despised insect to its own devices. Even when they have embraced an ant or other acceptable insect armed with jaws, in such a position that the captured insect touches the worm's body with its mouthparts, they instantly release it, probably from fear of injury and, without withdrawing into the sand, toss themselves and the prey back and forth in the funnel and keep repeating their embraces till it is securely held." Von Siebold also made an interesting observation, which I have often repeated when too many larvæ were confined in a dish containing sand mingled with small pebbles. Under such conditions the crowded pits become hexagonal or pentagonal for somewhat the same reasons as the cells of honey-bee combs assume the same shapes. After stating that the larvæ repair or excavate their pits by tossing out the sand only during the night, von Siebold says: "My larvæ were not in the least disturbed in their work when I carefully approached their dwellings with a light, and at such times their behavior was amusing. Among the closely adjacent funnels one of the larger pebbles would be tossed out by one of the larvæ and fall into a neighboring pit and was thence tossed back, so that some of these pebbles flew continually from one pit to another, and the busy creatures, though their pits were already completed, could find no rest on account of the forever returning missiles. Since, however, they always persevered patiently and tirelessly in this labor, they did finally secure relief from the disturbers of their rest, because in the end most of the pebbles, so incessantly tossed back and forth, accumulated on the few areas of sand where no pits had been made or in some cases came to lodge poised on the ridge between two craters." Von Siebold's larvæ remained alive in a warm room throughout the winter of 1858-59, though they were seldom fed. In the spring of 1859 they were again fed regularly and abundantly, but the pits decreased rapidly in number and the larvæ pupated in the sand, giving rise in a few weeks to flies. Some of the larvæ, however, failed to pupate and lived on through the summer of 1859, excavating as lustily and feeding as gluttonously as ever, till they had passed a second winter and pupated in the spring of 1860. From this von Siebold inferred that the larvæ normally require two years before attaining the imaginal stage.

In 1867 Courtiller published a description with some crude figures of the adult, pupa and larva of *Vermileo vermileo*. His account of the behavior of the larva not only adds little to what was previously known but is vitiated by a singular misconception. He mistook the posterior end of the larva for the head, the anus for the mouth and interpreted the four bristly caudal lobes as an organ for seizing the prey. He seems to have seen the posterior spiracles and to have thought they might be the eyes! And although he appears correctly to have distinguished the dorsal and ventral surfaces, he assigns the pseudopod to the ventral portion of the eighth instead of the fourth segment. Some of his statements are obvious exaggerations, as when he says that the anterior half of the larval body "acts with such force that I have often seen pebbles nearly as large as peas thrown to a distance of several centimeters." The following statement, too, is highly dubious, to say the least: "The life of these insects seems to be very tenacious, because I have kept some of them alive for five and six months, glued to pieces of cardboard in order to observe them better, and several of them have there transformed or sloughed their skin, so that after I had failed to keep them under observation, nothing was left but their exuviæ."

Brauer (1883), in an important paper on the morphology of Dipteran larvæ, compares the worm-lion with the larvæ of other Rhagionids (Ptiolina, Rhagio and Xylophagus) and gives a more detailed account of the head and mouthparts than Degeer and Réaumur. He also rectifies a peculiar blunder that may be easily overlooked in the accounts of these authors, namely, their mistaking of the dorsal for the ventral surface of the body. This was, indeed, an easy blunder to make, because the worm-lion actually crawls on its dorsal surface when placed on the sand or on any other plane surface and preserves the same orientation when it is lying quietly in its pit! I may add also that Brauer, like his predecessors, failed to notice that the young Vermileo larva at least possesses small eyes, and that, since the light can reach these organs only from the ventral side, as I shall show in the sequel, its habit of both crawling and lying on its back is its normal orientation. There are other peculiarities in the larva's structure, which I shall consider in the next chapter.

Falcoz (1927) found his Vermileo larvæ inhabiting dry powdery earth instead of sand. They were collected in May 1926 and kept in their native earth even in the laboratory. The following year, between June 20 and 28, several of them produced adult flies, but others persisted as larvæ. His account of their capturing the prey agrees with that of previous observers, except that he saw only small ants seized and devoured. "Other small animals that were presented to them, such as small flies and spiders, provoked no reaction on the part of the larvæ and remained immune." This is sufficiently contrary to the experience of previous observers and myself, but the most surprising statement concerning the larva is the following: "Such behavior (the seizing of the prey) obviously indicates its carnivorous appetites. But what shall we say of larvæ which, though kept in captivity for more than a year, in conditions preventing all access to prey, nevertheless metamorphosed in several instances? It was natural to infer that they nourished themselves at the expense of the only substance at their disposal, the subjacent earth. And, in fact, when one of them was dissected, I found its digestive tube filled with a brownish purée consisting in great part of débris of a vegetable nature clearly discernible under the microscope. This observation shows that the larva of *Vermileo degeeri* normally has a mixed alimentary regimen; carnivorous at times but mainly detritivorous, its principal food consisting of the organic particles contained in the soil in which the animal lives buried." This statement seems to me to be wildly improbable. Even if it were possible to keep the larvæ for a year without food, it is most unlikely that they would metamorphose. That they are not detritivorous is shown by the fact that I have kept many larvæ, not only of *V. vermileo* but also of *V. comstocki* and *Lampromyia canariensis* for many months in pure marble-dust, sterilized quartz sand and even pure kaolin, which, of course, contained no vegetable detritus, and have brought them to maturity with a diet of all sorts of small insects such as aphids, termites, many species of ants, caterpillars, various flies and gnats, spiders, etc. Furthermore, sections of larvæ taken directly from the sand or dust of their native habitats reveal no particles of vegetable detritus in the 'purée' filling their stomachs, but only granular and coagulated animal juices. The whole structure of the larva is, as I shall later endeavor to show, so highly specialized and so exquisitely adapted to an insectivorous mode of life that it is impossible to credit Falcoz's statements.

During the summer of 1925, as guests of Mr. Allison V. Armour on his yacht, the 'Utowana,' my friend Dr. David Fairchild and I were able to visit the three Balearic Islands, Iviza, Majorca and Minorca, and to explore many of their outlying districts for plants and insects. While on the same expedition I had previously found the larvæ of *Lampromyia canariensis* (see p. 248) on the Island of Teneriffe and was therefore constantly hoping to encounter those of *V. vermileo*. I could find no traces of them on Iviza, but secured many on Majorca and Minorca. On the former they were abundant in two localities. We reached Palma, Majorca, August 18 and the following day motored across the island to Soller. While descending the carretera from the Col de Soller to the town, I found some seven flourishing colonies of Vermileo larvæ on the right side of the road. Their pits were in fine gray dust which had been blown from the road and had accumulated at the bottoms of small cave-like cavities only a few feet deep that had been left when the fractured Jurassic limestone was cut down to make the highway. The pits measured from one to 4 cm. in diameter across the rim and the larvæ also varied greatly in size. They were of a grayish clay color, i.e., of the same color as the dust they inhabited. Nearly a hundred larvæ were collected in this place. I found that the most expeditious method of securing them was to scoop up the dust with a small wire tea-strainer and then to sift out the larvæ. Previous experience with other Vermileoninæ had taught me that this is also the best way to handle the larvæ and pupæ, not only in the field but also in the laboratory, since merely seeking them in the sand with the tweezers often leads to their being injured or overlooked on account of their cryptic coloration and peculiar habit of

FIG. 20. Typical habitat of *Vermileo vermileo* larvæ along the carretera on the Col de Soller, Majorca (about 1,000 ft.), with Dr. David Fairchild and Dr. José Porcel.

'feigning death.' A humorous description of the finding of the Vermileo larvæ in the Col de Soller is given in Dr. Fairchild's charming volume, 'Exploring for Plants' (1930, p. 245). To him I am indebted for the two photographs reproduced as FIGS. 20 and 21, representing one of the rock-cavities above mentioned, and a small group of the Vermileo pits.

FIG. 21. Pitfalls of *Vermileo vermileo* larvæ (½ natural size). Col de Soller, Majorca. (Photograph by Dr. David Fairchild.)

The second locality was also in the northwestern, mountainous portion (Jurassic limestone) of Majorca. We were motoring to Bañalbufar, a quaint little town whose inhabitants specialize in raising tomatoes, drying them and shipping them to Barcelona. Mr. Graham Fairchild and I had stopped to collect near Esporlas in a fine forest of *Pinus maritima* and *Quercus ilex* at an altitude of about 1000 ft. While we were walking along the road from the 18th to the 23rd kilometer stone from Palma to Bañalbufar to meet Dr. Fairchild and Dr. José Porcel, who had gone on in the car to investigate the tomato industry, we found no less than 20 Vermileo colonies, all on the left-hand side of the road in small niches in the limestone partly filled with white calcareous dust blown from the road. We collected about 60 larvæ and could have taken many more had we not been hurrying to overtake our companions. The larvæ varied greatly in size from a few millimeters to nearly full grown.

V. vermileo seems to be more widely distributed in Minorca than in Majorca. We found it first among the interesting neolithic monuments at Talati where the larval pits were made in the dust under the projecting edges of some of the monoliths. The Minorcan custom of enclosing all the small fields with stone walls six to eight feet high, which accumulate dust in their crevices, affords a favorable environment for Vermileo colonies, but more of them were found under the cliffs of Miocene limestone bordering some of the many barrancos which extend down to the sea, notably the Barrancos Simon, San Juan and Calemporter. The last, an unusually favorable locality, is on the estate of the Marquis de Menas Albas. The larval pits had been formed in great numbers in the dust accumulated under the projecting cliffs and detached rocks along the winding road to the sandy beach on which Dr. Fairchild and I found a great patch of the magnificent white lily, *Pancratium maritimum*.

The Vermileo larvæ collected in the Balearic Islands were kept in tins of dust and fine sand on board the 'Utowana' and fed with workers of a termite belonging to the genus Calotermes, which I had found in old stumps in the laurel forest at Las Mercedes on the Island of Teneriffe. When my supply of these insects was exhausted I had nothing with which to feed them between Aug. 31 and Sept. 22, but by the latter date I had arrived with them in

Boston and had established them in pans of fresh sand or of kaolin. They were then fed with various ants (*Tapinoma sessile, Lasius brevicornis* and *Formica subsericea*) till late October when they were consigned to a room kept at a temperature of 40° F. for the winter. They were returned to the heated laboratory the middle of March 1926 and were for some weeks abundantly fed with workers of a species of Calotermes from Arizona. They throve on this diet and began to pupate early in April. The first fly emerged April 18, and more and more of them appeared from day to day. June 13 I took the remaining larvæ, about one hundred in number, to Colebrook, in the Litchfield Hills of Connecticut. For several weeks the weather was unfavorable to the rapid development of the pupæ, because long spells of cold alternated with short, hot spells, and although the number of pupæ kept increasing, the emergence of the flies was rather irregular and continued throughout the summer. At Colebrook the larvæ had been fed so abundantly with our common termite, *Reticulitermes flavipes,* that even those that were very small when they were collected in the Balearic Islands during the preceding summer, had grown to their full size and produced flies. The last individual emerged Sept. 4. I feel confident, however, that many of the larvæ, had they remained in their native environment and been constrained to subsist on the few passing ants and other small insects that fell into their pits, would have matured much more slowly and have lived through a second winter before pupating. In other words, they would have behaved like the biennial larvæ described by von Siebold, who fed them with ants and miscellaneous insects, which are much less nutritious than fat worker termites.

The larva and pupa of the Balearic Vermileo are so similar to the corresponding stages of the other Vermileoninæ to be described in greater detail in Chapters V to VIII, that I shall here confine myself to a few general remarks. One point of interest which has not been sufficiently noticed by previous observers, relates to the ecdysis, or moulting of the larva. This occurs repeatedly during larval growth but apparently at rather irregular intervals, depending on the rate of growth, which in turn depends on the amount of food the larva has been able to capture and assimilate. To determine the precise number of moults and the time of their occurrence would require very careful rearing of a number of isolated larvæ from hatching to pupation, and this I have not been able to accomplish in the case of *V. vermileo.*

Just before ecdysis, the larva stretches out and becomes quiescent beneath the bottom of its pit, two to three centimeters below the surface of the sand. Its thin but tough cuticle then splits the full length of the body in the mid-dorsal line and is cast off as a flat, beautifully transparent ribbon, to the anterior end of which the sloughed dark brown cephalopharyngeal skeleton is attached. During ecdysis the surface of the larva's body remains dry or at any rate if there is any exuvial liquid secreted between the old and new cuticles it is not sufficiently sticky to cause any adherence of the surrounding sandgrains. As soon as the new cuticle has acquired sufficient consistency, the larva proceeds to repair its pit and while thus occupied tosses the ribbon-like moultskin out onto the surface of the sand, as if it were the exhausted carcass of a piece of prey. I have carefully preserved these moultskins, because they can be readily mounted in Canada balsam, without previous treatment with caustic potash and are useful in studying the tracheal spiracles, cephalopharyngeal apparatus, etc.

When the larva has reached maturity and begins to pupate, however, the last ecdysis is of a very different character. A layer of liquid accumulates between the old larval cuticle and that of the pupa. The former splits only in the head region and is gradually pushed back to the posterior end of the abdomen, as a tube, thrown into compact, accordion-like folds. It is not thrown off but remains attached to the caudal segments of the pupa as a much wrinkled and contracted tail or appendage. The liquid above mentioned clearly serves two purposes: first, it lubricates the surface of the pupa and facilitates the pushing back of the larval skin, and second, owing to its stickiness it causes the surrounding sandgrains to adhere firmly to the surface of the pupa. I have not been able to ascertain the source of this ecdysial liquid. We may conceive it to be either a secretion of scattered ecdysial glands in the hypodermis, as in the caterpillars of Lepidoptera, or a secretion of the poison glands (modified salivary glands) opening at the anterior end of the head, or a discharge from the anus either before or after the lumen of the midgut has become continuous with that of the hindgut. This latter alternative again suggests the possibility that the ecdysial liquid may be either a secretion of the Malpighian vessels, which, as we have seen, play such an important rôle during pupation in the Myrmeleontids, or merely the expelled residual content of the stomach (meconium). From the fact that the ecdysial liquid bathes the head and thorax of the pupa as well as its abdomen, I believe that it must be either derived from special glands in the integument or from the poison glands which no longer have the function of paralyzing the prey after the larva has begun to pupate.

The pupal period varies with the temperature and extends, according to my estimates, over two to three weeks. At first the pupa lies horizontally in the sand one to three centimeters beneath its surface, but when the time for the emergence of the fly arrives, it wriggles up head foremost and thrusts its head and thorax above the surface of the sand. The dorsal thoracic cuticle then ruptures with the usual 'orthorrhaph,' or T-shaped fissure and the imago slowly escapes. It is during the wriggling of the pupa to the surface that the sandgrains glued so firmly to its surface subserve, I believe, an important function. The abdomens of many Lepidopteran and Dipteran pupæ, that before eclosion wriggle through burrows or yielding substances such as soil or decomposing wood to a point where the delicate adult can at once issue unimpeded into the open air, are provided with rows of backwardly directed, chitinous teeth or spines, which facilitate locomotion like so many tiny claws, but the Vermileo pupa is furnished with only very feeble and therefore useless vestiges of such structures. Their function is assumed by the tightly adherent sandgrains which obviously afford an admirable substitute. Since the abdomen of the young pupa remains contracted and the intersegmental membranes are not exposed while the layer of sandgrains is being glued to its surface, it is possible for the adult pupa to move its abdominal segments very freely while climbing to the surface. One might maintain that the pupa in thus crudely selecting and fixing to its cuticle the sharp sandgrains of its immediate environment and in employing them as an aid in locomotion, is really behaving as a tool-using animal.

Unless there is some difficulty or abnormality that delays eclosion, the flies emerge only during the night and are found in the morning resting on the perpendicular sides of the dishes in the same position as other Rhagionids (Rhagio, Atherix, etc.), that is, with the head directed upward and the wings forming acute angles with the long axis of the abdomen as in the resting housefly. They may also rest, though much less frequently, with one wing overlapping the other, as described and figured by Degeer (see Appendix). This position of the wings is never assumed in many other Rhagionids (Rhagio, Atherix, Chrysopilus, Symphoromyia, etc.) The flight of *V. vermileo* when disturbed is like that of some gnats and Empidids, exquisitely light and graceful, and with the legs, especially the long hind pair, dangling.

The sexes are easily distinguished by the shape of the abdomen, that of the male being much narrower and more cylindrical than that of the female. Unfortunately, the adult insect, unlike the larva, is very delicate and short-lived. Not one of the numerous specimens which I reared survived more than 36 to 48 hours. Many of them, indeed, perished towards the end of the first day of their adult existence. I sought to prolong their lives by feeding them with honey or sugar-water but none of them would even imbibe water, though they have well-developed mouth-parts. Strangely, too, though both males and females often emerged during the same night and for several hours rested or flew about together, they exhibited not the slightest inclination to mate. I failed, therefore, to obtain any eggs or young larvæ. This failure was the more disappointing because no European entomologist has ever seen the eggs or early stages of any of the Vermileoninæ. As I shall show in Chapter VI, I have been much more successful with the Sierra worm-lion.

The *V. vermileo* flies which I reared are of a luteous yellow color. Even the wings are very faintly tinged with yellowish, the eyes in life are dark green, the head behind the insertions of the antennæ is black, the dorsal surface of the thorax ornamented with four parallel, longitudinal, brown stripes. The tips of the hind tibiæ and those of the hind femora on their extensor surfaces are fuscous, or dark brown, the first joint of the hind tarsi is pale yellow. The markings of the abdomen are conspicuous and differ in the two sexes. In the female there are three series of dark brown spots, a mid-dorsal and two lateral, consisting of three spots in a transverse row on the dorsal surface of each segment. In the male these spots coalesce on the anterior portion of the abdomen to form transverse bands.

The female measures 9-11 mm., its wings 8 mm., the male 8.5-9.5 mm., its wings 6-6.3 mm.

I have not been able to compare my specimens with material taken in Southern France, the type locality, in Tyrol or Italy, but the published descriptions indicate that the specimens from the Balearic Islands probably represent a distinct variety, for which I propose the name *balearicus* var. nov. The general yellow color of the body and appendages seems to be paler or duller. Other slight differences will probably be revealed by careful comparison with typical continental specimens.

The occurrence of a distinct variety of *V. vermileo* on Majorca and Minorca naturally leads one to speculate about its origin. That it must have inhabited the islands for a long time is, of course, indicated by its color deviation from the typical continental form. It is highly improbable that the fly could have flown to the islands from Spain even in the remote past or been carried to them on floating logs or other vegetation, since the insect is far too delicate and short-lived to have survived such a journey. Nor is it any more probable that the larvæ could have been introduced by man into two different islands in the sand or rock ballast of ships, as has occurred in the case of many plant-seeds in Eastern Australia and elsewhere. We must, therefore, suppose that Vermileo reached Majorca and Minorca at a time when these islands were still united with each other and the Iberian Peninsula. According to Scharff (1907), "the Balearic Islands have many species in common with the Spanish mainland, and seem to have been connected with it certainly in Pliocene times." A. von Jordans (1924-25, 1928), who has studied the avifauna of the Balearics intensively and has bestowed considerable attention on other groups of animals, cities 22 subspecies of birds as peculiar to the islands. He concludes that "the fauna of the region — and not only the avifauna — is very much more closely related to the fauna of Southeastern Spain and North Africa than to that of Northern Spain and especially the Tyrrhenian." The Iberian character of the Balearic fauna is very noticeable among the insects, though many of the species have been on the islands long enough to have developed indigenous varieties. Concerning the Mollusca Scharff remarks: "No less than twenty-eight species of land mollusks are peculiar to the islands. These are mostly related to Andalusian forms. One of the endemic snails, evidently a relic of early Tertiary times, is of particular interest, viz., *Tudora ferruginea.* Its only living relations inhabit the West Indies. On the mainland of Europe the genus is known from Miocene deposits." An ancient union of the Balearic Islands with the mainland and North Africa is also clearly indicated by the discovery of the remains of an extraordinary rodent-like goat, *Myotragus balearicus,* by Miss Dorothea Bate (1909, 1914) in the Pleistocene bone-brescia accumulated in several limestone caverns (of Jurassic age) on Majorca and Minorca. The peculiarities of this creature are succinctly described by Andrews (1909) as follows: "The dentition is remarkable. Instead of having three incisors and a canine on each side of the mandibular symphysis as is usual in the Bovidæ, the canines and the two outer pairs of incisors are wanting, while the median incisors are enormously enlarged rodent-like teeth, growing from persistent pulps. The premolars are reduced in number and the molars have very high crowns. The feet are remarkable for the shortness and stoutness of the metacarpals and metatarsals, which are quite similar to those of the Takin (Budorcas). The animal seems to have been adapted for climbing the steep crags and cliffs, and probably lived on very hard vegetation."[1] My friend Dr.

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[1] E. Ray Lankester has published an interesting account of Myotragus with excellent illustrations in the tenth chapter of his 'Science from an Easy Chair,' second series, 1913.

Thomas Barbour has called my attention to well-preserved skulls and teeth of this extraordinary animal in the paleontological collection of the Museum of Comparative Zoölogy. Since a ruminant so highly specialized could not reach the Balearics by swimming, we must assume a land-connection between these islands and the mainland during the Miocene or Pliocene. At about the same time the highly specialized *V. vermileo* may have migrated to the outlying portions of the Iberian Peninsula which were later isolated as Majorca and Minorca. The insect has managed to outlive its ancient contemporary, Myotragus, and may long survive, because its demands on its environment are so very modest and because its enemies, if indeed it has any, are so very few.

CHAPTER V

THE DISTRIBUTION AND STRUCTURE OF THE SIERRA WORM-LION

ONLY within recent years has it been ascertained that Vermileo is not a monotypic genus confined to the Mediterranean Region, but is also represented in North America. Probably this would have been known sooner were it not that the adults of our species are insignificant and easily overlooked by the collector owing to their resemblance in size and coloration to common gnats or mosquitoes and their occurrence only in the mountains of the far west and southwest at elevations rarely visited by entomologists in the early summer when the short-lived flies are abroad. The pits of the larvæ, too, are not carefully scrutinized because they are so similar to those of young ant-lions.

Professor J. H. Comstock was the first to encounter the larvæ of our Vermileo in the vicinity of the Yosemite Valley, and several years ago generously sent me the following notes on the various localities in which he observed them: "I first found the larva of Vermileo at Harden Lake, Aug. 11, 1907. This was at an altitude of 7600-7800 ft. and was the highest point at which I found it, although I looked carefully for it along the trail to Mono Pass. At

Harden Lake it was abundant. On our way into the Yosemite Valley, Aug. 29, 1907, I again found it on the trail opposite Indian Rock at an altitude of 7500 ft. Sept. 1, on our way out of the Valley I collected it at Old Gentry Mill. On the next day, Sept. 2, I took many larvæ at Gin Flat, Tuolumne County, and made the following note: Late this afternoon I observed the larvæ deepening their pitfalls.

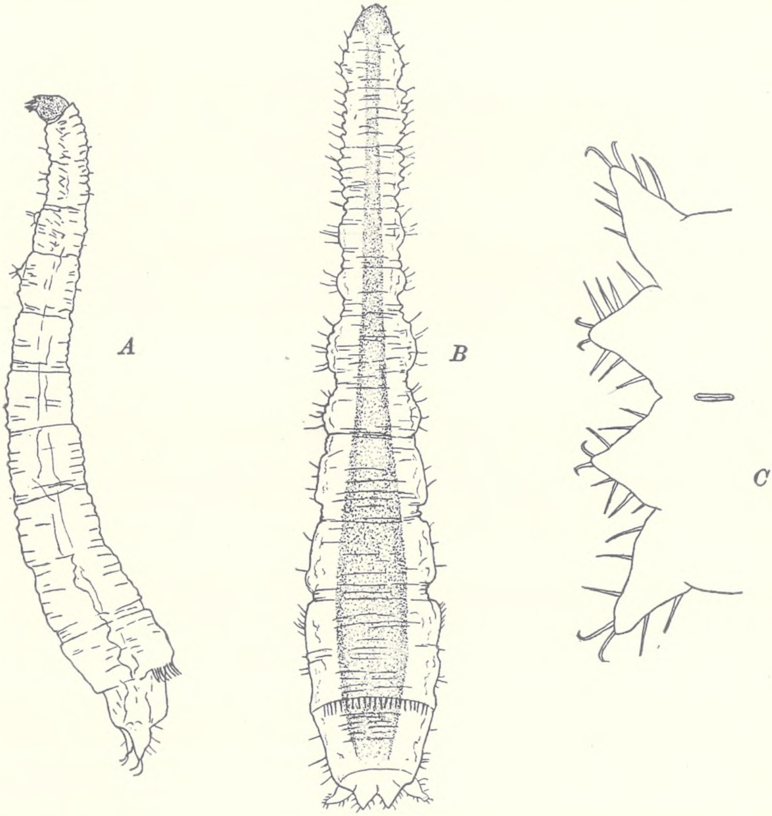

FIG. 22. Professor J. H. Comstock's original drawings of the *Vermileo comstocki* larva. *A,* lateral, *B,* dorsal view; *C,* ventral view of posterior end, with its four flattened appendages and slit-like anal opening.

The hind half of the body was anchored in the ground while the fore half was used for throwing out dirt and small pebbles. Frequently the larva would reach up and pull a pebble down beside the front end and wrapping this about it, suddenly throw it out of the pit. Frequently, when the sand is clean, the pitfall resembles in size and form the pitfall of an ant-lion, but in many cases, when there are pebbles and bits of vegetable matter mixed with the sand, the pitfalls are narrow and much deeper than wide. When the larva is dug from its burrow it 'plays possum', remaining motionless and resembling the bits of vegetable matter mixed with the sand. I have misplaced my map so that I cannot give the altitude of Gin Flat, but I think it must be the lowest point at which I observed the pitfalls. As the insect was very common here, it probably occurs at lower altitudes." [1] Professor Comstock subsequently recognized the larva as that of a Vermileo and presented me with his sketches, which are here reproduced as FIG. 22. Unfortunately, the specimens which he was attempting to rear in his laboratory at Ithaca were thrown away by a careless attendant.[2]

I first happened on the larvæ of Vermileo in 1917 while accompanying a party of Cornell instructors and students on a zoological expedition through the southwest. After spending a few days in Southern California we motored on August 22 to the Sequoia National Forest. The following day we took the eleven-mile trail to Alta Meadow,

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[1] On the U. S. Geological Survey map Gin Flat is near the Merced Grove of giant Sequoias and has an elevation of somewhat over 7000 feet. Harden Lake is a small body of water on the southern wall of the Grand Canyon of the Tuolumne River at an elevation of 7575 feet.

[2] The only published reference I have seen to Professor Comstock's observations is the following sentence in Professor J. M. Aldrich's monograph of the North American species of Symphoromyia (1915): "Professor Comstock showed me larvæ of a species (of Leptidæ) from the California Sierras which are ant-lions, like Vermileo of Europe; he did not succeed in rearing the adult, which remains unknown."

where we camped for several days at an altitude of 9000 ft. Here, along the upper border of the beautiful alpine meadow shown in the accompanying figure (FIG. 23), were great numbers of Vermileo pits in stretches of very fine glacial silt and dust surrounding the scattered boulders. Though the larvæ had made their pits close to the edges of the boulders, these were so deeply embedded in the silt that their rounded and receding sides afforded the insects no protection from the wind, rain and sun. The larvæ captured the many small insects that strayed from the adjoining meadow and coniferous trees and fell on the sand or were carried up from lower elevations by the diurnal air-currents. A more constant supply of food was certainly provided by the wandering workers from many colonies of ants (*Formica fusca*), which in many places had built their crater nests along the edges of the boulders or even among the Vermileo pits. Repeated experiment showed that the only other ant nesting in the same locality, namely the hard-shelled *Manica bradleyi,* when dropped into the larval pits, was seized but soon rejected. After devoting some days to observation of the larvæ I collected 200 of them and took them to Boston early in September. Here they were placed in dishes of fine sand and fed with a variety of ants and other small insects. After passing the winter in a cold room they pupated and produced flies during the following spring. As no species of Vermileo had been listed from North America I described my specimens as *V. comstocki* (1918). From a batch of eggs deposited by one of the flies I succeeded in rearing a second generation of larvæ, which, however, failed to survive the winter of 1918-19.

Since 1917 the insect has been taken in several other mountain localities of California by friends and correspondents who have generously supplied me with living specimens or with notes on their capture. On July 28, 1920, Professor E. M. East collected a number of larvæ for me along the

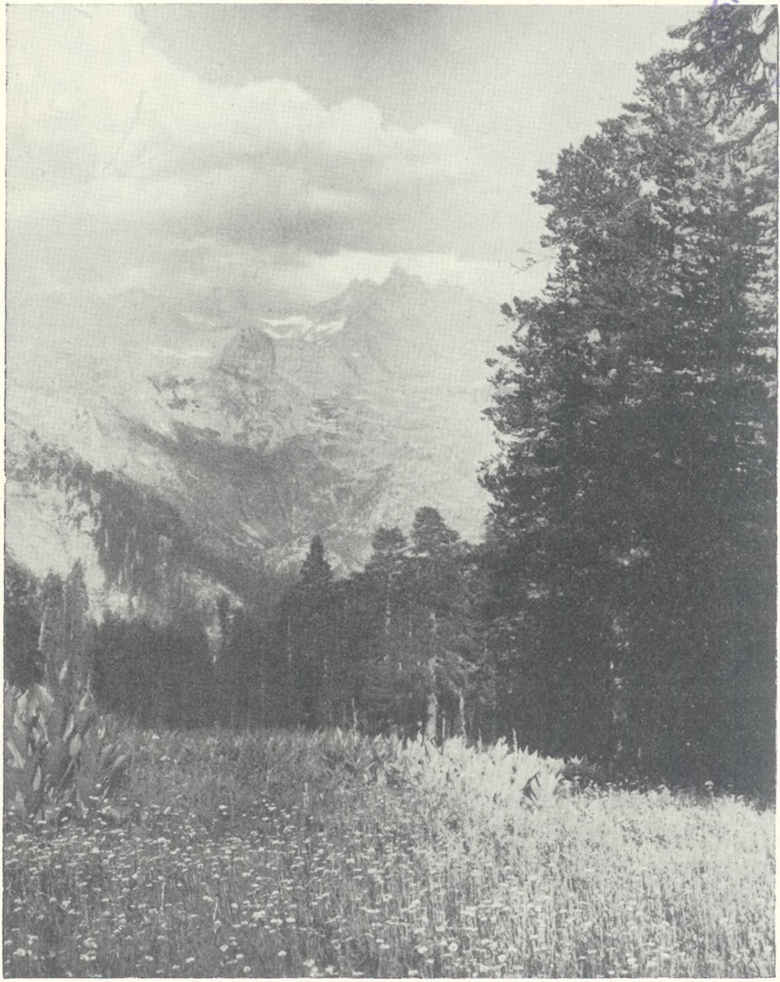

FIG. 23. Alta Meadow in the high Sierras of California, home of *Vermileo comstocki,* with view of Mt. Lippincott in the distance. (Photograph by Lindley Eddy.)

trail from Camp Curry to Vernal Falls, in the Yosemite. This trail is at an elevation of only 4000 to 5000 feet. During the same year Professor Harlow Shapley supplied me with several larvæ which he had taken on Sept. 11 and 12 at about the same elevation (5400 ft.) on the summit of Mt. Wilson in the Sierra Madre Range, near Pasadena. In 1927 Mr. Robert D. Harwood sent me the following note on finding *V. comstocki* larvæ during the preceding summer: "The first larvæ we found were in a stretch of coarse sand exposed to the direct rays of the sun at an elevation of about 7000 ft. near the north rim of the Yosemite Valley. That was during the first week in July. Then two weeks later we found them at Glacier Point on the south rim of the Valley at about the same elevation. The lowest elevation at which I found them was about 6500 ft. on the Pohona Trail near Old Fort Munroe." Professor C. T. Brues found some of the larvæ during the summer of 1927 in the Lassen National Park. Here the pits were in fine, partly calcareous dust which seemed to have been deposited by the hot springs in the vicinity. In August 1928 Professor E. O. Essig sent me some carefully preserved *comstocki* larvæ, which he had taken with a few of the adult flies on June 19 in the Yosemite, together with the following interesting note: "The larvæ were taken on the slopes of Sentinel Dome at an altitude of approximately 8000 ft. Their small pits were made in decomposed granite in a single locality, and although I looked over a considerable area I was unable to find them elsewhere. The larvæ were in various stages of development from exceedingly small ones not more than 3 or 4 mm. long to mature ones. Adults were also issuing, and the four which I collected seemed to be crawling around aimlessly on the surface of the ground and among the pine needles. I did not succeed in finding the pupæ." More recently, Mr. C. A. Harwell, naturalist of the Yosemite Park, sent me by air mail a few living larvæ which he had taken in the locality above described by Professor Essig. He wrote on Oct. 20, 1929, that three weeks previously he had collected a few of the larvæ while he was descending from Mt. Hoffmann on the May Lake Trail.

Wishing to obtain a more abundant supply of *comstocki* larvæ, I spent ten days, from May 22 to June 1, 1930, in the Yosemite. At first I had little hope of finding them, because the season proved to be too backward for collecting on the high rim of the Valley, where they had been found by most collectors. I soon discovered, however, that the larval pits were abundant along the edges of the valley floor at altitudes as low as 4000 ft., wherever there were boulders with projecting sides overhanging accumulations of fine dust. Starting at Camp Curry I found them everywhere along the beautiful trail up the Merced River to Vernal Falls and thence along the high trail to Nevada Falls, along the trail on the north side of the Valley from the new Yosemite Village to Mirror Lake and Tenaya Creek and westward on both sides of the valley floor from the new village to El Capitan and from Camp Curry to Bridal Veil Falls and thence up the road to Old Inspiration Point. Finally, after collecting so far afield, I found to my humiliation that the dust under the raised floor of the very cabin which I was occupying in Camp Curry was literally peppered with Vermileo pits and that the same was true of the dust under many of the other cabins and the great boulders at the base of the 3000 ft. precipice which rises behind the camp to Glacier Point. I was able, therefore, to secure an abundance of material without climbing to the rim of the Valley. The larvæ, of which I collected about 400, varied greatly in size from 5 or 6 mm. to 14 mm. and had all over-wintered from the preceding summer. They were always in accumulations of fine gray dust or silt protected from the rain or snow and in a few places were also taking advantage of the sandy soil under large prostrate logs not in actual contact with the ground. In other localities, especially near Mirror Lake, the Vermileo pits were mingled with those of ant-lions, but the latter were always very small. As a rule, the large larvæ of the common species of Myrmeleon in the Yosemite make their pits in open sunny places.

The foregoing citations of the localities in which *V. comstocki* has been found hitherto show that its known range extends along the Sierra Madre and Sierra Nevada Ranges from Mt. Wilson in Southern to Lassen Peak in Northern California, a distance of some 850 miles. Unlike the Mediterranean worm-lion, which lives at low elevations and even at sea-level, *comstocki* is a distinctly subalpine insect, occurring as high as 9000 ft. and, so far as known, not lower than the floor of the Yosemite Valley, or 4000 ft. Not improbably the small size of the Californian species, which is only half as long as *V. vermileo,* and its much darker color are alpine peculiarities. There is, however, a marked difference in the sites chosen for their pits by the larvæ that live at the two extremes of their altitudinal range. Thus in Alta Meadow at 9000 ft. the pits are not sheltered under the overhanging rocks but in the open sand or silt where they are fully exposed to the elements, whereas at 4000-5000 ft. in the Yosemite they are always in dust which is rarely or never wetted by rain or for long periods exposed to the rays of the sun. It will be noticed that none of the collectors above mentioned who have taken the larvæ at elevations of about 7000 ft. says anything about their being confined to spaces or cavities under overhanging rocks. It is difficult to account for this ecological discrepancy except on the supposition that *V. comstocki* is not strongly thermotactic and is therefore best adapted to the lower temperatures of higher altitudes. This would explain its preference for the shadier and cooler patches of dust along the often very warm borders of the valley floor in the Yosemite. In all cases, however, the Vermileo larvæ, unlike those of Myrmeleon, have an unmistakable penchant for making their pits very near, though not often in contact with, boulders or cliffs. I shall add some remarks on this idiosyncrasy in Chapter VI.

Since the publication of my description of *V. comstocki* in 1918, the dipterists have discovered that Coquillett as early as 1904 described as *Pheneus opacus* a fly taken by the late Dr. C. F. Baker at the head of King's Canyon, west of Carson City, in Ormsby County, Nevada. The type specimen, now in the National Museum, proves to be a true Vermileo and has been examined and compared with paratypes of *V. comstocki* from Alta Meadow by Professor J. M. Aldrich and Dr. M. D. Leonard. The former wrote me that the type of *opacus* "is a male with the abdomen broken off, except at the base. The body coloration is about the same (as in *comstocki*), tending a little more to yellow, but not materially different. There is a considerable difference in the width and form of the front which may be due to the difference of sexes." After I had sent him some males of *comstocki* for comparison, he added: "I believe there is no doubt that they are the same thing. There are some slight color differences, due principally to the fact that the type of *opacus* was a little immature." Dr. Leonard (1930), however, regards the two forms as distinct. He has discovered in the collections of the Philadelphia Academy of Sciences two more male specimens of *opacus* labelled "Alamogordo, New Mexico, May 2, 5, 1902."[1] The only differences which he records in his key relate to size and wing coloration, *comstocki* measuring 5.5-6 mm. and having the wings distinctly tinged with grayish or brownish, while *opacus* measures 5 mm. and has nearly hyaline wings. But perhaps the greater clearness of the wings in the latter form

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[1] I believe they must have been taken in the nearby Sacramento Mountains.

may be due to fading, since all three of the specimens examined by Leonard were taken more than twenty-five years ago. The size differences are rather insignificant. My specimens of *comstocki* (FIGS. 28 and 29) vary considerably in this respect, the females ranging from 5.5-6.5 mm., with wings 5-5.3 mm. in length, the males from 4.5-6 mm., with the wings 4.5-5 mm. The specimens from the Yosemite average somewhat smaller than those from Alta Meadow. It is certain, therefore, that the two forms are very much alike. Baker's Nevada specimen, moreover, was taken very near Lake Tahoe, in the high Sierras, where *comstocki* may be supposed to occur. I therefore incline to the opinion that *comstocki* is either identical with *opacus* or so slightly different as to constitute at most a variety of that species. On the other hand, it seems unlikely that the New Mexico form can belong to *comstocki*. Until more and better specimens of *opacus* have been obtained in Nevada and New Mexico, I propose to follow Leonard's example in retaining the name which I assigned to the Californian type.

The adult larva of *V. comstocki* (FIG. 24) measures 12-15 mm. and is pale grayish pink or flesh-colored. This coloration is not due to any pigment in the cuticle or hypodermis but to the internal organs and, in the posterior portion of the body, the dark contents of the stomach shining through the smooth, transparent, tough but only moderately thick integument. The surface of the cuticle is dull and opaque, not shining as in most Dipteran larvæ. The shape of the body is clearly that of a typical maggot and therefore essentially like the characteristic larval form of the Cyclorrhaph Diptera, but in Vermileo we can detect several singular modifications which are obviously so many subtle adaptations to its unusual mode of life and have been, as it were, superimposed on the primitive maggot archetype. It is, indeed, surprising that so rudimentary a form as the maggot, which was originally a larva simplified and specialized for living in the dark and in moist substances rich in nutriment, such as vegetable mold, fæces, and the decomposing or even living tissues of animals and plants, could, as the result of comparatively insignificant modifications of structure, become so admirably fitted for a very different environment and mode of life.

FIG. 24. Larva of *Vermileo comstocki.* Dorsolateral, ventrolateral and lateral views. (Photograph by C. T. Brues.)

The head of the larva is not only very small and imperfectly developed but is largely withdrawn into the body so that little of its structure is visible beyond the acute black tips of its mandibles. The body, like that of the typical maggots of the higher Diptera, consists of twelve segments, which gradually increase in size from the bluntly pointed anterior to the obliquely truncated posterior end. As in other maggots, the anterior segments are much more mobile than the posterior. Indeed, this mobility is much greater in Vermileo, as shown by the pronounced annulation of the individual segments, a condition most unusual among insects and recalling that of the leeches among the Annelid worms. In the larva of the Psychodidæ, the only other Diptera that exhibit an analogous subdivision of the segments, the annuli are less numerous than in Vermileo, which has five very distinct rings to each of the three postcephalic, or thoracic segments, and a less pronounced annulation of the succeeding segments, with the exception of the last two.

At first sight the Vermileo larva, like most maggots, seems to lack legs, but closer examination reveals the presence of a single unpaired, nipple-like pseudopod on the mid-ventral surface of the first abdominal segment (FIG. 25 *c, d*). This appendage, which was first seen and described by Degeer and Réaumur, reminds us that the maggot is phylogenetically a degenerate caterpillar and that though all traces of the ancestral legs and pseudopods have long since disappeared in most Dipteran larvæ, there are nevertheless a few groups which have retained by no means insignificant traces of these organs. Thus the larvæ of some gnats (Chironomidæ) and black-flies (Simuliidæ) have preserved a single well-developed, unpaired pseudopod on the first thoracic segment and a much closer relative of Vermileo, the Rhagionid Atherix (FIG. 35) actually has a pair of these appendages on each of its abdominal segments from the first to the seventh. We may infer, therefore, that the single pseudopod of Vermileo represents a fusion of the first pair of Atherix. The occurrence of such fusions even in forms with paired pseudopods on other segments is shown in a larva discovered near Ithaca, N. Y., by Needham (1903) and described as that of an "unknown Leptid", but which is clearly that of some one of our American species of Atherix (almost certainly *A. variegata*). Besides well-developed paired pseudopods on the first to seventh abdominal segments it has on the eighth a pair of these organs which are fused except at their tips (FIG. 35 *B*). The

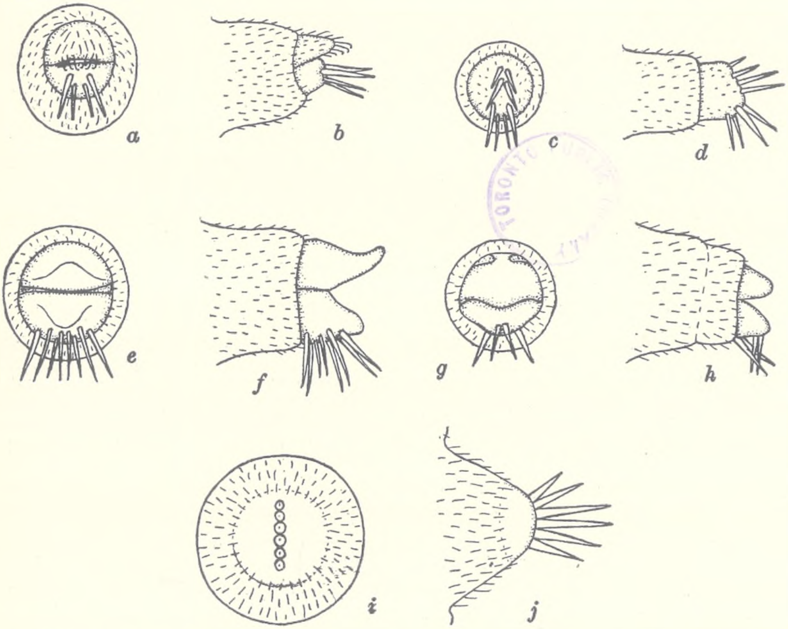

FIG. 25. The pseudopods of five species of Vermileoninæ. *a* and *b*, of *Vermileo vermileo*, from the end and in lateral view; *c* and *d*, of *V. comstocki; e* and *f*, of *Lampromyia canariensis; g* and *h*, of *L. sericea; i* and *j* of *Vermitigris fairchildi.*

Vermileo larva differs conspicuously from that of any other Diptera in having its last segment terminating in four flat, broadly finger-shaped lobes, the lateral pair of which are nearly twice as long as the median. Just anterior to the bases of this latter pair and on the mid-ventral line of the last segment there is a slit-shaped aperture, the anus (FIG. 30 *D an*).

The body of the *comstocki* larva is broader than high and therefore transversely elliptical in cross-section, owing to the development of a broad welt or swelling along each side of the body, with interruptions at the rather pronounced intersegmental constrictions. Each annulus of the three thoracic segments, moreover, is provided with a pair of lateral papillæ, and each of these in turn is capped with a long, stiff bristle, or seta (FIG. 30 *A*). When seen from above, therefore, the three thoracic segments have crenate lateral borders furnished with a regular fringe of bristles. The same arrangement is seen in *V. vermileo,* as Redtenbacher (1884) observed. He believed the fringe of bristles to be of use to the larva in throwing out the sand while excavating its pit, since the anterior end of the body is then curved in the form of a loop and the bristles would necessarily form a sieve somewhat like the hairs on the crossed mandibles of the excavating ant-lion. Redtenbacher's interpretation is not improbable, but it should be added that the long thoracic bristles are also undoubtedly sensillæ, which enable the larva to detect, while it is lying quietly in its pit, the slightest movement imparted to the surrounding sand or dust particles by any approaching insect. But there are other bristles or hairs on the worm-lion's body, that probably have the same sensory function, especially bunches of sparse, somewhat radiating bristles on the sides of the abdominal segments and a row of curved hairs which fringe the four finger-like caudal lobes. The pseudopod (FIG. 25 *c, d*) also bears at its tip several rigid bristles. More conspicuous is a regular comb-like series of about 16 large, basally broad and flat and apically rapidly tapering and recurved bristles on the raised posterodorsal border of the seventh abdominal segment. Degeer and Réaumur were the first to notice that this comb together with the spreading lobes of the last segment serves as an organ for anchoring the broadened hind end of the body in the sand while the larva is struggling with its prey. The comb may also function as a support or fulcrum while the larva is creeping over the sand on its dorsal surface.

The only other external features of the Vermileo larva besides those above mentioned, are the respiratory orifices, or spiracles. These structures (FIG. 30 *A, asp, E, psp*) are so inconspicuous that they are easily overlooked even in careful preparations of the chitinous cuticle, and when found are not easily interpreted. The larva is amphipneustic, i.e., possesses only two pairs of spiracles, one on the sides of the prothoracic, the other near the mid-dorsal line of the eighth abdominal segment. They form the anterior and posterior terminations of the pair of long tracheal trunks. The posterior spiracle when seen from the surface in cleared specimens presents the appearance of FIG. 31 *B*. It is oval and surrounded by delicate, concentric wrinkles of the general chitinous cuticle. The peritreme, or border of the spiracle is narrow and dark-colored towards the side of the body, but on the mesial side somewhat less than half of the circumference is occupied by a fan-shaped plate consisting of 19-21 minute, radiating, rod-like structures (*rt*), which under a very high magnification are seen to be hollow and tubular, with an opening at each end. The one at the peripheral end (*o*) is small, distinct and round, and opens to the outside, the position of the other is internal and not clear in surface view. At first sight the oval area enclosed by the peritreme seems to consist of an even chitinous membrane, the stigmatic plate (*sp*), but this really shows a differentiation into two regions, a peripheral which is dotted near the bases of the radiating tubules and a central portion, the central piece (*cp*), which surrounds a narrow crescentic orifice, the stigmatic opening (*so*). Numerous indistinct lines radiate from the periphery of the central piece of the peritreme. This whole apparently confused structure becomes clear when the spiracle and terminal portion of the tracheal trunk are examined in profile (FIG. 31 *A*) and in section (FIG. 31 *C*). Then we find that the central piece is continued as a clear, conical, chitinous plug for some distance down into a differentiated terminal portion of the tracheal tube known as the stigmatic chamber (*c*), or 'Filzkammer' of de Meijere (1895), and is traversed by a very narrow canal which is a continuation of the stigmatic opening. Numerous rather coarse, chitinous props, or trabeculæ (*tr*) run obliquely upward and inward from the chitinous lining of the stigmatic chamber to the surface of the central piece and also to the stigmatic plate at the base of the radial tubules. It is the insertions of these trabeculæ that appear as clear round dots (*B e*), and may readily be mistaken for minute openings. In the section (*C*) of the spiracle and stigmatic chamber, the inner opening of the radial tubules (*rt*) is seen to communicate with the cavity of the stigmatic chamber which is crossed by the trabeculæ. The anterior spiracle, as shown in FIG. 31 *D,* though much smaller and more difficult to analyze than the posterior, is nevertheless constructed on the same plan. The radial tubules, however, are only about half as numerous (8 to 10), and the central piece and its opening are very small. There is a distinct elongated Filzkammer traversed by oblique trabeculæ.

The spiracles of *V. comstocki* are of the type called 'multiphorous' and agree in general structure with those of certain other Orthorrhaphous Diptera, especially with such forms as Bibio, as described by de Meijere (1895) and the Asilid larvæ recently studied by Melin (1925). The spiracles of the Laphria larva described by the latter have, instead of my radial tubules, a regular series of radial 'props' between which lie the external openings of the stigmatic chamber. This chamber also has on its walls between the insertions of the trabeculæ a rather dense layer of chitinous hairs which are lacking in Vermileo.

Very recently Engel (1929) has described and figured the anterior and posterior spiracles of *Lampromyia sericea,* but his interpretation differs in important details from mine of Vermileo, probably because he failed to make any sections. In the anterior spiracle he figures a fan-shaped arrangement of dark, rod-like structures which he interprets as the stigmatic openings; in the posterior spiracle he erroneously interprets both the radial tubules and the small circular points of attachment of the trabeculæ as perforations or pores. He states that "besides the stigmatic openings, arranged peripherally, the whole (stigmatic) plate is covered by many small pores, from which tubes lead into the stigmatic chamber. From the latter other tubes lead directly into the body of the larva." And he adds: "I clearly saw the air pass by pressure through the stigmatic openings, but never through the fine pores which cover the surface of the plate, nor through the stigmatic scar or central piece." Obviously the air could not pass through the fine pores because they are not pores but the points at which the distal ends of the solid trabeculæ are attached to the stigmatic plate and central piece. I have been able to examine the anterior and posterior spiracles of some full-grown larvæ of the South African *Lampromyia sericea* kindly sent me by Dr. Hans Brauns, who also supplied Engel with his material. All the structures above described for *V. comstocki* are present in these larvæ and of essentially the same form, but larger and much clearer. The stigmatic chamber of the posterior spiracle is, however, shorter than in *V. comstocki* and the orifice of the central piece is much larger, more conspicuous and more eccentric. There are 18 to 19 radial tubules in the posterior but only six, as Engel noticed, in the anterior spiracle. The trabeculæ of the long stigmatic chamber of the latter are noticeably more distinct than in *V. comstocki.*

Fig. 26. Pupa of *Vermileo comstocki,* ventral and lateral views, showing covering of sandgrains and appended last larval skin. (Photograph by C. T. Brues.)

The functions of the various parts of the spiracles of Vermileo and Lampromyia are not easily determined. From his study of the similar spiracles in larval Asilids, Melin infers that during inhalation the air enters the stigmatic chamber, or 'Filzkammer,' through the radial passages, which correspond with my radial tubules, and passes out through the opening of the central body. He says that "in *inhalation* the orifice of the central piece is closed and the air passes in through the fine pores of the membrane; in *exhalation,* on the other hand, the orifice of the central piece is opened so much at least that the air can mainly pass out." This is a plausible hypothesis, but as yet we have no explanation of the mechanism, muscular or other, that opens and closes the orifice of the chitinous central piece. The stoutness and attachments of the trabeculæ suggest that the orifice in question might be opened by dilatation of the walls of the stigmatic chamber and this might be accomplished by muscles attached to its outer surface, and closure of the orifice may, perhaps, be due to the elasticity of the chitin of which the central piece consists. The trabeculæ are usually supposed to constitute an air-filter, but this can hardly be their function in Vermileo because the spaces between them are so much larger than the minute external orifices of the radial tubules, which would therefore constitute a much more efficient strainer than the trabeculæ. Then, too, the trabeculæ are coarse strands quite unlike the delicate chitinous hairs which in Asilid and other insect larvæ convert the stigmatic chamber into an adequate filtering apparatus. I believe, therefore, that the trabeculæ in Vermileo and Lampromyia and the similar structures in other Diptera, in addition to their possible function in enlarging the stigmatic orifice, may also act as struts in keeping the walls of the stigmatic chamber from collapsing under stress. Obviously this might be of considerable importance in a vigorously and spasmodically active larva like that of Vermileo. As Melin says: "The multiphorous type (of spiracle) with the wedge-shaped central piece is probably a mode of construction which can bear considerable strain." It is also evident from the foregoing description that the spiracles of the Vermileo and Lampromyia larva are beautifully adapted to respiration in fine dust or sand.

The characters of the pupa (FIG. 27) of *V. comstocki* are easily seen after the sandgrains adhering to its surface and the last larval skin attached to its posterior end have been removed with caustic potash. It measures 6.5 - 8 mm. and is dark amber brown, with the abdomen paler and more yellowish. The integument of the head and thorax are smooth, but the intersegmental regions of the abdominal segments and their borders and sides are covered with minute, rounded papillæ, which seem to represent the regular segmental rows of stiff spinules of other Rhagionid genera (Rhagio, Chrysopilus, etc.). The small spiracles

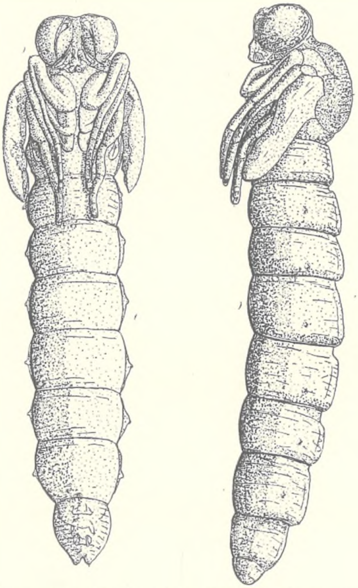

FIG. 27. Ventral and lateral aspects of pupa of *Vermileo comstocki* freed from its covering of sand grains and the last larval skin which invests the terminal abdominal segments.

(FIG. 31 *E* to *H*) are situated on distinct conical elevations and consist of groups of minute, elongated elliptical slits, radially arranged. They differ in number on the different segments, there being seven in each of the prothoracic spiracles (FIG. 31 *E*), which are the largest, and a gradually diminishing number on the more posterior segments, down to three in the last pair, which is on the eighth ab-

FIG. 28. Male imago of *Vermileo comstocki* taken in the Yosemite. (Photograph by E. O. Essig.)

dominal segment (FIG. 31 *H*). The last abdominal segment terminates in a pair of short, sharply conical appendages. Greene (1926) has published a good drawing of the *comstocki* pupa in dorsal view. His interpretation of the prothoracic and abdominal spiracles, however, seems to me to be incorrect, though it is clear that they are, as he has shown, quite unlike the pupal spiracles of other Rhagionids.

The larva and pupa of *V. comstocki* reveal so many idiosyncrasies of structure that a brief comparison with the corresponding stages of other Rhagionids may be of interest. Thanks to the patient researches of Perris (1870), Beling (1875, 1882), Brauer (1883), Townsend (1893), Austen (1899), Lundbeck (1907), R. Becker (1910), de Meijere (1917), Malloch (1917), Greene (1926) and Engel (1929), we have some acquaintance with the general form of the body and of the tracheal and cephalopharyngeal apparatus of a number of Rhagionids, representing the more important genera. It appears from all this study that the various larval forms are actually more diverse than the flies into which they develop. Though these have an extremely uniform habitus, the known larvæ may be referred to at least five or six different types, corresponding somewhat closely with the five groups or subfamilies based on taxonomic distinctions of the adults, namely the Xylomyinæ, Xylophaginæ, Cœnomyinæ, Vermileoninæ and Rhagioninæ.[1] Few dipterists, however, agree in including all five of these

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[1] It should be noted that there are two distinct types of larvæ in the subfamily Rhagioninæ, those of Rhagio and Atherix. In his revision of the Rhagionidæ of the Palæarctic Region, Lindner (1924) distinguishes six subfamilies: Erinninæ (=Xylophaginæ), Cœnomyinæ, Vermileoninæ, Bicalcarinæ (which includes only one species, *Bicalcar obscuripennis* Loew, described originally as a Chrysopilus), Rhagioninæ and Chrysopilinæ. Lindner's Bicalcarinæ, Rhagioninæ and Chrysopilinæ are only portions of the Rhagioninæ raised to subfamily rank. He does not include the Xylomyinæ among the Rhagionidæ. Bezzi (1926) has recently added another subfamily, the Arthrotelinæ, based on the South African *Arthroteles bombyliiformis* Bezzi.

groups in the Rhagionidæ. The three first are often regarded as so many distinct families, owing to the fact that their larvæ are so diversified, but no one has erected an independent family for the Vermileoninæ because the adult flies are so similar to the typical Rhagioninæ.

By common consent the Xylomyinæ, with the single genus Xylomyia (Solva), are regarded as the most primitive group of the series. The genus is, in fact, remarkably ancient and synthetic, with distinct larval affinities to the family Stratiomyidæ, or soldier flies as well as to the Xylophaginæ and Rhagioninæ. Eminent dipterists, including Osten Sacken, Verrall, Austen, Aldrich and Malloch, have actually placed it among the Stratiomyids. One of their most important arguments for this procedure is drawn from the fact that the Xylomyia larva pupates within the last larval skin, which, therefore, functions as a puparium. Before the adult fly emerges, however, as Townsend, Austen, Malloch, Lundbeck and Greene have shown, the larval skin ruptures with two transverse fissures, one between the pro- and mesothoracic segments, the other in the second abdominal segment and with a third mid-dorsal longitudinal fissure connecting the two, and then wriggles part way out of the larval skin before the fly emerges. In other words, the pupa retains for a time the last larval skin loosely enveloping the terminal segments of its abdomen. This peculiarity is supposed to ally the insect to the Stratiomyids, the larvæ of which are unusual among Orthorrhaphous Diptera in pupating within the larval skin, i.e., in possessing a puparium like the higher Diptera (Cyclorrhapha). But the fact seems to have been overlooked that the Vermileoninæ pupate in a manner strikingly comparable with that of the Xylomyinæ. As I have shown, the Vermileo pupa always retains the last larval skin firmly enclosing the terminal abdominal segments. The only difference between the two forms is that the Vermileo pupa does not form within the intact and hardened larval skin as in Xylomyia but pushes it back to the tip of the abdomen where it is permanently retained. The earliest stage of the Xylomyia pupa is, therefore, more like that of the Stratiomyidæ, but later, just before the emergence of the adult, more closely resembles that of the Vermileoninæ. Hence, so far as pupal peculiarities are concerned, there would seem to be as good an argument for retaining Xylomyia among the Rhagionidæ as among the Stratiomyidæ, and the argument acquires added force when we consider the obvious affinities between the adult Xylomyia and the Xylophaginæ.

There are, I believe, even more valid reasons for separating the Vermileoninæ from the Rhagionidæ if larval and pupal characters are to be given such decisive weight in classification. The Vermileo larva is unique among Rhagionids in the structure of the head skeleton, the annulation of the anterior segments, the presence of a single unpaired pseudopod on the first abdominal segment, the peculiar retinacular apparatus on the terminal segments, the structure of the spiracles, etc. All or nearly all of these characters are correlated with singular habits as are also certain unique features of the pupa, such as its use of sand-grains instead of spines as locomotor organs and perhaps also incidentally as a protective envelope, and the conical elevation of the abdominal spiracles. Greene calls attention to another peculiarity of the pupal spiracles when he says that "the spiracular plate in all the species [of Rhagionidæ, including Xylomyia!], except that belonging to the genus Vermileo, are very similar, and in all the spiracular entrance, the so-called spiracular opening, closely resembles the script capital letter E." Yet notwithstanding the uniqueness of these various larval and pupal characters, it seems to me that the dipterists are to be commended for not having assigned family status to the Vermileoninæ.

The foregoing discussion, however, involves only part

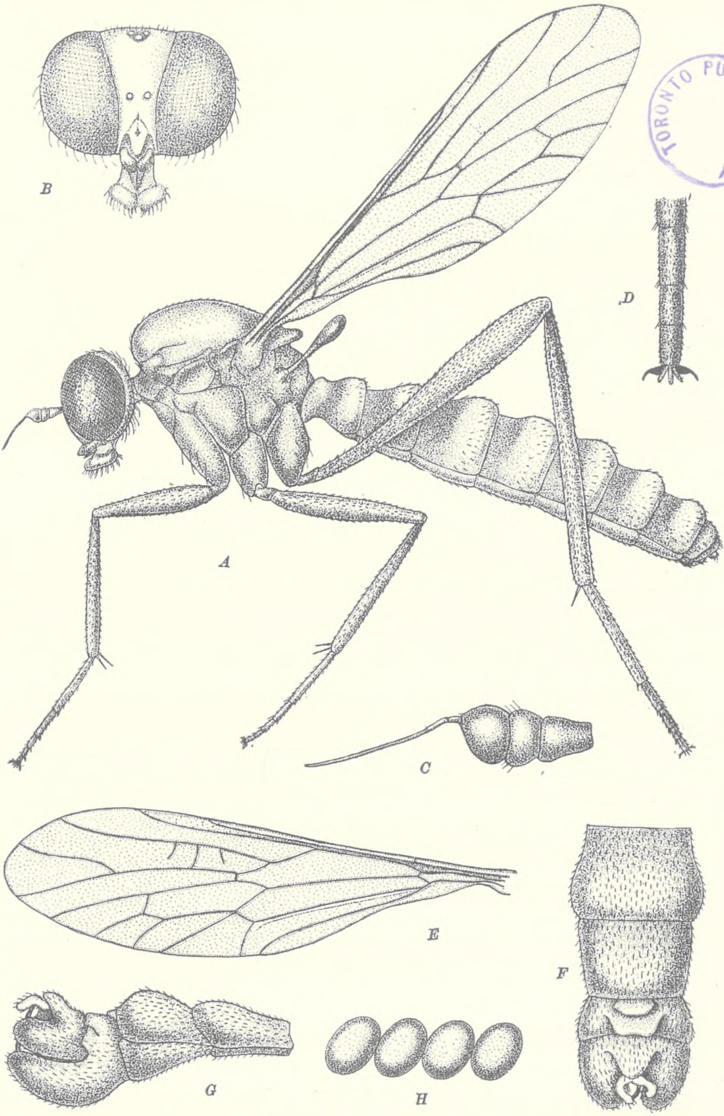

FIG. 29. *Vermileo comstocki. A,* female imago in profile; *B,* anterior view of head of same; *C,* antenna; *D,* tip of tarsus; *E,* wing of another individual with abnormal venation; *F,* tip of male abdomen showing genitalia from above; *G,* same in profile; *H,* eggs.

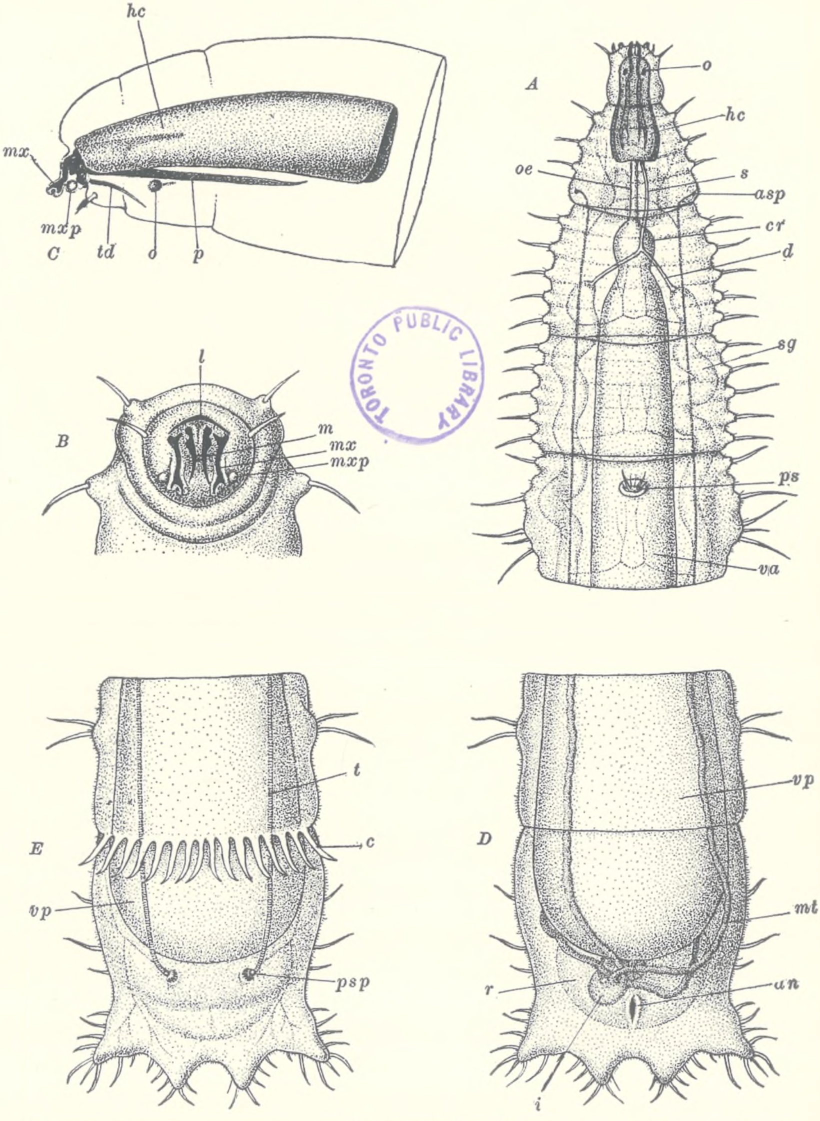

FIG. 30. *A,* anterior portion of body of *Vermileo comstocki* larva, viewed as a transparent object from the ventral side; *B,* head of living larva seen from front; *C,* head skeleton from side; *D,* posterior portion of larva, viewed as a transparent object from the ventral side; *E,* same from dorsal

of a more general question on which there is no clear consensus of opinion among systematists, namely the relative value to be attached to larval and imaginal characters in the classification of insects. Since it is generally admitted that one of the main objects of classifying organisms is to represent as adequately as possible their phylogenetic relationships, so far as they may be inferred from facts of morphological structure, ontogeny and geographic distribution, we are confronted with three questions: Are our classifications to be based on a balanced appreciation of all the characters displayed by a species in both its ontogenetic and adult stages? Or are adult characters to be given precedence and ontogenetic peculiarities to be ignored or used only when they support characters drawn from the adults? Or should the emphasis be placed on larval characters as having superior phyletic significance? Of course, the difficulty in answering these questions becomes acute when we are dealing with holometabolous insects which have three well-marked stages. We observe that in certain groups the adult forms are very similar while their larvæ are often conspicuously diverse, as in the mosquitoes (Culicidæ), whereas in other groups the adults are more diverse than their larvæ (Hymenoptera and higher Diptera), and in still others both the adults and their respective larvæ display considerable heterogeneity (Coleoptera, Lepidoptera, etc.). These observations imply that in holometabolous insects each stage has its own more or less independent phylogenetic history and that its singular characters have developed in specific adaptation to its own peculiar environment, and it is equally

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side. *an,* anus; *asp,* anterior spiracle; *c,* comb of flattered setæ; *cr,* crop, or proventriculus; *d,* paired salivary duct; *hc,* head capsule; *i,* small intestine; *m,* mandible; *mt,* Malpighian tubule; *mx,* maxilla; *mxp,* maxillary palp; *o,* eye; *oe,* œsophagus; *p,* ventral process of head skeleton; *ps,* pseudopod; *psp,* posterior spiracle; *r,* rectum; *s,* unpaired salivary duct; *sg,* salivary gland; *t,* trachea; *td,* unpaired chitinized tendon; *va,* anterior secretory portion of stomach; *vp,* posterior absorptive portion of same.

obvious that in such forms as the Diptera under consideration in this volume the most intimate and critical adjustment to the environment occurs during the larval stage, whereas in some other orders like the Hymenoptera this adjustment is more clearly exhibited by the imago. In the former insects we should therefore expect to find a greater diversity of larval, in the latter of adult morphological differentiation. These or similar considerations have undoubtedly deterred many systematists from placing too much emphasis on larval characters in classification. Conservative dipterists have therefore given more weight to the imaginal stage in classification and have employed such general characters as eucephaly and brachycephaly of the larva, the orthorrhaphy and cyclorrhaphy of the pupa, etc., only after they have been found to be correlated with general adult characters. De Meijere (1917) has contended that many special larval and pupal characters are really polyphyletic, or have developed independently in unrelated genera, and are therefore of little use in classification. The employment of such characters accounts for the failure of classifications based on the more obviously adaptive peculiarities in the various stages and the comparative success of those which have relied on such feebly or obscurely adaptive characters as the terminal antennal joints, the width of the face, the tarsal pulvilli, the tibial spurs, the chætotaxy of the body, the details of wing venation, structure of the male genitalia, etc.

I have not been able, of course, to investigate the whole internal anatomy of *V. comstocki*. Such a study would, in fact, require a volume for its adequate presentation. I therefore confine myself in the following paragraphs to a detailed description of two organ complexes only, the head-skeleton and the alimentary tract, and to adding a few brief notes on the nervous system, musculature and fat-body, because these structures are most important in connection with certain aspects of the larva's behavior to be considered in the next chapter. My investigations were made on *V. comstocki* before I was able to secure material of the larger and more favorable *V. vermileo, Lampromyia canariensis* and *sericea,* but the anatomical structure of these species is so very similar that the description will very probably apply to all Vermileonine larvæ.

The chitinous head-skeleton, or cephalopharyngeal apparatus as it is usually called, of Dipteran larvæ has been so long an object of study and so useful for diagnostic purposes that it has given rise to an extensive literature. Here only the accounts of the Rhagionidæ can be considered. Brauer (1883) was the first to describe the structure of the head in this family, selecting as his material the larvæ of *Ptiolina nigripes* and *Vermileo vermileo.* Marchal (1897) subsequently investigated the same region in *Lampromyia pallida,* Becker (1910) in Atherix, de Meijere (1917) in Rhagio, Greene (1926) in *Vermileo comstocki* and Engel (1929) in *Lampromyia sericea* and *pallida.* It will be seen therefore that the head-skeleton of the Vermileoninæ has received more attention than that of any other subfamily. And yet the results are somewhat disappointing. Brauer's description and figures of *V. vermileo* are very defective, not to say misleading; Greene's figures of *V. comstocki* are too small and the parts are neither designated nor described in the text; Marchal's figure of *L. pallida* (FIG. 43, *14*) and Engel's of *L. sericea* are much better, but both fail to call attention to several different sclerites that were in all probability present in their preparations.

When the head of the living *comstocki* larva is viewed from the front (FIG. 30 *B*) the only visible sclerites are the blackish anterior tip of the labrum (*l*), the stylet-like mandibles (*m*) and the maxillæ (*mx*), with their enlarged tips and palpi (*mxp*). In order to obtain a more satisfactory knowledge of the entire skeleton, all the soft parts have to be dissolved away in caustic potash and the chitinous parts mounted in Canada balsam under slight pressure in order to separate their sclerites. The drawings in FIG. 32, made from such preparations, show the head-capsule, which is withdrawn into the first thoracic segment, as a large, dark-colored, scoop-shaped structure, evenly arched above, open below and when seen in either of these positions broader behind than in front and somewhat violin-shaped. It is decidedly more slender in *V. vermileo* than in any of the other species which I have examined. Two short vertical plates, one on each side of the median line, are fused by their upper borders to the roof of the head-capsule and extend

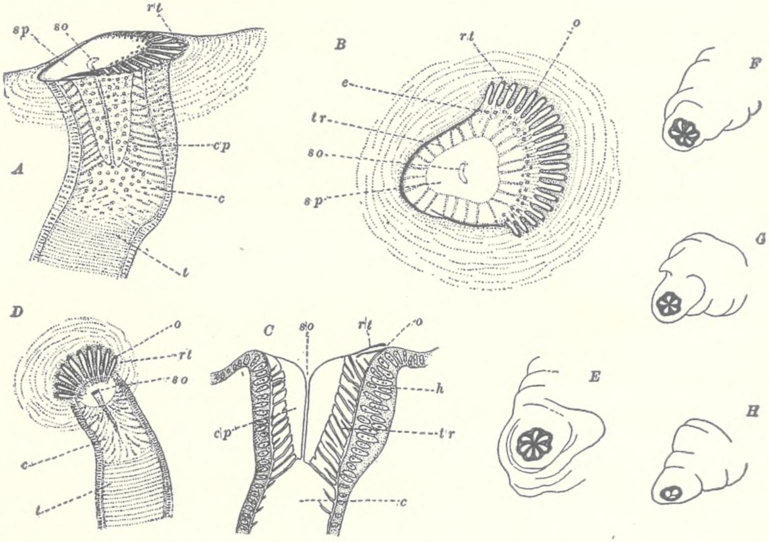

FIG. 31. A, posterior spiracle of *Vermileo comstocki* larva in profile; B, same seen from surface; C, same in longitudinal section; D, anterior spiracle in profile; E, prothoracic spiracle of pupa; F, first abdominal; G, fourth abdominal and H, eighth abdominal spiracle of same; *t,* tracheal trunk; *c,* stigmatic chamber ('Filzkammer'); *so,* stigmatic opening; *rt,* radial tubule; *o,* opening of same; *cp,* central piece; *tr,* trabecula; *sp,* stigmatic plate; *h,* hypodermis.

backward and somewhat downward as long, slender, ventral processes (*vp*). Between these and nearly in contact with them lies a flat, linear, parallel-sided sclerite (*g*), which has been overlooked by previous observers. It is narrowed anteriorly and terminates in a short bifurcation. Its posterior, incompletely chitinized end is transversely truncated. Within the space formed by the head-capsule as the roof, the linear sclerite as the floor and the ventral processes and their anterior plates as the sides, lies the pharynx, with its well-developed musculature attached to the walls formed by these chitinous structures. The ventral and lateral portions of these walls are more moveable and elastic than the head-capsule. The anterior portion of the head-skeleton consists of several small, dark-colored sclerites, partly paired and partly unpaired. The head-capsule is continued forward as an unpaired, median, narrow, acutely pointed piece, with crenated borders, the labrum (*lb*), or upper lip, not unlike the rostrum of a lobster. This projection is embraced by the mandibles (*m*), which are falcate and laterally compressed, with finely serrated ventral borders and fine ridges, continuous with the serrations and extending over their surfaces, so that they appear to be transversely striated. Two much larger sclerites, the maxillæ (*mx*) lie next to the mandibles and project well beyond them anteriorly. They are large rods, curved downward and laterally, with expanded, calyculate distal ends, covered with a thick layer of colorless chitin, and each enclosing in the impression at the tip a rounded sense-organ. The proximal ends of the mandible and maxilla on each side are articulated to the ends of a very peculiar sclerite, bent like a hook, which may be called the uncinate sclerite (*a*). It surrounds a perpendicular, elliptical piece (*l*) which is expanded and laterally compressed ventrally. This seems to be interpreted as the labium, or lower lip, in Engel's figure of *L. sericea*. In addition to these more conspicuous sclerites

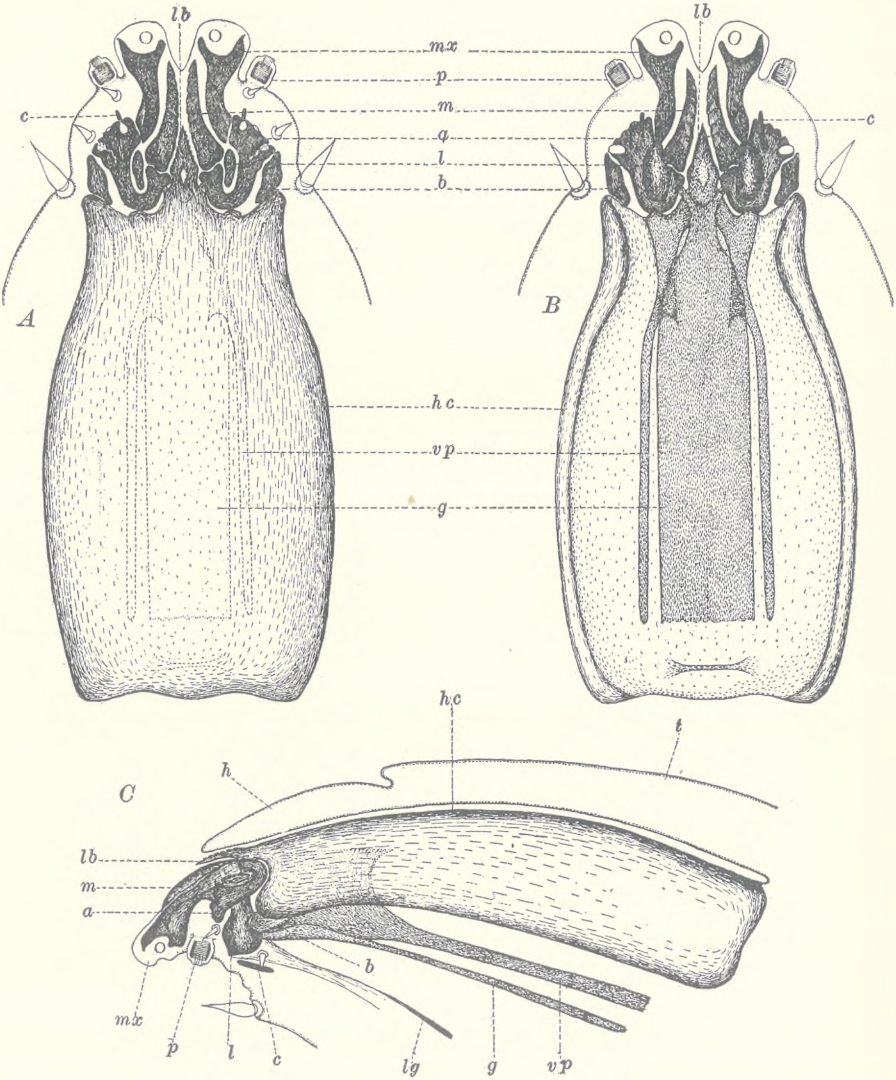

FIG. 32. Head skeleton of *Vermileo comstocki* larva. *A*, dorsal, *B*, ventral view, both from preparations somewhat compressed in order to separate the anterior sclerites. *C*, lateral view. *lb*, labrum; *mx*, maxilla; *p*, maxillary palp; *m*, mandible; *a*, uncinate sclerite; *l*, labium (?); *b*, lateral sclerite; *hc*, head-capsule; *vp*, ventral process of same; *g*, gula (?); *lg*, chitinized ligament; *c*, small lineal sclerite; *h*, head segment of larva; *t*, first thoracic segment.

I find the following, which are not mentioned by previous observers: first, a thick, scale-like sclerite at each of the anterolateral corners of the head-capsule (*b*); second a pair of small, slender, isolated, rod-like structures (*c*) rather far forward on the ventral side; and third, a slender, unpaired, median, chitinized tendon (*lg*) belonging to a long muscle that apparently draws down the floor of the mouth. Lateral to the maxilla on each side and rather isolated from the other structures is the conspicuous, keg-shaped maxillary palpus (*p*) which has been clearly figured by Marchal (FIG. 43) and Engel. It is evidently an important sense-organ. The anterior portion of the head is also furnished below on each side with some smaller sense-organs in the form of short, stout sense-hairs. The form and position of all the structures above mentioned are so clearly shown in the accompanying three views of the head-skeleton (FIG. 32) that more minute description is unnecessary.

It is very difficult to determine the homologies of these sclerites, with the exception of the head-capsule, labrum, mandibles and maxillæ, all of which are easily referable to corresponding structures in many Nematoceran and Brachyceran larvæ. I am inclined to regard the linear sclerite as the homologue of the gula in other insects and perhaps the vertical elements enclosed by the uncinate sclerites really represent the labium, as Engel implies. Some of the numerous sclerites can, no doubt, be homologized with those in the much simpler head-skeleton of the higher, Cyclorrhaph Diptera, but this would require a special comparative investigation. I merely call attention in passing to the singular resemblance of the Vermileo head-skeleton to that of the Syrphid Microdon as figured by Holmgren (1904, FIG. 4). Comparison of Vermileo and Lampromyia with the few other Rhagionids that have been studied in detail (Atherix, Rhagio, Ptiolina) reveals numerous resemblances, but also

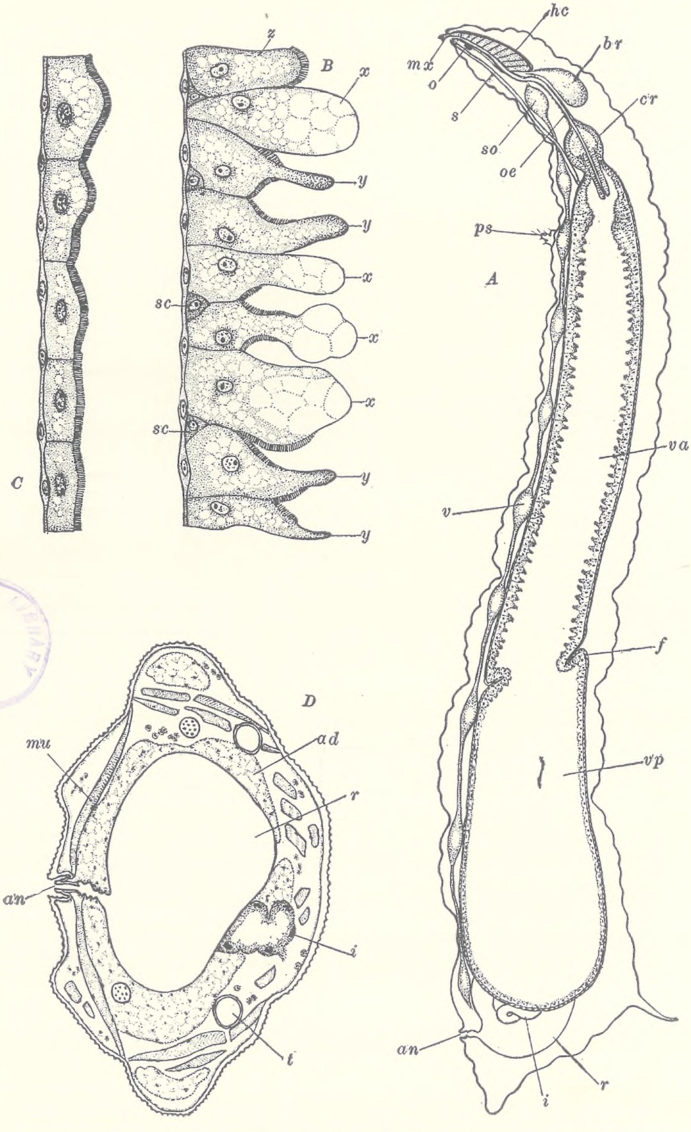

FIG. 33. *A,* median sagittal section of *Vermileo comstocki* larva; *B,* section of epithelial lining of secretive portion of stomach (*va*); *C,* section of epithelial lining of absorptive portion of stomach (*vp*); *D,* transverse section through anal and rectal

striking differences, as will be found by the curious reader who cares to consult the figures of Brauer, Becker and de Meijere.

The entomological literature contains no description of the alimentary tract of the Vermileo larva. Dissection and sections show that it is fundamentally of the same type as in other Diptera, with one important difference to be noticed in the sequel. The minute and not easily detected mouth-opening, situated between and under the mandibles, leads into the slender, tubular pharynx, the thick, muscular walls of which, attached to the inner surfaces of the head-capsule and the adjacent lateral and ventral sclerites, were mentioned above. The tract is continued back as a short œsophagus, or gullet (Fig. 33 *A oe*), traversing the simple, bulb-shaped proventriculus, or crop (*cr*) and projecting into the cavity of the stomach. The latter is the largest and longest portion of the alimentary tract and extends backward with gradually increasing diameter through the greater portion of the body. A short distance behind the middle it is incompletely divided by a transversely oblique fold (*f*) into an anterior, narrower (*va*), and a posterior, broader region (*vp*). These have different functions since the epithelial cells lining the walls of the former are very largely, if not exclusively, concerned with the secretion of the gastric juices, whereas the cells of the latter, at least in great part, absorb the products of digestion.

I find that the cavity of the stomach does not communicate with that of the hindgut as in other Dipteran larvæ,

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region. *ad,* fat-body; *an,* anus; *br,* brain; *cr,* crop, or proventriculus; *f,* fold separating secretive and absorptive portions of stomach; *hc,* head-capsule; *i,* small intestine; *mu,* muscle; *mx,* maxilla; *o,* eye; *oe,* œsophagus; *ps,* pseudopod; *r,* rectum; *s,* unpaired salivary duct; *sc,* substitution cell ('Ersatzzelle'); *so,* subœsophageal ganglion; *v,* ventral ganglion; *va,* anterior or secretive portion of stomach; *vp,* posterior or absorptive portion of stomach; *x,* actively secreting cell; *y,* cells after expulsion of secretion; *z,* absorptive, or resting cell.

but is closed off as in the ant-lion. Sections (FIG. 34) show that the epithelial lining of the hindgut where it joins the small intestine (*pr*) forms a large thickening or proliferation, not unlike that figured by Rengel (1908) for the ant-lion, and thus occludes the lumen, so that the dark granular contents of the stomach (*ct*) end sharply with a convex, more or less hemispherical surface and are never seen to be continued into the intestine. Nor is it possible by

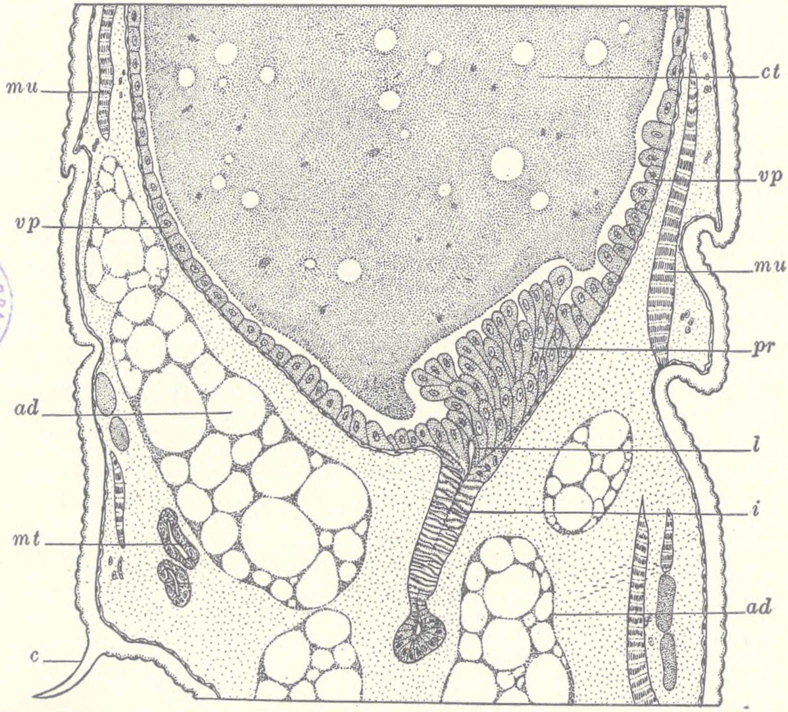

FIG. 34. Portion of a sagittal section through the posterior end of the stomach and beginning of the small intestine of a *Vermileo comstocki* larva. *vp*, epithelial lining of stomach; *ct*, granular contents of stomach. The clear circular spaces are filled with fat-globules in the living larva; *pr*, proliferation, or thickening of the epithelium at the point where the small intestine (*i*) is continuous with the stomach; *l*, remains of lumen; *ad*, fat-body; *mt*, section of Malpighian tubule; *mu*, muscle; *c*, seta of dorsal comb.

pressure or manipulation of the stomach of a living or recently killed larva to force any of the stomach contents back beyond this point. The small intestine (*i*) is long and very slender and applied as a coil to the hemispherical posterior surface of the stomach. It is therefore easily overlooked in dissections and by no means easy to unravel in serial sections. It possesses a narrow lumen (*l*), obscure in the anterior portion and never containing any traces of food or fæces. At its point of attachment to the posterior end of the stomach it is somewhat swollen and rounded and here gives off the Malpighian tubules (FIG. 30 *D mt*). These are four in number. Their proximal portion is very slender and its cells are filled with yellowish green granules, but the longer apical portion is considerably thicker and, in larvæ that have been well fed and then left to fast for some time, filled with minute urate crystals, so that it appears pure white in reflected and black in transmitted light. These tubules bend forward just beyond their insertions and accompany the walls of the stomach for some distance into the anterior portion of the body (FIG. 30 *D mt*). The small intestine (*i*) behind the insertions of the Malpighian tubules narrows to a mere thread, as in the ant-lion, but widens somewhat and has a larger lumen before it enters the rectum (FIG. 33 *r*), which is a large, thin-walled vesicular structure, functioning apparently during larval life as a bladder, or receptacle for the liquid excretion of the Malpighian tubules. It terminates on the ventral side as the slit-shaped anus (*an*) by means of a short tube with wrinkled walls. Thus, owing to the occlusion of the alimentary tract at the hind end of the stomach throughout larval life, the whole hindgut becomes subordinated, as in the ant-lion, to the excretory function of the Malpighian tubules, but the Vermileo larva does not spin a cocoon so that the tubules do not secrete silk. The cavities of the stomach and hindgut become continuous just before pupation, and the dark unassimilated contents of the stomach and the urates accumulated in the Malpighian tubules are then voided as the 'meconium.' In the ant-lion, as we have seen, the evacuation of these larval food residues is postponed till the imaginal stage. Our entomological textbooks cite only three groups of insects that have the stomach, or midgut shut off from the hindgut during the larval stage, namely the Neuroptera (Planipennia), the Strepsiptera and the Hymenoptera, with the exception of the sub-order Phytophaga. To these we must now add a fourth group, the Vermileoninæ, among the Diptera.

The epithelial lining of the stomach of the Vermileo larva is an unusually favorable object for the cytological study of secretion and absorption. In sections like the one shown in FIG. 33 *B,* through the wall of the anterior division (*va*) of the stomach, we find epithelial cells of four different forms: First, very actively secreting cells of the form indicated at *x*. These are high and columnar, with numerous small vacuoles surrounding the nuclei and, especially in their free ends, projecting into the lumen with huge vacuoles or droplets of secretion which break off and fall into the digestive cavity. These droplets evidently burst through the finely striated border, or rhabdorium, leaving only portions of it surrounding the protrusion. Second, there are the cells (*y*) that have obviously extruded their load of vacuoles and are slowly returning to another secreting phase. Their apical ends are much narrowed, cylindrical and pointed, and consist of dense and rather deeply staining cytoplasm. The third type of cell (*z*) is rare in the anterior division of the stomach. It is regularly columnar, with intact rhabdorium over its apical surface, and is evidently in the 'resting', or absorbing phase. Finally, the fourth type is represented by the small, triangular, deeply staining substitution cells (*sc*), or 'Ersatzzellen', interspersed between the bases of the large functioning cells (*x, y*) and destined to grow up and replace the latter after they are worn out with repeated secreting and drop into the digestive cavity to be themselves digested. The epithelium in the posterior division of the stomach (*vp*) is peculiar in consisting of cells of the flattened, or pavement type, but with distinct and perfect rhabdorial border, as shown in FIG. 33 *C*. This more stable type of cell is evidently 'resting', or rather absorbing. We see, therefore, that unlike the ant-lion stomach, in which all the epithelial cells are alike and undergo alternating phases of secretion and absorption, the stomach of Vermileo exhibits a segregation of these functions between the cells of its anterior and those of its posterior division. The stomach epithelium of Vermileo is also unlike that of the ant-lion in producing no peritrophic membranes.

The stomach epithelium of *V. comstocki* bears a close resemblance to that of the Tipulid fly *Ptychoptera contaminata* described in a classical paper by Van Gehuchten (1890). More recently Shinoda (1927) has detected similar conditions in another Dipteron, *Psychoda sexpunctata*. This investigator, after a study of the stomach epithelium in representatives of many orders of insects, concludes that the Diptera present very simple conditions which he believes to be secondary, or the result of specialization, rather than primitive, or ancestral. He also finds that the anterior portion of the Dipteran stomach is more secretive, the posterior more absorptive. Van Gehuchten found a similar regional differentiation in Ptychoptera, though in this form the median portion of the stomach is absorptive and the anterior and posterior ends secretive.

In our study of the ant-lion larva we found that the source of the venom employed in paralysing or killing the prey is unknown and we could only surmise that it is secreted by the maxillary or salivary glands. In the Vermileo larva, however, there can be little doubt that it is a salivary secretion that produces the paralyzing or lethal effects. Indeed, it is well known that the salivary glands often produce such substances in mosquitoes and other biting flies, but in all cases this statement applies only to the adult flies and not to their larvæ. The resemblance is somewhat closer between the Vermileo larva and the adults of such forms as the Asilidæ, or robber-flies, which actually capture and paralyze insect prey. This subject has been considered at length by Melin (1923), with citation of the pertinent literature.

There is space for only a few summary remarks on the nervous system, musculature and fat-body of *V. comstocki.* In FIG. 33 *A,* I have represented the main ganglia of the central nervous system, i.e., the brain (*br*), which is rather well developed and situated above the gullet and behind the head-skeleton in the second thoracic segment. The connectives which unite the brain with the subœsophageal ganglion (*so*), lying under the gullet, are not represented on account of the plane of section. The ventral nerve chain consists of a series of nine smaller ganglia, one of which is shown at *v,* and their longitudinal connectives. The position of the brain behind instead of within the head-capsule is very unusual in insects. Bugnion (1922, 1929), however, has recently shown that the same displacement occurs in the larva of a very different group, the fire-flies (Lampyridæ). Their larvæ have sucking mouthparts constructed on somewhat the same plan as those of the ant-lion. Bugnion believes that "the cause of the displacement of the brain may be explained without much trouble. The sucking apparatus requires a highly developed musculature and the brain has moved back of the head-capsule in order that the dilator muscles of the pharynx may have more extensive insertions." This explanation probably applies also to the worm-lion, though not to the ant-lion, which retains its brain *in* the head-capsule.

One of the most interesting organs connected with the nervous system of Vermileo is the eyes, which have been overlooked by previous investigators. In *V. comstocki* these appear as a pair of small, subspherical, deeply pigmented bodies (FIGS. 30 *o* and 33 *A o*) under the anterior end of the head-capsule in all very young and most older larvæ. In the latter they are not always easily detected, apparently because they sometimes lose their pigment. When well-developed they closely resemble the eyes of some other Rhagionids (Rhagio, Atherix). Their structure, of course, is much simpler than that of the ant-lion's eyes, being in fact little more than a cluster of cells filled with blackish pigment granules. They therefore at best merely enable the larva to distinguish between light and darkness. I find that the eyes of *V. vermileo* are very variable, being sometimes distinct even in half-grown larvæ and at other times indistinguishable, probably owing to defect of pigment. Even adult larvæ of *Lampromyia canariensis,* however, sometimes have very distinct, deeply pigmented eyes. As will be explained in the next chapter, the position of these sense-organs under the head-capsule may be important in connection with the larva's inveterate habit of lying and walking with its ventral side uppermost.

The musculature of the Vermileo larva would be well worth careful cytological study, because its fibres, as indicated by the great distinctness of their discs, or striations, are so highly differentiated (FIG. 34 *mu*). This might be expected in an organism that is capable of executing such vigorous and rapid movements. Like the ant-lion, the larva of Vermileo has a voluminous fat-body (FIG. 34 *ad*), consisting of white strands of adipocytes, or fat-cells, filling all the spaces between the integument and the alimentary tract not occupied by other organs. The adipocytes, of course, store up the fat and proteids that will be drawn upon during the pupal stage to build up the body of the imaginal insect.

CHAPTER VI

THE BEHAVIOR AND DEVELOPMENT OF THE SIERRA WORM-LION

BEFORE describing the behavior of *Vermileo comstocki* in detail it seems advisable to dwell somewhat on the known habits of other Rhagionidæ. The literature contains brief, scattered data on the larval and adult behavior of all the more prominent genera. Concerning the ecological or native environment of the larvæ, interesting facts have been recorded by Dufour (1862), Perris (1870), Beling (1875, 1882), Brauer (1883), Needham (1903), Malloch (1917), Lindner (1924), Greene (1926), Leonard (1930) and others. The larvæ of Rhagio and Chrysopilus live in damp mould, under decaying leaves, in compost or in decaying wood. Brauer describes the emerald green larva of *Ptiolina nigripes* as occurring under Hypnum moss covering the surface of rocks, in company with the larvæ of the snow-insect, *Boreus hiemalis*. The only observation on Symphoromyia was made by Beling (1882), who found the larva of *S. crassicornis* in sod at the edge of a beech forest. The very sluggish larvæ of Cœnomyia live not only in the soil of fields, but also in decaying wood; those of Xylomyia and Xylophagus beneath the bark of trees. In nearly all cases the food of the various larval Rhagionids has been found to be other insects and especially larvæ. The larvæ of the largest species in the family, the European and North American *Cænomyia ferruginea,* have actually been seen to feed on white grubs (Lachnosterna) in a field near Chicago (Malloch). A few records, however, refer to the species of Xylomyia and Chrysopilus as subsisting on decayed vegetable matter. Unlike these terrestrial forms, the singular larva of Atherix (FIG. 35) lives in the water of rapidly flowing streams. Besides its numerous pairs of pseudopods which make it resemble a caterpillar, it bears at the posterior end a pair of long ciliated gills and has smaller lateral and dorsal appendages which may, perhaps, have the same function. The specimens observed by Needham (1903) were 16 mm. long and lived "in the crevices of the stones in rushing waters associated with stone fly and caddice fly larvæ." Of the pseudopods with their double circlets of hooks he says: "This grappling apparatus is doubtless correlated with a life spent clinging to the surfaces of rocks in the current of rushing streams." But the larva, according to Aldrich, "also has the power of raising

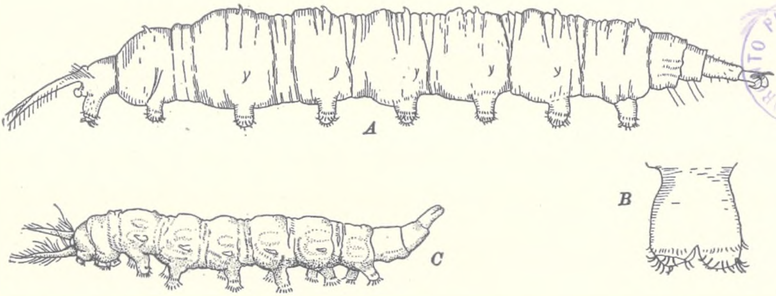

FIG. 35. *A,* Larva of an American species of Atherix after Needham; *B,* fused eighth pair of abdominal legs of same; *C,* Larva of *Atherix ibis* of Europe, after Lindner.

itself in the water by an incessant undulating motion in a vertical plane."

The adult Rhagionids are rather delicate flies which soon die of exhaustion, the males after mating, the females after oviposition. Owing to the similarity of the sexes there seem to be only feeble indications of courtship in some species and the general behavior is on the whole rather uninteresting. Certain genera, however, contain species of economic importance because they are blood-suckers and may, like the mosquitoes, horseflies, blackflies, etc., actually attack man. This is true of some North American species of Symphoromyia, as has been shown by Knab and Cooley (1912), Knab (1915), Shannon (1915), Aldrich (1915), Leonard (1930) and others. Knab (1912) has also produced evidence that in Mexico *Atherix longipes* is a fierce biter and blood-sucker and cites Philippi as having observed this habit in *Dasyomma obscurum* in Chile. Bezzi (1926) believes that the South African *Atherimorpha albipennis* may have the same propensity. The genus Atherimorpha was originally described by White (1915) from Tasmania, but he says nothing about its being a blood-sucker. He does, however, make this assertion of another peculiar Tasmanian Rhagionid, *Spaniopsis tabaniformis,* which has a proboscis somewhat longer than its head and seems to be a connecting-link between the Rhagionidæ and Tabanidæ. Judging from G. H. Hardy's observations, quoted by White, its behavior must be very unusual for a Rhagionid, since "it occurs locally in swarms, like mosquitoes, which when flying around one, it is easily mistaken for."

A number of European entomologists — Walker, Schiner, Verrall, Sharp, Egger, Chapman, Tournier and Preudhomme de Borre (1874), Pérez, Billups (1889), Giard (1902) and Lindner (1924) — have shown that *Atherix ibis* possesses the singular habit of clustering and ovipositing in the immediate neighborhood of the streams in which its larvæ live, and Ives (1890), Riley and Howard (1890), Aldrich (1912) and Engelhardt (cited by Bequaert 1921) have called attention to the very same behavior in our North American *A. variegata.* Thousands of the female flies congregate on tree-trunks, piles or stones overhanging or emerging from the water, in dense pear-shaped or spherical clusters often several inches in diameter and die *in situ* after depositing their eggs. These are found embedded among the dead flies as whitish, agglutinated masses from which the hatching larvæ fall into the water. Tournier (1874) conjectured that the larvæ feed at first on the corpses of their mothers and later, after entering the water, on carrion ("dead dogs and cats and other refuse"), but this was regarded as improbable by Giard (1911) who seems to have inferred from Dufour's (1862) account that they live on decayed and submerged wood. It seems more probable that their food consists of small insect larvæ.[1] Billups (1889), who published a good figure of a cluster of Atherix flies, bred from their eggs two minute Hymenopterous parasites, a Trichogramma and a Megaspilus. Aldrich, in an interesting paper (1912), has shown that the extraordinarily abundant clusters of an undetermined species of Atherix were annually collected, mashed, baked into loaves and eaten by the Modoc and Pitt River Indians of California and Oregon. A similar clustering habit has been observed also in the South African *Pachybates braunsi* by Dr. H. Brauns. Bequaert (1921), who first described this fly as an Atherix, quotes Brauns' remark that "it is at home along the margin of swiftly running brooks near Cape Town. One finds females and males of it on stones that emerge above the water (the female is smaller and black), bunched together in masses as large as a man's head; every

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[1] Dufour, who believed that the larva he was describing was that of Sepedon, says nothing about its food. He merely gives its habitat as "under the bark of immersed piles and also in decayed wood in the River Adour near Saint-Sever."

moment pieces the size of a fist break away from the mass and, as soon as they drop in the water, are greedily eaten by the trout with which the streams have been stocked." Nothing is said in this account about oviposition and there are flies of both sexes in the clusters. Apparently only ovipositing females form the clusters of the European and North American Atherix.

It will be seen from the foregoing paragraphs that Atherix must be regarded as a highly specialized insect and as having diverged as far from the majority of Rhagionid genera in the direction of hygrophily as the Vermileoninæ in the direction of psammophily. That the larval behavior of most of the genera is more primitive or conservative than that of the imagines is confirmed by the general agreement of Rhagio, Chrysopilus, Xylophagus, etc., at least in larval habits, with several other Brachyceran families, notably the Therevidæ, Asilidæ, Tabanidæ, Empididæ and Dolichopodidæ. The larvæ of all of these groups live in soil, vegetable mould or decaying wood, though there are considerable differences in their humidity requirements. Thus Tabanid larvæ prefer very moist soil, or mud, the Therevidæ dry soil, sand or even dust, and the Asilidæ show a considerable range of predilection from moist earth and decaying wood to dry sand. So far as their psammophily is concerned, therefore, the Vermileoninæ are in all probability descended from forms with essentially the same habits as the arenicolous Therevids and Asilids. Leaving further discussion of this matter to be continued in connection with the paleontological history of the Rhagionidæ in Chapter IX, I take up the behavior of *Vermileo comstocki.*

Very little has been added to our knowledge of the imaginal or adult behavior of the Vermileoninæ since Degeer and Réaumur recorded their few observations on the flight and wing-postures of *V. vermileo,* and my own observations on this species (p. 162) have failed to yield more information. During the spring and summer of 1918, however, I was able to complete the life-history of *V. comstocki* with data on its mating, oviposition and earliest larval behavior. The older larvæ collected in Alta Meadow during August, 1917, were kept in a cold room from November 12 to December 31 and then transferred to a hothouse. After making their pits and feeding for some weeks they pupated during March and the first imago, a female, emerged April 1. Thereafter till the end of the month a few flies of one or both sexes emerged each day. That their development had been accelerated by shortening the period of larval hibernation is proved by the fact that the overwintered larvæ collected in the Yosemite during May, 1930, did not produce flies till June, which as Essig has shown

FIG. 36. Four just unearthed *Vermileo comstocki* larvæ, showing the characteristic U-shaped posture. (Photograph by E. O. Essig)

(p. 172) is the time of emergence in their native environment.

The fly escapes from the pupa at night and is usually found in the early morning resting fully pigmented and mature on the side of the dish in which it lived so many months as a larva. In a few cases of delayed emergence I saw the insect in the act of disengaging itself from the pupal envelopes. Its wings are quickly spread and its coloration, at first reddish or yellowish, rapidly deepens to the dark brown adult hue. Its eyes are uniformly dull olive green. Like *V. vermileo,* the resting fly carries its wings in one of two positions, either over-lapping on the dorsal surface of the abdomen or separated and standing off obliquely from the sides of the body. The former, I believe, is the posture of more complete rest. On a perpendicular surface it assumes the same posture as our species of Rhagio and Atherix, that is, with the long axis of the body perpendicular and the head uppermost and facing the light. It is, therefore, positively phototactic, and when released in a room flies directly to the illumined window-panes. Its flight is very light and graceful, but it soon settles down and when undisturbed may remain motionless for a long time as if unable to shake off the stupor of its larval and pupal stages.

My flies declined to imbibe either water or syrup, and since dissection of females showed that their eggs were fully mature in their ovaries and ready to be laid, it is probable that the short-lived imaginal insect requires no food. On the day following emergence several pairs of flies mated. During copulation, which lasted about half an hour, both sexes spread their wings somewhat, the male rested on the back of the female, with his abdomen parallel with hers, but with its posterior segments twisted to the left side and the genitalia at the tip turned upward and firmly applied to those of his mate. This is precisely like the mating pose of Empis, and is called by Richards (1927), who has studied the various copulatory postures in Diptera, the "false male vertical pose." A few hours after mating several of the females oviposited. They thrust the extensible tip of the abdomen down into the sand to a depth of about 3 mm., standing meanwhile on their hind legs, with the anterior pairs of legs stretched out into the air and the tips of the delicate wings so forcibly applied to the sand that they were often broken or torn. All the eggs, more than fifty in number, are extruded at one time, and the female dies soon after withdrawing the tip of her abdomen. Of the eggs laid by the females in 1917 only one batch hatched, but in 1930 many batches of fertile eggs were obtained, and a casual observation showed that the females, when placed in a situation simulating a small zone of sand under an overhanging rock, are careful to select a particular spot for oviposition. A small dish with widely sloping sides had been placed in the center of the sand in a much larger covered dish containing a number of mated flies. The females, when they came to oviposit, invariably laid their eggs in the sand close to the glass of the small dish and therefore well under its sloping sides instead of in the larger area of open sand near the receding walls of the large dish. This ovipositional preference on the part of the females is so pronounced that I can only regard it as a natural propensity and as partially accounting for the fact that in the field Vermileo larvæ are invariably found very near the surfaces of rocks and usually under their overhanging sides.

The pale cream-colored, broadly elliptical eggs measure only .6 mm. in length and .4 mm. in width and adhere to one another in rows as shown in Fig. 29 *H*. The chorion, or shell, is thin, transparent and, under a high magnification, finely granular. The hatching of the single fertile batch of eggs, laid April 20, was awaited with impatience, because it seemed probable that the first stage larvæ would be very different from the older larvæ, which were the only stages known to all previous observers. As it seemed to me unlikely that the minute just-hatched Vermileo could secure its food by means of a pitfall, I expected to see an active, wandering larva not unlike the first-stage larvæ of such parasitic insects as the Acroceridæ, Bombyliidæ, Nemestrinidæ and certain Tachinidæ among the Diptera or the Trigonalidæ, Eucharidæ, Perilampidæ and Chrysididæ among Hymenoptera. But my expectations proved to be unfounded. The eggs, left undisturbed in the sand in which they had been deposited by the female, hatched simultaneously April 28 as minute larvæ of essentially the same structure and behavior as the older larvæ with which I was familiar. Though only 2 mm. long and .2 mm. broad the just-hatched differed from the older larvæ only in being more transparent, with clearly visible

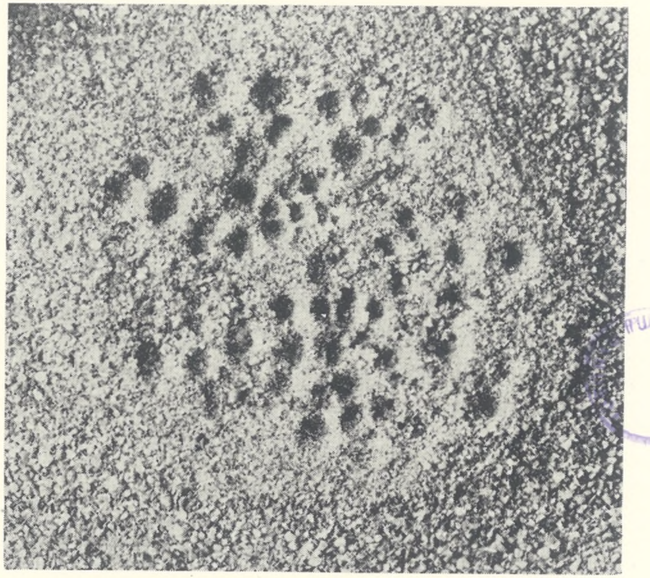
FIG. 37. Cluster of pits made by a group of first-stage *Vermileo comstocki* larvæ (natural size). (Photograph by C. T. Brues)

alimentary tract and tracheal trunks, of more uniform width, owing to the proportionally larger head, head-skeleton and thoracic segments, and in having more distinct eyespots and fewer and proportionally longer setæ. These tactile organs were, in fact, as long as two thirds of the body width. The larvæ had crawled only a short distance through the sand from the spot where the eggs were laid, and the first sign of their existence was a dense cluster, about the size of a silver fifty-cent piece, of minute pits, each only 2-3 mm. in diameter and depth and occupied by a minute worm-lion. Notes on this colony, kept under close observation throughout the summer and fall of 1918, fill several pages of my note-book, but I shall transcribe only the more interesting data. Most of them were confirmed by observation of the more numerous colonies obtained during the summer of 1930.

Owing to their small size, the just-hatched *comstocki* larvæ could not, of course, be fed with insects as large as those given the older larvæ. I therefore selected Aphids, which could be readily obtained in considerable numbers. They proved to be most acceptable. But what is the food of these larvæ in their native environment? I am at loss to conjecture unless it be minute gnats (Chironomids), migrant plant-lice and mites which happen from time to time to be scattered over the sand by the wind. There is certainly no species of ant in the high Sierras small or abundant enough to furnish an important part of the diet of such diminutive creatures.

The small cluster of about sixty individuals at first behaved like a colony. They showed no inclination to disperse and their pits were so close together as to be separated only by narrow partitions of sand. The sedentary propensity of the larvæ was shown also by the fact that within a few days the bottoms of the pits became rounded and bag-like, so that they were broader below than at the rim. From the first the larvæ were very alert and active and showed no tendency to avoid the daylight. They often stood perpendicularly in their pits with the anterior half of the body exposed and the posterior half anchored in the sand. They were so sensitive that when an Aphid fell into one of the pits, the larvæ in all the others at once squirmed and tossed out sand as if the prey were within their reach. The compact colonial arrangement may therefore be advantageous to the individual larvæ since it must increase the chances of the prey's capture by some larva, even if it happens to escape from the one into whose pit it has fallen. The strength of the first-stage larvæ, considering their size, is remarkable. While making or repairing their pits they deftly tossed out sandgrains and small pebbles fully six or eight times as wide as their bodies, a performance almost as astonishing to the observer as if he were to behold a man seizing a grand piano with one hand and hurling it across the street. Behavior like that described by von Siebold (see p. 151) for *V. vermileo* living in crowded pits, may be witnessed daily in colonies of first-stage *comstocki* larvæ, because they keep tossing the coarser particles of sand back and forth from one pit to another, till they come to rest on the intervening network of sandy ridges or partitions.

When an Aphid fell into one of the small pits the young worm-lion reacted promptly, either by disappearing under the sand or striking at the prey violently and repeatedly till it could fix its mandibles in some portion of its body. Sometimes it succeeded only in seizing one of the Aphid's legs. As soon as a hold had been secured it pumped venom into its victim and then commenced imbibing its juices, as was proved by the stream of green Aphis blood flowing into the larval stomach. Feeding usually occurred in the open, because the larvæ in this stage neither coil around the prey nor drag it under the sand. Even those that had disappeared when the Aphids fell into their pits were seen cautiously approaching and attacking their prey from beneath. In a few instances their mandibles were so firmly implanted that the Aphids dragged the larvæ out of their pits and some distance over the sand before the injected poison could take effect.

When removed from their pits and placed in a watch-glass the first stage were much more active than old larvæ. They feigned death with the body in the usual S-shaped posture, but the feint was brief and the tiny creatures soon straightened out and began to crawl away. Then an interesting difference in locomotion between the very young and the older larva was disclosed. The latter invariably walks on its back, but the former, after proceeding some distance in this manner, sometimes turns over and walks on its belly. The first-stage larva is therefore ambigrade, or both dorsi- and ventrigrade, the older larva exclusively dorsigrade. Thus for a brief period after hatching the larva retains vestiges of the ancestral mode of locomotion so rigidly adhered to by nearly all other insect larvæ. That there are other instances of this peculiar ambigression among Dipteran larvæ may be inferred from an observation by Wille (1923), who found that the common cheese-skipper (*Piophila casei*), though usually ventrigrade, may occasionally walk on its back.

By May 4 the first-stage larvæ, on a diet of Aphids, had visibly increased in size and were much more like the older larvæ in behavior. They now encircled the prey when it was not too bulky, abandoned their upright position, became more sluggish and lay on their backs, with sand-grains sprinkled over their ventral surfaces, across the floors of their pits. They were still too small to drag the Aphids under the sand and therefore continued to imbibe their juices in the open. The pits had also increased in size, so that the whole colony occupied more space on the surface of the sand. In the colonies of this and the immediately following stages reared in 1930 there was considerable mortality. Aphids were scarce and the weather at the low elevation of Boston apparently far too warm and humid for the little creatures. But in their native Sierras mortality from lack of food and unfavorable exposure to heat or cold must be even greater, since the pits of the older larvæ in the small patches of dust or sand under overhanging rocks are by no means as numerous as would be expected from the fecundity of the females, and sometimes many of the pits have been made and abandoned by the same individuals. No parasites have ever been reared from Vermileo larvæ. While sifting the dust under boulders in the Yosemite I occasionally found long, slender Therevid larvæ that looked as if they might prey on the worm-lions, but when these were confined for several weeks with the suspects in a small dish of sand, they remained unmolested. Nor could any cannibalistic proclivities be detected among the young *comstocki* larvæ. When one of them happened to fall into a neighbor's pit, it was not attacked but promptly ejected, as if it were a pebble or a bit of exhausted prey.

By May 9, when the colony was photographed (FIG. 37) the *comstocki* larvæ averaged 3 to 3.5 mm. in length. On the following day they were fed on various small insects, including the minute workers of the common thief ant (*Solenopsis molesta*) and young termites (*Reticulitermes flavipes*). The latter proved to be the more acceptable, though they were too large to be drawn under the sand. By May 15 the larvæ had grown another millimeter in length and their pits were 6-7 mm. in diameter. A number of small moth caterpillars (Tortricids) dropped into them were promptly paralyzed and deprived of their juices. On May 22 some of the larvæ were 4-5 mm. long and their pits nearly 10 mm. in diameter. The latter were now farther apart and the colonial bonds which had their inception in the batch of eggs deposited by the mother fly were obviously loosening. The following day the first moult-skins

FIG. 38. Pits made by half-grown *Vermileo comstocki* larvæ in a dish of sand (⅔ natural size). (Photograph by E. O. Essig)

were found, marking the termination of the first larval stage.

On June 4 I tried to feed the larvæ with a small black thrips (*Anthothrips niger*) which is extremely common on the flowers of the ox-eye daisy. This insect proved to be very favorable for testing the perseverance and trial and error behavior of the larva, because it is so slender, hard and slippery that it eludes seizure and the implanting of the mandibles. One thrips, which I closely watched under the lens, repeatedly slipped through the coils of a lusty young larva. Again and again it was tossed about in the pit and seized in different positions, but always managed to escape uninjured. Finally, after twenty minutes of frantic effort, the larva gave up the task, disappeared under the sand and gave no further heed to the thrips, though in its subsequent struggles to escape from the pit it exposed the larva's body and kept crawling over it. None of the other larvæ had any better success.

The second moult occurred about June 13, when the larvæ were nearly one fourth grown and were large enough to feed on ants (Lasius), full-grown termites and various large Aphids. The pits were now 1.5-2 cm. across. Among many observations on the feeding behavior of the larvæ I will cite only two which show that it is by no means a stereotyped reflex. An ant (*Lasius nearcticus*) was dropped into one of the pits. The larva suddenly roused itself and without encircling the ant, bit the base of one of its hind legs and then disappeared beneath the sand. The ant seemed lame at first but soon regained its feet and crawled about, though unable to scale the walls of the pit. Nearly ten minutes later the larva suddenly popped up, struck at the ant several times, encircled its thorax and began to feed. It held the ant in this position for another ten minutes before dragging it partly under the sand. In this case the various acts in overcoming the prey are separated by long periods and in part reversed. Normally the biting follows the encircling and the withdrawal into the sand is not so long delayed. Ants of the typical subgenus Lasius, like the one observed on this occasion, are usually seized and sucked out with avidity, but those of the subgenus Acanthomyops, which have a strong odor of lemon verbena, are rejected. A number of *A. latipes* dropped into the pits July 10 were promptly encircled and drawn into the sand, but all of them were ejected in a few moments, probably as soon as the larva had brought the sense-organs of its maxillary palpi in contact with their aromatic surfaces. Ants of the same species were also fed to four young ant-lions (*Myrmeleon immaculatus*) and were likewise promptly killed and thrown out. And when soon afterwards I placed fresh Acanthomyops in the pits in contact with their mandibles they quickly backed into the sand and would have nothing to do with them.

The concluding history of the colony of *V. comstocki* larvæ may be briefly told. They grew to nearly full size by the last of September. There was a third moult about July 1, a fourth about July 25, and a fifth about August 30. After the first of October they would neither take food nor repair their pits, but remained buried in the sand. That this was the beginning of hibernation was shown by the same behavior, also during the first days of October, of the more numerous larvæ reared from eggs during the summer of 1930. Since the larvæ on both occasions were kept in a warm room, their dormancy could not be due to temperature. Those reared in 1918 lived till late February in a hot-house and were then transferred to an unheated cold frame in the garden. When they were brought into the laboratory, April 8, 1919, it was found that they had not survived the damp and cold of the New England March. There is every reason to believe that had they survived they would have reached the imaginal stage without ever having imbibed water, except in the juices of their prey.

The following descriptive behavioristic account of the Sierra worm-lion may serve as an introduction to a more penetrating quantitative study by some future entomologist. The just-hatched larvæ, as we have seen, may be regarded as gregarious, but as they grow larger and establish their pits farther from their birthplace and from one another they become solitary insects. The pits of old larvæ vary from 2 to 3 cm. in diameter and 1.5 to 2 cm. in depth, and are smaller and have steeper walls than ant-lion pits. A worm-lion that is frequently fed may occupy the same pit for several days. If it is excavated in fine dust or kaolin it is apt to become broader at the bottom, owing to the activities of the larva, and its cavity may assume the shape of a truncated instead of a pointed, inverted cone. A pit long inhabited may even become broader at the bottom than across its rim and therefore very unlike an ant-lion's pit.

The frequent crowding of the larger pits in a small area in the natural environment is not due to a gregarious propensity on the part of the larvæ, but partly to their confinement to a very limited rock-sheltered strip of sand or dust and partly, I believe, to a vague attraction of the rocks or cliffs similar to that which probably induces the mother fly to lay her eggs close to their bases. This may be inferred from the following observations. During 1917-18 the larvæ were kept in square terra-cotta seed pans somewhat more than a foot in diameter. After each pan had been half filled with fine, dry sand, a dozen larvæ were placed in the center. A few days later it was found that most of them had made their pits in the positions indicated by the black dots in Fig. 39. It will be seen that the larvæ avoided the central portions of the sand and excavated their pits near or occasionally in actual contact with the sides of the pans. In the field, also, the pits are most numerous next to the rocks or cliffs and more scattered towards the periphery of the narrow zone of dust. Here shade and a lower temperature may be important factors in attracting the larvæ, but the fact that the pans had outwardly sloping sides and were uniformly lighted from above, and the further fact that in Alta Meadow the pits also showed a pronounced tendency to greater aggregation close to the bases of the rocks, though they projected only slightly above the sand, indicate that the behavior is not due to agoraphobia, or a fear of open spaces, but rather to a kind of attraction towards massive solids. The feebler air-currents and slightly greater

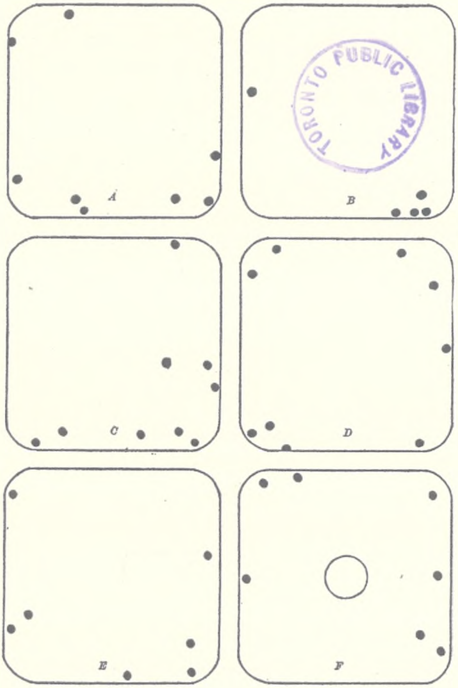

FIG. 39. Diagram of six large pans containing *Vermileo comstocki* larvæ showing their tendency to make their pits (represented by black spots) near the walls.

humidity near the rocks and their longer retention of heat during the night than the adjacent soil might also be supposed to attract the larvæ, but these conditions did not exist in the warm laboratory, where the pans and sand were uniformly dry and covered with glass plates and the difference between the temperature of the sand and the containers must have been inappreciable.

I can think of only one other possible explanation of the peculiar tendency of the Vermileo larvæ to prefer the immediate neighborhood of rocks and that is the more abundant supply of food they may afford. In fact, observation shows that certain terrestrial insects and particularly certain ants do not as a rule cross rocks or boulders by climbing over their high and projecting surfaces, but prefer the shorter path along their line of contact with the surface of the soil. This preference is very marked in *Liometopum occidentale,* a common ant in the Yosemite Valley between 4,000 and 5,000 feet, where it forages on the ground and vegetation in interminable files. I feel confident that most of the worm-lion's food, in that locality at least, consists of these ants, though two less abundant species, *Formica sibylla* and *Tapinoma sessile,* are not infrequently captured in the pits.

When the larva is removed from the sand, either with the tweezers or with the sieve, it always lies on its side and is bent in the form of a letter S or of a U, with one of the limbs recurved at the tip (FIG. 36). The more voluminous portion of the body, consisting of the dorsally concave abdomen, represents the large curve of the S and the smaller downwardly curved head and ventrally concave thoracic segments represent the small curve of the S or the recurved limb of the U. Starved larvæ or those with little food in their stomachs are apt to be less gracefully curved than well-fed individuals, because their posterior abdominal segments are closely applied to the more anterior segments and the head and thoracic segments are in close contact with the ventral surface of the abdomen. The larva remains perfectly immobile, or 'feigns death' in the more or less S-shaped posture for several minutes. Since its body when it lies in the sand is more or less extended we must suppose that the feint and the peculiar posture are induced by the unavoidable shock of its exhumation. If the immobile body of the larva, lying on its side, is now carefully explored with the point of a needle there may be no reaction at first, though pinching it with the tweezers, especially near the middle, will cause it to wriggle violently but at once resume its immobile S-shaped posture as soon as the pressure is removed. Certain regions of the body seem to be more sensitive than others to gentle contact, especially the basal abdominal segments, the obliquely truncated posterior end and the tip of the head. Touching these parts with the needle causes the larva to leap suddenly into the air and to land on its side 2 to 5 cm. away, with precisely the same S-shaped flexure and continuation of its feint, but after it has been stimulated to make a few leaps in quick succession, touching the body or its sense-hairs at any point with the needle will induce the sudden reaction. The threshold of stimulation therefore falls rapidly, probably as a result of the larva's very gradual recovery from its feint. The movements of the leaping larva are quite simple and not too rapid to prevent analysis. They consist of two phases, a sudden, violent contraction of the antagonistic muscles, producing a complete reversal of the S-shaped flexure of the body, and as sudden a return to the original posture. Though the larva is lying on its side, the first contraction throws it off of the substratum, and the second occurs in the air or just as it is landing. This leaping is never spontaneous and cannot be induced by bright light, but only by mechanical contact or pressure, and certain gases, such as chloroform. It is therefore often resorted to when the larva happens to fall into the pit of another larva and is encircled or bitten.

It is interesting to compare the leaping of the worm-lion with that of some other Dipteran maggots that exhibit this behavior in a more spectacular form. The best known of these is the common cheese-skipper, *Piophila casei,* which has been studied by several investigators, especially Taschenberg (1880), Haycraft (1898), Krausse (1909), Bachmann (1918) and Wille (1923). The cheese-skipper, according to Wille, does not acquire the power of leaping till the fifth of its six days of larval life. His experiments show that mechanical stimulation will not induce it to leap, but that it will leap spontaneously in dry air or in bright light, either solar or artificial, or even when immersed in water. Being negatively phototactic it leaps away from the light and therefore after it has matured and left its food normally pupates in some dark spot. Its manner of leaping is very different from that of the worm-lion and the act is not a response to stimulation during immobility or death-feigning. The larva merely stops while crawling along on its ventral surface, forms a vertical loop by bending its head backward and underneath its abdomen and seizes with its hook-shaped mandibles a transverse fold which is stretched between a pair of processes at the caudal end. The extensor musculature of the body is then tensely contracted, the mandibles suddenly release their hold and the larva is hurled forward through the air, hind end foremost in the direction in which it was proceding before the leap. In this manner the cheese-skipper, though only 8 mm. long may, according to Krausse and Bachmann, leap to a height of 20 cm, and to a horizontal distance of 23 cm.

Leaping is also observed in the larvæ of two other groups of Diptera, the gall-gnats (Cecidomyidæ) and the fruit-flies (Ceratites). Kieffer (1913) cites the habit as occurring in no less than fifteen different Cecidomyid genera, and says that the larva "loops its body by bringing its anal segment forward to the ventral surface of the prothorax and thus forms an arc perpendicular to the plane of position. Then by unbending like a tense spring it is projected to a distance of several centimeters, though rarely farther than a decimeter." In the Cecidomyid larva, therefore, the posterior end of the larva is curled forward to the prothorax, instead of the head being curled back to the anal segment as in the cheese-skipper. There is considerable literature on the fruit-flies, because of their economic importance, but I have been unable to find any detailed observations on their leaping, comparable with those on the cheese-skipper. Accounts and figures of the Mediterranean fruit-fly (*Ceratitis capitata*) indicate, however, that it leaps in the same manner as Piophila. From Woglum's statement (1929) that "full grown larvæ have the peculiar habit, if taken out of the fruit of curling up and jumping from one to six inches," I infer that the young larva, like the young cheese-skipper, can only crawl. Vermileo larvæ, however, will leap when they are only 3 to 4 mm. long. The leaping of this insect is obviously a pure reflex and of little or no use, except perhaps in enabling it to escape capture by some other larva into whose pit it has chanced to fall, but the greater leaping powers of the mature, unprotected larvæ of Piophila and Ceratitis may enable them to reach snug places for pupation either in the soil or under débris much more expeditiously than by crawling.

When left undisturbed on a hard, smooth surface the death-feigning worm-lion begins, after a few minutes, and especially if it is placed in bright sunlight, to move the anterior end of its body and gradually straightens out. The head twists about till the thoracic and somewhat later the abdominal segments are turned over and the whole body comes to lie on its back. Then it begins to crawl slowly and awkwardly merely by alternately and rhythmically extending and contracting its anterior segments and dragging the less mobile posterior segments forward with each contraction. While the body is thus lumbering along, the head is moved first to one side and then to the other and the back of the head and thoracic segments is with each of these movements brought down to the substratum in an obvious effort to seize it with the mandibles. This always fails, of course, on hard surfaces like those of glass, wood or paper, but at once succeeds when the larva is lying on any powdery substance like sand, dust, salt or sugar. When placed on the sand the larva bends its head and anterior segments backward and downward in line with the remainder of its body and, thrusting its head into the sand, while still rhythmically contracting and expanding its segments in anteroposterior sequence, begins at once to penetrate it, as shown in FIG. 40 *A*. Progress is now more rapid, because the larva can use its mandibles in dragging its body forward, and the anterior segments can secure a firmer purchase in the sand. The creature therefore soon disappears from sight.

Even in the sand the larva continues to lie on its back. If sufficiently hungry and if left undisturbed in dim light or darkness it may within a few hours set about making its pit. The procedure is very simple compared with the usual circuitous performance of the ant-lion, because the worm-lion merely curls its anterior end after thrusting it in the sand and then suddenly straightens it, thus tossing the sand out onto the surface. At the same time it rotates more or less on its long axis, so that the direction in which the sand is thrown differs somewhat with each discharge. In this manner a small conical pit, with the larva at its apex, is soon formed (FIG. 40 *B*) and may be enlarged and deepened during the same night or on subsequent occasions till it has the proper dimensions. When the pit is completed the larva sometimes awaits its prey by merely leaning its head and thoracic segments with their ventral surface exposed, against the wall. Usually, however, it lies horizontally on its back (FIG. 40 *C*) with its posterior half buried in the sand and its thoracic and first abdominal segments crossing the floor of the pit like a bar and covered with a very thin layer of sand. It will be recalled that the thoracic segments are fringed on each side with long tactile hairs (FIG. 30 *A*) and it is these and the very sensitive ventral integument of the same segments that first come in contact with the falling prey and act like the release of the spring in a steel trap. It will also be recalled that the eyes of the larva (FIG. 30 *Co*) are situated on the ventral side of the opaque head-capsule

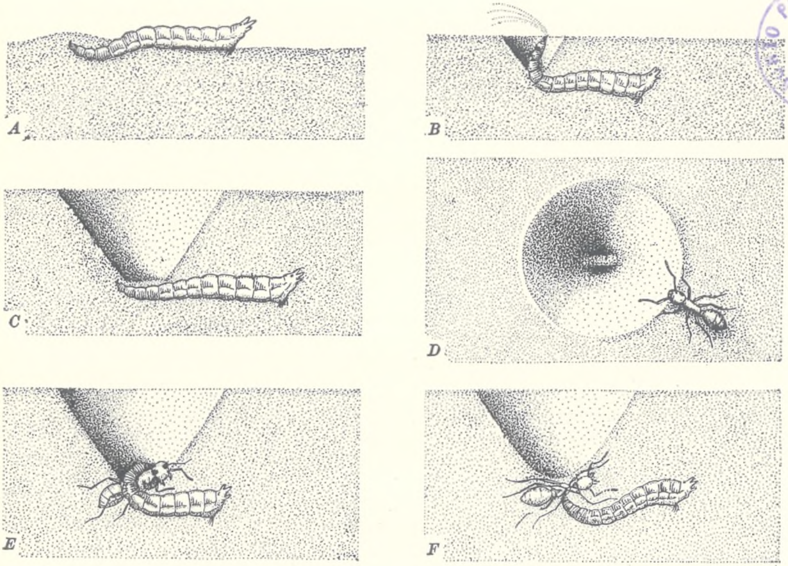

FIG. 40. Activities of the *Vermileo comstocki* larva. *A,* creeping on its back on the surface of the sand and just entering it with the anterior end; *B,* making the pit by tossing out the sand in jets; *C,* lying in wait at the bottom of the pit, lateral view; *D,* Pit as seen from the surface with the sand-powdered anterior end of the larva across its floor; *E,* method of seizing the prey; *F,* absorbing the juices of the prey after it has been paralyzed and dragged under the sand.

where they are exposed to the light only when the larva is lying on its back. We may assume, perhaps, that these sense-organs are not too simple or vestigial to be of some slight service in detecting the sudden eclipse of the light when the prey falls to the bottom of the pit. At any rate, the larva seems to be so well aware of the shape and position of the prey that it nearly always embraces it instantly and holds it firmly, unless it is too voluminous.

As soon as the prey is seized the tight grip of the larva's thoracic segments forces it against or somewhat into the sand at the bottom of the pit and thus prevents it from struggling too actively. Under a lens it is easy to see that while the thoracic segments remain fixed the tip of the head moves about, carefully exploring the hard integument of the victim till it finds a suture or an intersegmental membrane. As soon as such a vulnerable point is found the larva thrusts its serrated mandibles into it and at once injects its venom. I have assumed that this comes from the salivary glands and that the digestive fluid is secreted by the anterior portion of the stomach and is injected into the prey either simultaneously or somewhat later. Perhaps the powerful and prolonged contraction of the thoracic musculature of the larva compresses the salivary glands and anterior portion of the stomach and thus facilitates the extrusion of both liquids. Since medium-sized ants and termites are paralyzed in three to five minutes, the venom can hardly be less powerful than that of the ant-lion. While the prey is succumbing the larva improves the time by securing its mandibles firmly in the wound, and as soon as it has succeeded, makes a sudden twisting and uncoiling movement with its anterior end and whisks the prey partly or completely under the sand (FIG. 40 *F*) where its liquefied and digested tissues can be leisurely imbibed. After this is accomplished the carcass, now reduced to an empty chitinous skeleton, is pushed up through the floor of the pit and when the latter is being repaired during the night, tossed out onto the surface of the sand.

The Sierra worm-lion is as omnivorous as the ant-lion, and also feeds mainly on worker ants, because these happen to be the most numerous and easily captured insects in its natural environment. But in the laboratory both the worm-lion and the ant-lion thrive better on worker termites, a prey with which they have never had any previous acquaintance. The worm-lion usually manages to avoid the mandibles of its prey, but I once saw a termite seize the head of an attacking individual. After telescoping its head into its thoracic segments and quietly holding the latter

FIG. 41. Nocturnal tracks made by wandering *Vermileo comstocki* larvæ on the surface of fine white sand. (Photograph by C. T. Brues)

aloft for some time till the termite released its hold, the worm-lion behaved as if it had been injured and immediately concealed itself in the sand when I removed the aggressive termite and placed another in the pit. On several occasions when I dropped large larvæ of ants or nut-weevils (Balaninus) into the pits, their occupants exhibited the same behavior, but when I removed the prey with the tweezers the worm-lions were dragged out at the same time, affixed by their mandibles. They had come up unobserved beneath the bulky larvæ and had begun to ingest their juices. Older worm-lions, like the very young individuals previously described, reject heavily chitinized insects, such as beetles and Myrmicine ants, and insects with powerful odors (Acanthomyops and certain bugs).

The worm-lion is less sedentary than might be supposed from casual observation in field or laboratory. During the summer months, when food is most abundant, it not infrequently abandons its pit to make a new one some centimeters away. This may not be due to hunger, because it was also observed in the laboratory among larvæ that were fed daily. When the dishes were covered with cardboard or placed in the dark for several days, the larvæ sometimes emerged from the sand and wandered about on its surface. On exposure to the light they soon buried themselves again. They leave on the surface of the sand a characteristic trail (FIG. 41) consisting of a sinuous groove, made by the creeping body, and on each side a series of punctures, the impressions of the exploring head as it is moved first to one side and then to the other. But new pits may be made and occupied by larvæ that have wandered through instead of over the sand, as is proved by the absence of any trails on the surface between old and recently excavated pits.

Towards the end of the summer the older worm-lions descended more deeply into the sand and reacted feebly or not at all to prey thrown into their pits. They made no attempt to repair the old or to excavate new pits after the sand in the dishes had been shaken down till its surface was perfectly level. By the first week in October all the worm-lions seemed to be hibernating, though summer temperatures still prevailed in the laboratory. If removed from the sand they feigned death and would leap when stimulated. When left undisturbed on the surface of the sand they slowly revived and at once buried themselves. I unearthed them once a week or oftener but except for these brief responses they could not be aroused from their lethargy.

We must, I believe, distinguish three different kinds or states of immobility in the worm-lion: first, death feigning which, as Rabaud (1919) has shown in many insects, is a reflex, peripherally induced by a more or less localized mechanical stimulus or shock; second, the immobility of lying in wait in the pit, a spontaneous, tense and alert state from which the insect can be quickly aroused to vigorous action by even very delicate mechanical stimuli, and third, the immobility of hibernation, estivation, etc., also spontaneous, due to internal stimuli and readily yielding to the first state. The same three states are met with in the ant-lion and one or all of them in many insects, millepeds, spiders and crustaceans. Rabaud calls the first of these states 'reflex immobility', the second, 'simple immobility' and the third 'sleep', or slumber (*sommeil*). For the last such neutral terms as 'stupor' or 'torpor' might be more appropriate, because the sleep of the higher vertebrates seems to be a very different phenomenon. The worm-lion's stupor is quite a different physiological state from its lying in wait for the prey. The latter is obviously comparable with the more or less alert quiescence of many other Arthropods, such as the ant-lion, the praying mantis, the flower-spiders (Thomisids), water-scorpions, many moths, etc. Rabaud's statement, however, that "the distinctive difference between the immobilized [i.e. death-feigning] animal and the [simply] immobile animal resides in the persistence or suppression of the contact of the tarsi with the substratum", will not apply to the worm-lion for the simple reason that it has no tarsi. It probably remains immobile as soon as it has entered the sand for much the same reason that the Amphipod crustacean Talorchestia, as described by Holmes (1903), remains immobile as soon as it is immersed in the same medium and has brought as much as possible of its body surface in contact with it. Holmes is therefore probably right in regarding this behavior as positively thigmotactic, though it is at the same time negatively phototactic, as Rabaud suggests. As an internal or physiological state, nevertheless, the stuporous immobility of the worm-lion is quite different from its quiescent but alert state. Like other insects the worm-lion is more easily induced to feign death while in the former than in the latter.

The stuporous form of immobility is interesting when considered in connection with certain other organisms like the spiders and venomous serpents, which behave not unlike the worm-lion and ant-lion. Physiologically the lethargy of all these animals would seem to be due to autointoxication induced either by the ingestion of their own venom with their food, or to inability to rid themselves of the waste products of their muscular activity or of their general metabolism. It seems improbable that the ingested venom would be toxic to the animals that secrete it, nor is it probable that the stupor of the worm-lion and antlion is due to the fatigue products of their muscular activity since this is much more intermittent than in many other larvæ that exhibit no such protracted periods of immobility. It is therefore more probable, in the worm-lion and ant-lion at least, that the toxic substances consist of the urates and other excretory products and the unassimilated remains of all the food that has been ingested during their long larval stages.

That the worm-lion's stupor is due to autointoxication with the substances above mentioned becomes highly probable in the light of Roubaud's important researches (1922) on various blowflies (Calliphora, Sarcophaga, Lucilia, Mydæa, etc.). He found that the full-grown (preimaginal) maggots of these insects pass the winter in a torpid condition, because their fat-body and sometimes their other tissues are charged with urates, which have to be eliminated before development can proceed. The cold inhibits all metabolic activities except those of the excretory organs. During this diapause,[1] or period of developmental inhibition the larva is in a condition of 'asthenobiosis', to use Roubaud's term, owing to autointoxication with urinary products. The urates, at first accumulated in the fat-body, which functions as a storage kidney, are gradually transferred to the Malpighian tubules, whence they can be excreted before pupation. There is a sudden revival of the general metabolism and development as soon as this 'depuration' occurs. "The period of cold is therefore a period of repose and of excretion, made necessary by the general intoxication of the larva, a period of relief owing to the continuous functioning of the urinary organs, on which the return to vitality of the species depends. As a result of this preparatory repose accompanied by depuration, the functional energy of the Malpighian tubes may itself take on new vigor. The excretory epithelium, as soon as it is brought up to the temperature of general activity, functions with even greater intensity and in such a manner as to insure the complete depuration of the organism." The

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[1] As Roubaud implies, the word *diapause* (from διάπαυσις, an arrest or interruption of activity) was introduced by me (1893, p. 68) to designate a pause during the embryonic development of insects and was later applied by Henneguy (1904, p. 424 *et seq.*) to other developmental pauses, embryonic, larval or pupal.

tissues of the larva, previously suffering, so to speak, from a prolonged attack of gout, are rejuvenated after the urates have been eliminated, and pupation, or the rapid elaboration of the imaginal structure, is the result. Roubaud is probably justified in believing that the conclusions drawn from his study of the asthenobiosis of fly larvæ have important bearings on such common biological phenomena as metamorphosis, hibernation, estivation, encystment, sporulation, etc.

Dissection of old or hibernating worm-lions shows that they resemble the blowfly larvæ described by Roubaud in certain important peculiarities. I find no urates in the voluminous fat-body, but the Malpighian tubules very closely resemble those of the Mydæa larva figured by Roubaud in having their distal portions swollen and distended with compacted urate crystals, so that they appear as very conspicuous white strands as soon as the posterior segments of the larva are opened. When we consider that the worm-lion lives in an environment in which it is unable to obtain any water, except from the juices of its prey, and that it must be constantly losing small amounts of water in respiration, we can understand why the solution of the abundant urates and their evacuation must be a slow and difficult process. The worm-lion does, nevertheless, excrete a small amount of liquid urine. Pressure on the posterior part of its body will often cause extrusion from the anal orifice of a small drop of clear liquid, which has been slowly accumulated in the rectal sac and must be an excretion of the slender, greenish, proximal portions of the Malpighian tubules, because their distal portions are charged with urates and evidently function for the time being merely as storage kidneys. All the evidence, therefore, goes to show that the older and especially the hibernating worm-lion, like the Dipteran larvæ observed by Roubaud, is suffering from uric acid poisoning and has to devote months to depuration before it can pass on to its pupal and imaginal stages. Accordingly, the stuporous condition and lengthening of larval life are not attributable so much to scarcity of food as to auto-intoxication resulting from difficulty in evacuating the excreta from the renal tubules and alimentary tract.

The immobility of the worm-lion pupa, like that of the pupæ of other holometabolous insects, is due, of course, to conditions the very reverse of those we have been considering. The pupa is really a second embryo, and is quiescent for the reason that there is actively going on within it so much building up of new tissues and organs that it cannot move about. Hence the pupæ of the great majority of insects may be said to have no 'behavior'. This is not altogether true of the worm-lion pupa, because it does exhibit a very limited behavior just as it is about to become an imago. As we have seen, it then wriggles up to the surface of the sand and exposes its head and thorax and often more or less of its abdomen. The delicate imago, which could hardly make its way through even a few centimeters of sand, is thus enabled to issue into the air without difficulty. Sometimes the pupa does not cease all activity after it reaches the surface but continues to wriggle, with its hind end fixed like a pivot in the sand, till it produces a funnel-shaped pit precisely like that of the larva though smaller. According to Brauns (p. 260) the pupa of *Lampromyia sericea* may leap like the larva. Since I have never observed this behavior in the species of Lampromyia and Vermileo which I have reared, I believe that it must be exceptional and perhaps peculiar to very young pupæ.

We may now compare very briefly the behavior pattern of the Vermileo larva, as described in this chapter, with that of the ant-lion. The parallelism is, indeed, striking. It will be seen that many of my remarks on the behavior of the ant-lion may be applied almost *verbatim* to Vermileo. But there is one difference of considerable theoretical importance: the worm-lion is more nearly a reflex automaton. Its behavior, like its structure, is certainly simpler, and this may account for the fact that it is less successful than the ant-lion, or rather possesses considerably less amplitude of response, though it occupies very nearly the same ecological environment. But this does not mean that it is a tropistic and reflex organism through and through. Although most of its activities seem to be singularly mechanical and stereotyped, its feeding responses, as shown by several observations recorded in preceding paragraphs, are clearly modifiable in conformity with differences in the size and behavior of its prey and with differences in its own physiological states.

CHAPTER VII

THE WORM-LIONS OF THE GENUS LAMPROMYIA

THE adult flies of the genus Lampromyia are so rarely encountered by collectors of insects that they are known to few dipterists. This is not astonishing, perhaps, because most Rhagionid genera are rarely seen in nature. Many of them, indeed, like our North American Glutops, are known from very few specimens, and all the commoner species in Europe and America belong to only four genera: Rhagio, Atherix, Chrysopilus and Symphoromyia. Lampromyia is certainly very closely related to Vermileo, but its affinities are obscured by the great length of its proboscis, which, except in one of the seven known species, is two-thirds or more the length of the body (FIGS. 43, *1* and 45 *A*). Even expert dipterists, therefore, have been led to place the genus in some Orthorrhaph family in which species with a long, slender proboscis are of frequent occurrence. Thus Fabricius (1794) and Macquart (1835) assigned the earliest known species of Lampromyia to the genus Empis of the family Empididæ. Bigot (1879) at first assigned the genus to the family of the bee-flies (Bombyliidæ) and Brauer (1882) regarded it as a robber-fly, or Asilid. Although Macquart, at a later date (1840), and Schiner in 1862 had detected its true affinities to Vermileo

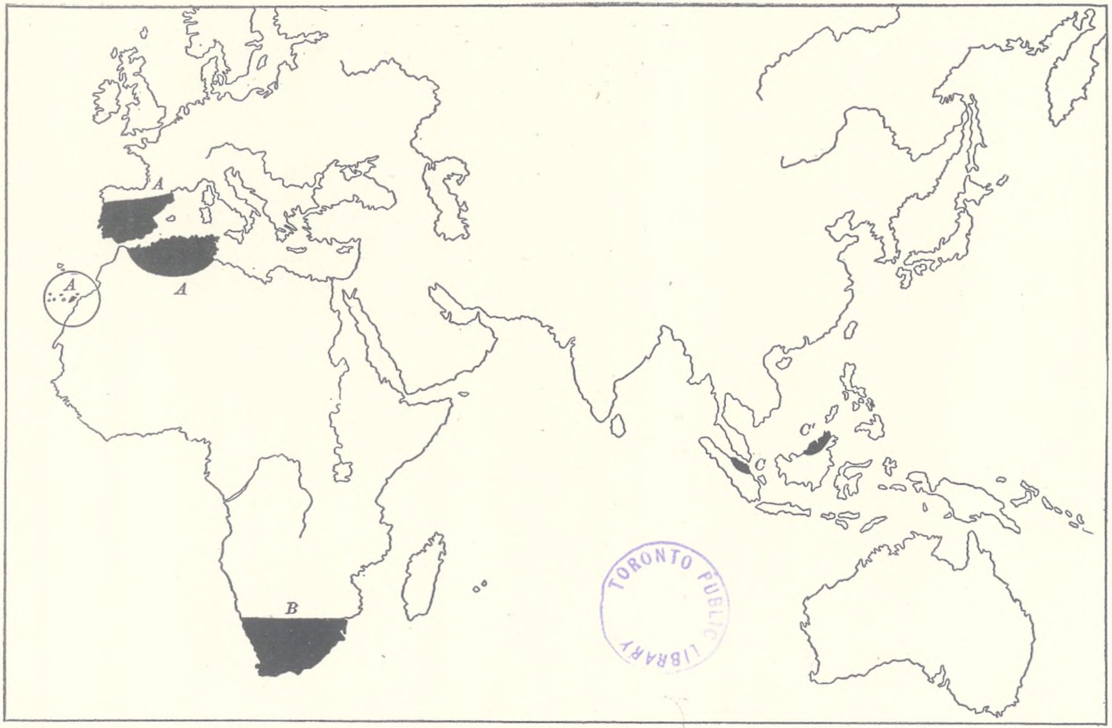

FIG. 42. Map of Old World showing known distribution of species of Lampromyia and Vermitigris. *A*, distribution of northern; *B*, of southern group of Lampromyia; *C*, of *Vermitigris fairchildi* sp. nov; *C'*, of Vermitigris sp. (probably *fairchildi*).

among the Rhagionidæ, this allocation was not definitely established till the larva of one of the species was discovered by Paul Marchal (1896, 1897). He first showed that the larvæ of the two genera have the same habits and differ structurally only in trivial characters. Bezzi's recent discovery (1926) of *L. brevirostris*, a species with a proboscis intermediate in length between that of the other members of the genus and Vermileo, may be said to link the two genera still more closely.

To the biogeographer the genus Lampromyia presents an interesting problem on account of the peculiar discontinuous distribution of its species. Of these there is a northern and a southern group (FIG. 42). The former comprises *pallida* Macquart, *cylindrica* Fabricius and *canariensis* Macquart. All of these have been recorded by Th. Becker (1921-'22) as occurring in the Canary Islands, but *pallida* and *cylindrica* are known to occur also in Spain and Africa north of the Sahara. These are, in fact, the regions in which they were first taken. The other group of species comprises *sericea* Westwood, *argentata* Bigot, *appendiculata* Bezzi and *brevirostris* Bezzi, all from the tip of Africa south of a line connecting Zululand and Namaqualand. This distribution shows that the genus Lampromyia is peculiarly African, since all the species occur on that continent, or in the case of *canariensis*, on one of its outlying groups of islands, though two of the species have extended their range into Spain.[1] Even if future investigation fails to reveal any species in the Ethiopian Region north of Cape Province, we must nevertheless assume that the genus occupied this area during some bygone geological age and has been confined more recently to the two widely separated northern and southern ranges. We may also conjecture that this separation was due to temperature as well as aridity, since both

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[1] Lindner (1924) records *pallida* also from Southern France, but on what authority I know not.

the present ranges have a more temperate climate than the intermediate region.

We may now take up in order the various species of Lampromyia, beginning with the northern forms which were earliest seen by European observers. The first form to become known was *L. cylindrica,* originally described as an Empis, as long ago as 1794 by the famous entomologist Fabricius from specimens taken by Desfontaines somewhere in North Africa ("Barbaria"). The same species was redescribed in 1850 as *Lampromyia funebris* by another illustrious entomologist, Léon Dufour, from specimens taken in Spain. He published some good colored figures of the insect, which measures 9-10 mm. and is dark rust brown, with a deep rust yellow thorax, ornamented above with three dull black longitudinal stripes and some spots of the same color on the pleuræ. The abdomen is entirely shining black, the legs are rust yellow, the tarsi and tips of the hind femora and tibiæ are fuscous. The wings are rather uniformly blackish brown, the halteres dark ferruginous brown. The larva of this species has never been found, and even the adult, judging from its infrequent mention in the European literature, must be very rare or local.

The best known species of Lampromyia is *pallida,* the type of the genus, which was based by Macquart (1835) on specimens taken in Oran. The fly is larger than *L. cylindrica,* measuring 12-14 mm., and is pale yellow, with two pale brown stripes on the thoracic dorsum and black spots on the pleuræ. The abdominal segments, except the first, have large triangular black spots. The legs are pale yellow, the hind tibiæ infuscated at their tips, the wings yellowish, with the transverse veins and branchings of the longitudinal veins bordered with brown. The adult or larval *pallida* has been taken repeatedly in North Africa. Baron Osten Sacken (1883) mentions possessing specimens of the fly collected near Tunis by the Marquis Doria of Genoa. The celebrated French entomologist Paul Marchal (1906, 1907) discovered the larvæ at the base of the ruined walls of the old Turkish fortification at Tunis, and a decade later Th. Becker (1906) collected them in the same spot. In May 1910 Bequaert (1921-'22) found larvæ of this species in Algiers on the outskirts of Mustapha Supérieur, along the highway to Blidah, in the suburb of the Colonne Voirol. Rabaud (1927) has published a few remarks on the larvæ of *L. pallida,* but fails to mention the locality in which they were taken.

Becker and Bequaert, and especially Marchal, have published valuable data on the behavior of *L. pallida.* Marchal collected both larvæ and pupæ in April and brought a few of them to Paris for observation. The larva, as shown in his figures 12 and 13, which I reproduce (FIG. 43, *12, 13*) assumes a peculiar position while lying in wait for its prey. It stands perpendicularly under the bottom of the pitfall, with its anterior end coiled horizontally and thinly covered with sand. Marchal determined this fact by carefully sweeping away the sand from the larva with a brush. He shows that the 'death-feigning' of the *pallida* larva and its methods of seizing, overcoming and burying its prey are essentially the same as the corresponding behavior of Vermileo, and concludes that "the biological adaptation of this insect (*pallida*) in the larval state is therefore one of rare simplicity. It consists in passing most of its larval existence in complete immobility and in responding only to a perfectly definite stimulus. Let us add also the rare faculty of making gyratory movements, which characterizes all vermiform animals and was evidently the point of origin of the funnel-making instinct of the larva. It should be noted that if the larva be withdrawn from its funnel and placed in the hand, it seems to be completely dead; it is inert, flaccid and absolutely motionless. But if it then be placed on the surface of the sand, it begins, after a few moments, to move its an-

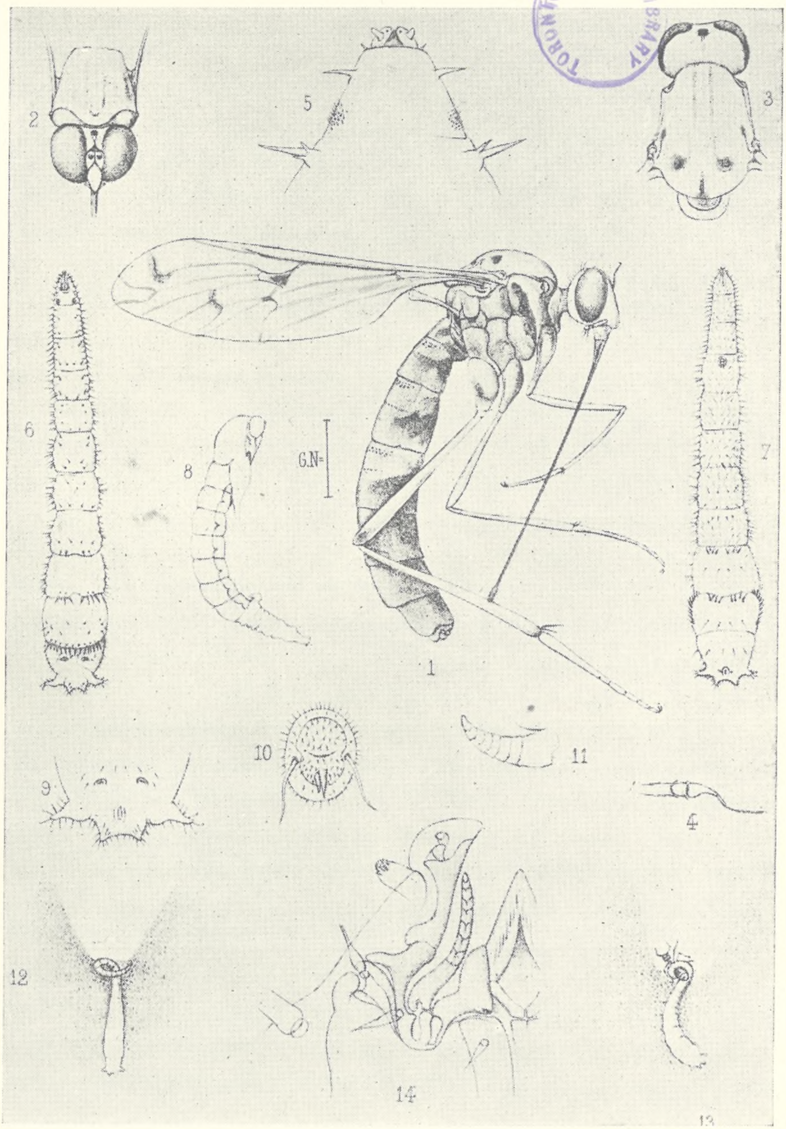

FIG. 43. *Lampromyia pallida* of North Africa after P. Marchal. 1, female imago in profile; 2, head and thorax of same, anterior view; 3, dorsal view of same; 4, antenna; 5, head of larva; 6, larva, dorsal view; 7, same, ventral view; 8, pupa in profile; 9, caudal end of larva, dorsal view; 10, pseudopod; 11, mandible; 12, position of larva at bottom of pit; 13, larva capturing prey; 14, anterior sclerites of left half of larval head.

terior extremity in order to burrow into the sand; it thereupon penetrates it obliquely, making a very acute angle with the surface. The funnel, which I did not see in process of construction, is then excavated a short distance in front of the point at which the larva disappeared." Marchal gives a careful description of the three stages of *pallida* and correctly distinguishes the dorsal and ventral surfaces of the larva. His is also the first careful description of the pseudopod (FIG. 43, *10*) "which presents at its extremity two fleshy valves separated by a deep fissure. The posterior valve bears two strong chitinous spines placed one behind the other." Marchal described the imago as *L. miki* but later recognized its identity with Macquart's *pallida*. In conclusion, after discussing the taxonomy of Lampromyia, he announces his agreement with Schiner in placing the genus "at the head of the Leptidæ, next to Vermileo and immediately after the Asilidæ."

Th. Becker confirmed the French entomologist's observations on the *pallida* larvæ which he found in the same Tunisian locality during April and May, 1906. He transported a considerable number of them to Germany and found that "the animals stood the journey well and developed an enormous appetite. While they were in Tunis they probably fed largely on ants, but I feed them with flies, which are allowed to crawl over the sand after their wings have been removed. During the course of the summer several larvæ developed into imagines, the last one on October 10; since that time development seems to have been retarded." I understand this to mean that some of the larvæ failed to pupate and prepared to overwinter again before metamorphosis. Bequaert records the following interesting data on *L. pallida* in Algeria: "Wherever the soft sandstones of the road banks happened to be excavated or weathered into miniature caves, one was sure to find the dry, powdery dust beneath the shelter of the overhanging rock fairly dotted with the funneled pits of Lampromyia. At that season (June, 1910) adult flies were frequently seen resting on the rocky ceilings of the excavations. I found that the most common victims of these larvæ were workers of the little *Tapinoma erraticum* (Latreille)." The observations of Marchal and Bequaert thus agree in indicating that the mature overwintered larvæ of *L. pallida* produce adults in June, just as does *Vermileo comstocki,* and Becker's observations suggest that at least some of the larvæ need two years to complete their development.

The third northern species of Lampromyia, *canariensis,* is confined to the Canary Islands. A male specimen was briefly and rather inaccurately described and figured as long ago as 1840 by Macquart in the Dipterous section of Barker-Webb and Berthelot's 'Histoire Naturelle des Iles Canaries' (1836-1844). Macquart believed that the specimen might represent merely a variety of his *L. pallida,* but more recently Th. Becker (1908) has redescribed *canariensis* from two males taken by Dr. Cabrera in Teneriffe and pronounces it to be a valid species. Cabrera's specimens were seen flying about the burrows of some terrestrial bees in a rocky locality. Becker surmises that "perhaps the sand funnels of the larvæ were also present in this vicinity, where overhanging cliffs give protection from the rain and where the weathering process of the stone is sufficiently advanced to supply the necessary sand." Becker himself, notwithstanding all his efforts, was unable to find the larvæ.

In July, 1925, while visiting the Island of Teneriffe on Mr. Allison Armour's yacht, the 'Utowana', I succeeded in obtaining *canariensis* larvæ and later in rearing a considerable number of adults of both sexes. The male fly measures 10-12 mm. and is rust red, with three broad, dull black and almost confluent stripes on the thoracic dorsum, the lateral stripes being abbreviated anteriorly and posteriorly. The pleuræ and coxæ are spotted with black. The face and vertex are reddish brown, clouded with black and covered with gray pollen. The antennæ and proboscis are black, the former reddish at the base, the latter as long as the abdomen. The abdomen is darker than the thorax and usually black, with rust-red intersegmental regions and a silver gray transverse band across the anterior portion of each of the six posterior segments. The tips of the tibiæ and tarsi are infuscated, the hind tibiæ sometimes entirely black. The wings are sooty brownish, with blackened costal cell, cross-veins and vein-branchings. The halteres are blackish brown. The male genitalia (FIG. 45 *B*) are large, shaped in profile somewhat like a human foot and covered with short, black hairs. The female (FIG. 45 *A*), which has not been described, averages somewhat larger than the male, measuring 12-13 mm., and differs in having a

FIG. 44. Volcanic cliff on which La Paz is situated near Puerto Orotava, Teneriffe, home of *Lampromyia canariensis*. The larvæ had made their pits in deposits of red ochre at the points indicated by white crosses. (Photograph by Dr. David Fairchild)

longer proboscis, a slightly broader face, a broader abdomen and much less conspicuous genital appendages.

Mr. Graham Fairchild and I first found the larvæ of this insect near Puerto Orotava on the face of the volcanic cliff which forms one side of the Barranco Martianez and on the top of which is situated La Paz, where Alexander von Humboldt lived in June, 1799, while he was investigating the Pico de Teyde, and where, during the Great War the German Anthropological Station was situated in which Wolfgang Koehler carried on his brilliant studies on the behavior of chimpanzees. In the sides of the cliff, of which I reproduce a photograph (FIG. 44) kindly made for me by Dr. David Fairchild, and about 200 feet above the sea, there is a large cave that was used as a burial site by the ancient Guanches and has yielded a considerable number of their bones and mummies during recent years.[1] Just below this cave there is a thin stratum of red ochre weathered into cavities only a few feet deep and in the dust on the floor of these cavities we found several colonies of *canariensis* larvæ. The larval pits, owing to the fineness and compactness of the red dust, were not funnel-shaped like those of Vermileo but bag-shaped, that is, broader at the bottom than at the top. In this locality the larvæ were entirely confined to the ochre dust. The ordinary dust on the top of the cliff and at the bases of old weathered adobe

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[1] Concerning this picturesque locality I find the following remarks in Brown's "Madeira, Canary Islands and Azores," 12th edit., 1922, p. L 40. "On the east of the town (Puerto Orotava) is the Barranco Martianez, from which a fine avenue of palms leads down to the Thermal Palace and the bathing beach. Immediately beyond are the cliffs of La Paz, once a rendezvous where games of skill were held by the Guanches and where it is said that the articles of peace between the natives and the Spanish invaders were formally ratified. The path which crosses the Barranco near the sea, leads up the cliff by a steep path below an old Guanche burying cave. It then passes the Fuente Martianez (¼ hour) and follows the face of the cliff by a small path below and above the most extraordinary volcanic rocks and air chambers in the lava, now exposed owing to the inroads of the sea. There is also a deposit of red ochre and many wild flowers and maidenhair ferns can be picked."

walls contained only the larger, funnel-shaped pitfalls of the common ant-lion of Teneriffe (*Neseurus alternans* Brullé). The *canariensis* larvæ were placed in a jar of red ochre and promptly made pits during the night. They placed themselves horizontally, ventral side uppermost, at the bottoms of these in precisely the same position as Vermileo larvæ and not perpendicularly like the larvæ of *L. pallida* as described and figured by Marchal.

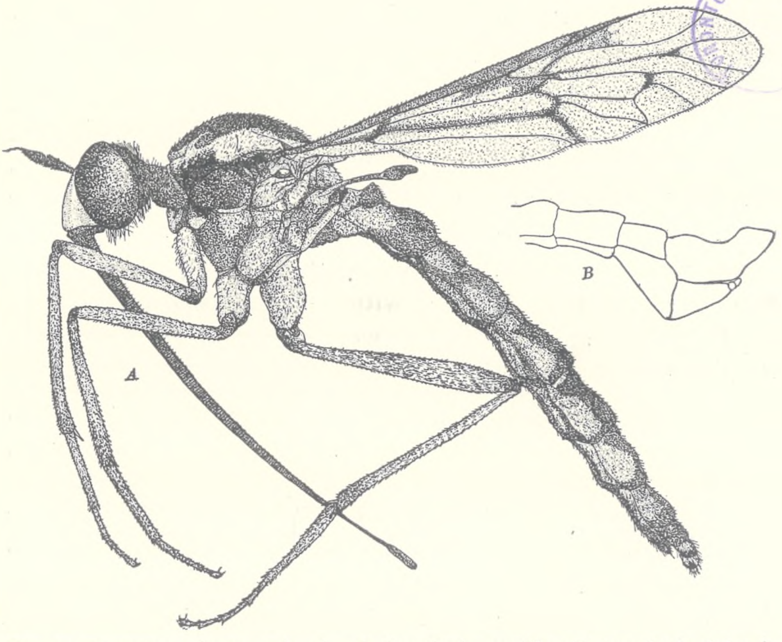

FIG. 45. *Lampromyia canariensis. A,* female in profile; *B,* terminal abdominal segments of male.

On July 10, I found *canariensis* larvæ also in three other localities. In one of them, Santa Ursula, near the town of Orotava, they were living in red ochre dust in the small cavities of a volcanic cliff precisely as in the Barranco Martianez. The two other localities were between Puerto Orotava and San Juan de la Rambla, on the highway leading to the western end of the island. Near the latter town, there were larval pits in the walls of the Barranco Ruiz, in small cavities sheltered from the wind and partially filled with ordinary dust. Here the pits of Lampromyia were mingled with those of Neseurus and varied greatly in size, from five to 30 or 40 mm. across the rim. Only the larger pits contained larvæ and these were somewhat more than half grown. Finally, many colonies were found between the Barrancos Ruiz and Realejo, along the sides of the highway where it had been cut through the lava to a considerable depth. The perpendicular walls, here a few hundred feet above sea level, are studded with a peculiar stone-crop, *Æonium tabulæforme,* which forms flat rosettes, closely applied to the rocky surface and sometimes as much as 16 inches in diameter. In the walls, within easy reach from the road are many small niches partly filled with the fine dust raised by the passing vehicles. The larvæ were very abundant in this locality but only in the larger niches. Although I sought them diligently on the islands of Gran Canaria, Palma and Lanzarote, which we visited later in the month, I failed to find any traces of them. I examined many small sheltered cavities in cliffs or under rocks, but the sand or weathered volcanic materials was always much coarser than the red ochre and fine dust of Teneriffe, and this probably accounted for the absence of the worm-lions.

The *canariensis* larva is pinkish or flesh-colored, shading into dark gray or brown posteriorly, and when full-grown measures 15-18 mm. It is more like the larva of *V. comstocki* than that of *V. vermileo* in having the head-capsule relatively broad and short, but the latter consists of paler chitin ventrally. The eyes are clearly discernible even in the adult larva, as two small pigmented bodies in the usual position under the anterior end of the head-capsule and behind the labial sclerites. The pseudopodial papilla (FIG. 25, *e,f*) is deeply cleft transversely into two protruding, beak-like processes, the posterior of which bears on its hinder surface a group of 6 to 8 backwardly directed spines. The four finger-shaped anal lobes seem to be shorter than in the Vermileo larva and this is true also both of the hairs along the sides of the thorax and abdomen and of the recurved setæ forming the transverse comb on the seventh abdominal segment. These setæ, however, are more numerous, there being 18 of them instead of 10 or 12 as in Vermileo.

The larvæ which I collected in Teneriffe, all survived their journey to Boston. They were installed in dishes of fresh sand, dust or kaolin on September 22. During the autumn of 1925 and the spring of 1926, after being kept in a cool room during the winter, they were fed mostly with termites (Calotermes and Reticulitermes), but occasionally with ants and other insects. On one occasion I placed some half-grown wasp grubs in their pits. Instead of attempting to grasp them, they retreated under the sand, exhibiting the usual reaction towards large or bulky insects, but several of them were seen to approach the wasp grubs from beneath, to fix their jaws in their sides and eventually to suck out their juices. On another occasion, when I dropped a codling moth caterpillar two centimeters long into one of the pits, there was an interesting demonstration of the gradual paralysis of the prey. The *canariensis* larva happened to embrace the last segment of the caterpillar. It writhed violently and emitted from its mouth great quantities of silk, but the larva held on and soon thrust its mandibles into one of its anal prolegs. The progressive paralysis induced by the injected poisonous saliva could be clearly followed in a posteroanterior direction, segment by segment, till the whole caterpillar was completely immobilized. This required five minutes. Observation was possible under the pocket lens because the long body of the caterpillar was stretched out in such a position that it could not be dragged under the sand with the sudden twist always adopted in the case of shorter and smaller prey. It seemed to me that the larvæ of Lampromyia, perhaps on account of their greater size, were more alert, vigorous and rapacious than those of *Vermileo vermileo* and *V. comstocki.* I have been unable to detect any other differences in behavior between the species of the two genera.

FIG. 46. Pupa of *Lampromyia sericea* (After Engel.)

The Lampromyia larvæ after undergoing ecrysis from time to time, reached maturity by the beginning of May 1926 and began to pupate in the same manner as Vermileo. The first adult fly emerged during the night preceding May 27, and from time to time till August 2 the remainder of the larvæ produced imagines. Most of the flies emerged between July 7 and 13. The pupa, which is very much like that of *L. sericea* (FIG. 46), measures 13-15 mm. and has the head and thorax dark brown, the abdomen more yellowish with pale brown segmental annulations. The surface, as in other species of the genus and in Vermileo, is covered with agglutinated sandgrains and bears the shrunken last larval skin attached to the terminal abdominal segments. When the larval skin and sand are removed by immersion in caustic potash solution the abdomen is seen to end in two backwardly directed, parallel appendages and each of its segments from the first to the seventh bears, on each side near the middle, a large, pointed, spine-shaped tubercle. The abdominal spiracles are also on tubercles and are much as in *V. comstocki* but larger. The integument of the head and thorax is smooth but that of the abdomen is very finely and transversely rugulose, with areas of small rounded tubercles, especially on the sides and more posteriorly also on the intersegmental membranes. The antepenultimate segment bears a pair of posterolateral appendage-like swellings covered with minute, backwardly directed spines.

The beautiful dark colored flies were very inactive. They rested with overlapping wings and the head and anterior portion of the thorax elevated, the abdomen lowered and the long, needle-like proboscis directed backward and downward between the legs. Both sexes appeared in about equal numbers, but for some unknown reason showed no inclination to mate. I also failed to induce them to take any of the liquid foods—honey, syrup or sugar-water—with which they were provided. The function of the singular proboscis therefore remains a complete enigma. That the adult Lampromyias do not visit flowers is indicated, perhaps, by the observations of Bequaert, who found *L. pallida* resting on the walls of the cavities which sheltered the larvæ. Since it is also improbable that Lampromyia feeds on the juices of insects, we can only suggest that the proboscis may perhaps be used as an instrument during oviposition in the sand. All of the flies which I reared, were, like those of Vermileo, very short-lived; many of them lived scarcely more than 24 hours, others lingered on for two or three days.

According to Becker, all three of the northern Lampromyia species occur in the Canary Islands, where, in fact, he asserts (1921-22) that he has himself taken them. *L. canariensis,* so far as known, is confined to Teneriffe, and for the reason stated above, it seems probable that the two other species occur on the same island. All three must obviously be regarded as survivors from some remoter geological age, since as Kobelt (1902) maintains, "we can definitely designate the fauna of the Canaries as a relict fauna, a remnant of an early Tertiary period, and the conclusion is not unwarranted that during this period the islands were still united with or had just separated from the mainland, so that their inhabitants, protected from competition with other species, have maintained themselves down to the present time." *L. canariensis* is, therefore, a very obvious relict, whereas the other species, *pallida* and *cylindrica,* as we have seen, still manage to survive in scattered localities on the formerly united African mainland and Iberian Peninsula.

Bezzi (1926) has recently considered the South African Lampromyias in a general monograph on the Rhagionidæ. This paper contains a purely taxonomic revision of *L. sericea* described by Westwood in 1876, and *argentata* described by Bigot in 1885, together with descriptions of two new species, *appendiculata* and *brevirostris,* discovered in the collections of the South African Museum. The Cape region, in fact, would seem to be the center of distribution of the genus and may harbor a number of undescribed species. This I infer from a communication received from the late Dr. Hans Brauns, a very competent observer, who was more familiar with the larvæ of these insects than any other South African entomologist. In reply to a request for larvæ, he sent me not only a number of preserved but also a lot of living specimens of *L. sericea.* Unfortunately, the latter all died on the long voyage from Cape Town. I quote his letter of November 1, 1927, because it contains some interesting taxonomic reflections and the only field observations I have seen on the South African worm-lions.[1] "Your letter of October 4 was received last week. I shall probably be able to collect and send you during this month the desired material (larvæ and pupæ of *V. sericea* Westw.). Last year I collected both of these stages here in Stellenbosch in considerable numbers and reared from them *sericea* Westw. I also sent living material to my friend Dr. O. Engel in Munich, Bavaria, who succeeded in rearing several individuals despite the German winter. He fed them with hibernating mosquitoes from his cellar and therefore had occasion during several months to observe the behavior of the species. He confirmed the identification which I had made from Bezzi's monograph in the Annals of the South African Museum. Engel has now completed a paper which, he writes me, will probably soon appear in the Annals of the Cape Colony Museum. This will contain a revision of the species together with his observations on behavior, the data with which I have supplied him, and several illustrations. Bezzi, as you are aware, has monographed the South African species of Rhagionidæ and has replaced the name Vermileo by that of Lampromyia. He has made some errors in regard to the spinulation of the fore tibiæ, which Engel will probably correct. We shall have to await, therefore, the publication of the latter's work. It seems to me that Vermileo should be retained, for

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[1] Dr. Brauns' remarks on the identity of Vermileo and Lampromyia represent his personal opinion and are interesting because they adumbrate a possible future taxonomic lumping of the two genera.

I have taken three males of a Palearctic species, close to *canariensis,* here in Cape Colony, near Lady Grey, in the eastern part of the province. . . . I cannot give you the name of the species till I return to Willowmore which will not be till the end of December. Near Willowmore, I took the male of a second species which, though very close to *sericea,* is certainly distinct. It, too, has been sent to Engel for determination or description. As yet I have found no larvæ of this species. Bezzi has described several species in his monograph. I have myself seen larval funnels near Van Rhynsdorp, in Namaqualand. Moreover, colonies of funnels are found right on the sea-beach near Hermanus, which is on the Indian Ocean, about one hundred miles north of Cape Town. These, too, may belong to a species differing from *sericea.* I shall endeavor to visit that locality with my motor. Unfortunately, my attempt to reach it last year was prevented by the severe rains. Some years ago I saw some Vermileo larvæ from which a Wesleyan pastor had reared a large, dark colored species. These larvæ came from Natal. It would seem, therefore, that a considerable number of species of Vermileo are distributed over South Africa. Arnold in Bulawayo, Southern Rhodesia, probably reared imagines from living *sericea* larvæ, which I sent him from here, but has hitherto found no endemic species in tropical South Africa. These are all the data I possess on geographical distribution. It seems to me that Vermileo and Lampromyia are not generically distinct. The occurrence of terminal spines on the fore tibiæ, emphasized by Bezzi, is evidently variable even in the same species. Perhaps Engel's critical work will elucidate this matter. . . . 'Vermileo (Lampromyia) is cannibalistically inclined, and has a developmental cycle covering more than a single year. Of a considerable number of larvæ sent to Engel only a small number survived. Here I find larvæ of all sizes and sometimes also pupæ at the same season (November and December). The funnels are made in sandy soil, singly or frequently in pseudocolonies. The larvæ are somewhat fastidious in regard to diet and toss unsuitable prey out of the funnel even after they have dragged it under the sand. They seize their prey with lightning rapidity by encircling it and quickly thrust their stylets into it. They can go without food for a long time and some of them readily hibernate here during the months from June to October. This is the usual rainy season in Southern Cape Colony. After showers several days often elapse before they repair their funnels. This work, according to my observations, is carried on mainly in the evening or during the night. I have often observed the larvæ at work in the evening under electric light. They then raise their bodies almost as far as the anal end from the bottom of the funnel, wildly whirl their anterior end like a tiny snake about its axis and thus succeed in giving the funnel its beautifully symmetrical shape. Failure to repair their funnels for some days is a sign that they are either digesting, moulting or about to pupate. Perhaps it would be well for you to sprinkle them with water occasionally. They must then be exposed to the sun. The imagines should be permitted to develop without disturbance. Engel found that after he had left the larvæ without food for months and believed all life to be extinct, there were still several plump individuals in the sand (also an indication of cannibalism). They often make their funnels some distance from the spot in which they entered the sand and therefore wander about under the surface. Sometimes there are funnels of ant-lions among the Vermileo colonies. When the funnels are dug up in the field, the larvæ lie motionless for a time and are, on that account, difficult to find. On such occasions they assume a very characteristic, somewhat curved posture, which closely resembles that of certain Geometrid caterpillars. Only under strong sun-light and heat do they begin to move and then they often leap some distance. The pupæ, too, are able to leap. The dark change of color which the larvæ undergo in alcohol or other preserving fluids is disagreeable. Engel was unable to tell me of any way to avoid this discoloration. The larvæ, even after starving for a long period and having, therefore, emptied their intestines, became darker in alcohol and in the course of time, quite black.' "[1]

L. sericea, the first South African species to be bred from the larva by Dr. Brauns, was described by Westwood from specimens received from Damaraland as the type of a new genus, Leptynoma. Bezzi records it also from Matroosberg, 3500 feet (R. M. Lightfoot). The insect (male) is 13 mm. long, with a proboscis of 6 mm. Its face, occiput, proboscis and terminal antennal joint are black, the occiput covered with gray dust; the thorax and abdomen are reddish, the former with a silky sheen, and its dorsum ornamented with a median black stripe edged with whitish and a broad reddish brown stripe on each side, interrupted at the transverse suture. The halteres are yellowish, with a black knob. The abdomen is without markings and covered with silvery dust throughout. The fore and middle legs are entirely yellowish with apically blackened tarsi; the hind pair is reddish with the tips of the femora, tibiæ and tarsi infuscated. The wings are grayish hyaline and iridescent, with fuscous spots on the præfurca and below the stigma,

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[1] The dark discoloration mentioned by Dr. Brauns is, indeed, a serious obstacle to the proper preservation of Vermileonine larvæ, either as museum specimens or for histological purposes. It is due to the solubility of the black stomach-contents, which in alcoholic material gradually soak through the thin wall of the gut and discolor the musculature and other tissues. I have found that beautifully distended specimens of the larvæ can be obtained by dropping them into water heated to 80°C and then transferring them through 35% and 70% to 90% alcohol for preservation. But after some months such specimens, though perfectly retaining the form of the body and, of course, of all the chitinous elements, become discolored and the musculature often breaks down. Much better results both for *in toto* preservation and for histological purposes were obtained by dropping the larvæ into hot corrosive sublimate solution and then passing them through the different grades of alcohol.

forming a dark band in the narrowed median portion of the marginal cell. The apical portion of the second vein is bordered with fuscous and the veins in general are yellowish basally and darker apically. The genitalia are erect, reddish, with short white pubescence.

Engel's interesting study of the larva and pupa (FIG. 46) of *L. sericea,* based on material received from Dr. Brauns, appeared in 1929. He describes the living larva as reddish ochraceous but darker anally, owing to the black contents of the stomach. I have already mentioned his observations on the spiracles and head skeleton (p. 183). He also gives an account of the pseudopod, which I am unable to harmonize with my own observations. He describes a diverticulum of the intestine as extending into it. The structure in question is certainly no portion of the alimentary tract but a complex of tissues consisting of hypodermis and the retractor musculature of the appendage. I am also unable to agree with his description of the terminal segment, or papilla of the pseudopod. He says that "the papilla itself is composed of three processes, the median one having the form of an anchor and the lateral ones being of simple cylindrical form. The mouthparts seize the median process from behind, so that the four preceding segments form the upper part of a Roman S. Then the larva stretches the body a little, the mouthparts glide off from their hold, and the head acts like the strained end of an elastic steel which has been bowed together by its two ends, for the rest of the body remains firmly anchored in the sand of the pitfall. The movement is too quick for one to see more than the effect of the mechanism. As the anal end remains fixed to one point in the depth of the homogeneous fine sand, it is easy to understand how the conical form of the pitfall is constructed by the larva." And after his description of feeding the larvæ with mosquitoes (Culex), he continues: "Seeing that the intervals between these pitfalls, each of which had a diameter of almost 4 cm., were not very large, it often happened that a struggling *Culex* removed sand-grains from the wall of one pitfall which fell into the center of another, and this was promptly answered by eruptions of sand, falling again on the head of the next larva, so that in a short time a regular bombardment spread over all the eight pitfalls. These eruptions are produced in the following manner: The larva, which is firmly anchored by its thickset anal end in the sand below the center of the pitfall, so that only the first six or seven segments are visible, bows the head and fixes the mouthparts on the papilla, lying ventrally on the fifth segment. It then lets loose the wart, and, throwing the head backwards with a sudden jerk, hurls the objects from out the pitfall. The sucked-out bodies of the victims, and even the cast skins of the larva itself, are removed in this way."

Engel's contention that the larva grasps the pseudopodial papilla with its mouthparts, seems to me to be very doubtful, first, because I have been unable to witness this behavior in any of the four species of Vermileoninæ which I have had under observation, and because Engel himself admits that actual observation of the seizure of the papilla is impossible when he says that "the movement is too quick for one to see more than the effect of the mechanism." Second, the structure of the papilla in *L. sericea* (FIG. 25 *g,h*) does not agree with Engel's description. It is, as in other species of Lampromyia and in *Vermileo vermileo* (FIG. 25 *a,b*), cleft transversely into two valves or processes and not longitudinally into three, and the only structure that might, perhaps, by a considerable stretch of the imagination, be described as anchor-shaped is the anterior valve. Third, I fail to see how the papilla in *sericea* or in any of the other Vermileoninæ in which it has been studied, is at all suited for seizure by the mandibles or maxillæ of the larva, since it is far too delicately chitinized to stand the strain of the vigorous extensor muscles of the thorax. Fourth, we should expect the papilla to be used in the manner described by Engel when the larva is leaping, but at such times it certainly does not grasp the appendage with its mouthparts though there is a very violent retroflexion of the thorax. And fifth, according to my observations, several of the anterior abdominal segments in addition to the three thoracic segments, are implicated in all the abrupt movements performed by the larva while making its burrow, striking at its prey or tossing out exhausted carcasses.

But, if we cannot accept Engel's interpretation of the pseudopod as a catch or ratchet for the spring-like movement of the neck, what is the function of the appendage? Most observers of Vermileo and Lampromyia larvæ have assumed that it must act like the human thumb when opposed to the fore finger—represented by the anterior segments of the larva—in grasping and holding the prey. But the only species in which the organ would seem to be fairly well adapted to such a purpose is the one described in the next chapter (p. 272); in all the others it is too small and delicate to function very efficiently in this manner. It occurs to me, therefore, that it may act as a strigil, or rather as a toothbrush, for cleaning the larval mandibles and maxillæ. That these organs may occasionally become clogged with particles of sand or dust while the larva is making its funnel or feeding subterraneously on its prey, seems, indeed, highly probable. And certainly the tuft or series of backwardly directed spines, with which the pseudopodial papilla is furnished would seem to be admirably suited for cleansing the mouthparts. For obvious reasons, however, it will not be easy to observe this act.

Engel has published a good figure of the *L. sericea* larva and has also described and figured in detail the pupa (FIG. 46), which I have not seen. It varies in length from 11 to 18 mm. and very closely resembles the pupa of *L.*

canariensis. Like other Vermileoninæ it retains the wrinkled larval skin firmly attached to the last abdominal segments and its surface is covered with a layer of agglutinated sand-grains. The abdomen does not seem to be as smooth as that of the *canariensis* pupa, since, according to the description "the integument of the intersegmental parts of the abdomen is transversely rugose; that of the segments shows densely set, minute spines, all directed anally."

It is interesting to note that in Bavaria Engel's *sericea* larvæ became flies at precisely the same season as they would have in their South African homeland. He says: "After three months, in the middle of May, just at a time when our Palæarctic insect life begins to awaken, all my larvæ refused to take food and the pitfalls began to fall in. This period lasted till the 5th of October, when two new pitfalls, but of smaller dimensions than usual were constructed. Those of the first season measured from 3 to 3.5 cm. in diameter, while they now reached scarcely 2 cm. Four larvæ were present, but only two took food, and even this at intervals of from two to four days. On the 14th of October no more larvæ were to be seen. On 21st October a fine male fly emerged from a pupa. All the others proved to be females, the last of these emerging on 1st March." In other words, the flies emerged during the Bavarian winter months corresponding with the summer season in Cape Colony, after the larvæ had hibernated, so to speak, during the Bavarian summer. I have already called attention to the less remarkable coincidence of the emergence of the flies of *V. comstocki* from larvæ reared in Massachusetts with the normal emergence of the flies in the Sierras of California.

Concerning the development and behavior of the three other known South African species of Lampromyia, *argentata, appendiculata* and *brevirostris,* nothing is known. According to Bezzi, *argentata* "is possibly only a form of *sericea*." He examined Bigot's type, which was taken on the Hex River, Cape Province. It differs from *sericea* in having the front and occiput more densely dusted with white, the antennæ entirely red, the thorax, abdomen and legs paler, the thorax with brown stripes. The wings are distinctly more yellowish and characterized by several peculiarities in venation.

The type of *L. appendiculata* Bezzi, a male taken by R. M. Lightfoot at Matroosberg (alt. 4500 ft.), is also closely related to *sericea*. Its antennæ are entirely pale, the proboscis a little longer, the color of the body paler, and the thorax lacking the dark lateral stripes above the notopleural line. There is a dark stripe on the posterior portion of the venter. The genitalia are shorter and have the upper lamella truncated at the tip. The wings are similarly colored but with a slightly different venation, the fourth vein having a long stalk and all the veins in the apical portion of the wing being stouter and blacker than in *sericea*.

L. brevirostris was described by Bezzi from two males, one from M'fongosi, Zululand, taken by W. E. Jones and one from East London, taken by H. K. Monro, and a female without locality label but bearing the note: "Bred by Rev. N. Abraham from a larva kept for two years in captivity, April 1920." These specimens measure 11-12 mm. and differ from all the other known species of Lampromyia in having the proboscis very short and robust, only a little longer than the vertical diameter of the head. The antennæ are long, the general color of the body is like that of *sericea*, but the thorax has three black stripes above, the abdomen in both sexes is without silvery dust and has black spots at the posterior border and along the sides of each segment. In the male the three last segments are entirely black above. The legs and wings are colored somewhat as in *sericea*. In the shortness of its proboscis, *L. brevirostris* seems to constitute an interesting transition between Vermileo and Lampromyia, and would seem to justify the erection of a new genus or subgenus for its accommodation, or a lumping of the two genera, as suggested by Dr. Brauns in the letter above quoted.

CHAPTER VIII

THE WORM-TIGERS OF INDONESIA

THE occurrence of two genera of worm-lions on the African continent would lead one to seek them also in Southern Asia, but though India, Burma, Malaya, Indochina and southern China have long been favorite collecting grounds for many enthusiastic and competent entomologists, the literature contains no mention of the occurrence of any Vermileoninæ in those regions. This is not true, however, of one of the larger adjacent islands. Nearly thirty years ago, R. H. Shelford (1901) discovered on Mt. Penrissen, which rises to an elevation of about 4000 feet in the province of Sarawak, Northern Borneo, a larva which in structure and behavior so closely resembled the larva of Vermileo, that it was assigned to that genus. I quote the whole account which was published in a rather inaccessible periodical: "During a recent visit to Mt. Penrissen, Sarawak, I found in sand beneath some overhanging cliffs numerous small pitfalls exactly like those made by the antlion; some of these when examined were found to contain a curious worm-like larva which has since proved to belong to a fly of the genus Vermileo, family Leptidæ. The body consists of 11 segments, into the first of which the head can be completely retracted, five annuli can plainly be distinguished on segments 2, 3 and 4, but are less well marked on the others; the 10th consists only of three. The middle annulus of the fourth segment bears on the ventral surface a fleshy knob (abdominal pseudopod) which is surmounted by a small semicircular chitinous comb longitudinally placed; the eighth segment ventrally bears a median tuft of setæ, and a fringe of similar setæ marks the posterior border of the 9th segment. This also carries on its ventral surface 2 median setigerous papillæ. The 10th segment, which is set at somewhat of an angle to the 9th, bears on the dorsal surface at its posterior border a fringe of very strong setæ directed backwards. The 11th and last segment terminates in four finger-like processes clothed with delicate hairs, the anus opens on its ventral, two stigmata on its dorsal surface. The last three segments are markedly larger than any of the preceding ones. The larva burrows into the sand head first, until completely buried, and then proceeds to form its pitfall in the following manner: the more deeply buried tail-end acting as a fixed point, the anterior half of the body is curved about in all directions, each curving motion being followed by a rapid straightening out, which jerks the sand away for some distance; since the tail is fixed, the result of many of these motions is to produce a circular depression with sloping sides; at the bottom of this lies the larva, ventral surface uppermost, the posterior half of the body still buried, the anterior half exposed and straightened out. If now an ant is introduced into the pitfall, the exposed part of the larva suddenly curls up in a spiral coil, the prey being generally included in the coil and impaled by pressure on the chitinous comb of the 4th segment; a hold is then gained with the mouth, and after a few minutes, with a rapid sinuous motion, the larva straightens out and disappears below the sand, carrying its prey with it. If the larva is not successful in catching its prey the first time, it flings sand about in all directions by rapid switching movements, and the victim, unable to obtain a foothold on the sliding sides of the pitfall, falls down to the bottom; or occasionally the larva actually strikes like a snake at the victim as it endeavors to escape from the toils, indeed, many of the actions of this larva are quite snake-like, and an ant enclosed in one of its coils reminds one of nothing so much as of a small mammal in the grasp of a python. Occasionally the prey seems somewhat out of proportion to the larva, but by means of the numerous setæ on the large posterior segments a very firm grip is obtained in the sand, and I have never yet seen an insect of moderate size make good his escape after having been once seized. I brought down to Kuching alive several of these larvæ, and one or two pupated; shortly before pupation, the larva leaves its pitfall and lies close to the surface of the sand, though completely covered; the anterior segments become much swollen and retracted, until the integument bursts, revealing beneath the brownish pupa; by some convulsive movements the whole pupa now appears at the surface, the larval skin being slowly shuffled off backwards, but never becoming entirely freed, so that the posterior end of the pupa always presents a somewhat ragged appearance. Unfortunately the heat of Kuching proved too much for these pupæ, and none came to maturity, but shrivelled up; some Leptid flies which I obtained on Penrissen are, however, I am sure, the adult stage."

It will be seen that though there is very little in this account to distinguish the Bornean larva from that of Vermileo, Shelford's statement that it was proved to belong to that genus is decidedly doubtful, both because he failed to rear the adult fly and because there is nothing in his description to show that the larva is not a Lampromyia or even a member of some hitherto undescribed genus. Unfortunately he gives no description of the Rhagionid which he took on Mt. Penrissen, and regarded as the adult form of his larva. While there can be no doubt, therefore, that Shelford's insect is a true Vermileonine, its generic allocation must remain in doubt till some future investigator succeeds in rearing it to maturity.

In a letter of March 26, 1926, from Kaban Djahe, Sumatra, Mr. Graham Fairchild, who had helped me collect Vermileo and Lampromyia in the Balearic and Canary Islands, informed me that he had just discovered some Vermileonine larvæ on March 17 at Konde, in the province of Deli, Northern Sumatra, at an altitude of 1500 to 2000 feet. He described the situation in which the larvæ were living as an accumulation of coarse dust under a deeply shelving ledge by the side of a trail through moderately heavy jungle. "The dust," he wrote, "seemed to be decomposed volcanic tufa. The larval pitfalls were interspersed with those of a small species of ant-lion and were difficult to distinguish because they were only slightly smaller. The largest larvæ measured about half an inch, the smallest about a quarter. They appeared to lie horizontally in their pits, sometimes with the anterior portion of the body curled up, at other times outstretched and applied to the sloping wall of the pit, ready to snap over on a victim. When taken from their pits they assumed the usual motionless S-shaped posture like the larvæ of Vermileo and Lampromyia we took last summer. I succeeded in securing only 11 larvæ and shall preserve three and try to rear the others." Mr. Fairchild wrote again June 27 that he had reached Naples with the larvæ but that only two of them had survived the journey from Sumatra. "The long voyage was too much for them and I had no opportunity to feed or examine them *en route*. It seems probable that these two devoured the others as they are still of good size and only the skins of the others remain." He intrusted the survivors to Dr. H. B. Osborne who kindly delivered them to me in Boston on July 25.

The two precious insects were at once placed in a dish of sifted road-dust mixed with fine sand. By the following morning they had made very symmetrical pits and were lying horizontally across their floors. They were quite as large as full-grown Vermileo larvæ and of a dull pinkish-gray color. They seemed to be very hungry because each of them during the day managed to kill and devour two *Reticulitermes flavipes* workers. On the morning of July 17th each again took a termite though they would have nothing to do with a couple of *Formica subsericea* workers, which I dropped into their pits, but hid under the sand while the ants were scrambling about just above them.

During the next fortnight the larvæ fed ravenously on termites and increased considerably in size. One of them was now nearly 20 mm. long and quite the most active and formidable larva I have seen. Its behavior was singularly snake-like and vicious, like the Bornean larvæ studied by Shelford. The other individual was growing more slowly and seemed much less healthy. On August 10 it lay motionless on the sand. When I felt sure that it could not recover I fixed it in water heated to 80° C. and preserved it in 80% alcohol. By this date the single surviving larva was fully 22 mm. long and made pits 3 to 4 cm. in diameter and shaped exactly like those of our common ant-lions. When removed from the sand it assumed the usual motionless S-shaped attitude but differed from the Vermileo and Lampromyia larva in having its four anterior segments tightly coiled up ventrally like a small snail-shell with a flattened spire. Towards the end of August it ceased to feed and wandered about during the night, leaving a record of its path as a groove on the surface of the fine sand, but hid beneath the surface during the day. This behavior continued till August 28th. After September 1 it no longer came to the surface and on sifting the sand on September 7, I found that it had transformed into a large pupa. The probable date of pupation was September 1, which may correspond with the normal period of metamorphosis in its native habitat. Although I carefully buried the pupa again in the sand, I found on October 11 that it had died after nearly reaching maturity. Thus I had no better success than Shelford in rearing the Indonesian insect, and can only give a description of the larva and pupa and offer some comments on their probable taxonomic significance.

The full-grown, outstretched larva measures 23 to 24 mm. and is therefore larger than that of any other known species of Vermileoninæ. At first sight it closely resembles the larvæ of Vermileo and Lampromyia, but closer examination reveals several peculiarities. The most striking of these is the structure of the pseudopod (FIG. 25 *i,j*) on the ventral side of the first abdominal segment. In profile the tip of this appendage is evenly rounded and hemispherical, with a distinctly differentiated and uncleft papilla and with a low median longitudinal thickening bearing a series of straight, rigid, radiating spines, shorter at the ends of the series than in the middle. These spines vary in number, apparently, with the age of the larva, a full grown specimen having six, the smallest four and an individual of intermediate size, five. The body of the larva is covered with very short, fine, uneven hairs and there are the usual long hairs on the sides of the thoracic annuli, the sides of the thoracic segments and the borders of the four anal lobes, which are rather short and thick. There are, however, several much longer, stouter, recurved bristles of a dark brown or blackish color. One series of these forms the comb on the posterior border of the eighth abdominal segment, but there are only twelve of them, six on each side of the median line, and they are not flattened at the base as in Vermileo and Lampromyia but cylindrical and alternating with them is a second series of similar and much shorter bristles. There are also series of three stout dark-colored bristles on each side of the middle line and arising from paired transverse swellings or welts on the dorsal and ventral sides of the seventh and the dorsal side of the sixth abdominal segment. The mouthparts and cephalopharyngeal apparatus are much like those of Lampromyia, the head-capsule being black, robust, heavily chitinized and scarcely more than twice as long as broad, but the ventral tendon, which is very narrow and incompletely chitinized in Vermileo and Lampromyia, forms a distinct linear sclerite, like the piece which I have called the gula, but shorter. The mandibles are stout, with rather coarsely serrated borders. The spiracles are large and distinctly chitinized and their radial tubules, which number six in the anterior and ten in the posterior pair, are unusually large and distinct.

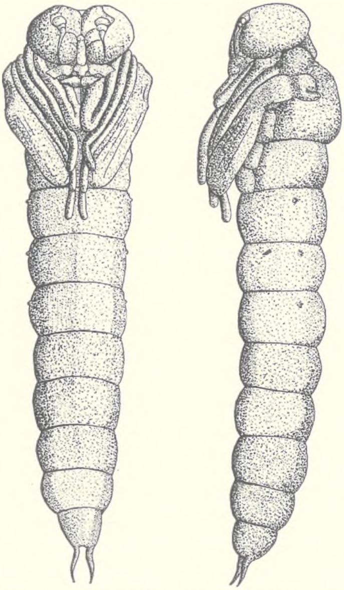

FIG. 47. Ventral and dorsal aspect of pupa of *Vermitigris fairchildi* freed from the last larval skin which invests the abdominal segments.

The pupa (FIG. 47) measures 15 mm. and is dark brown, with thicker, more brittle and smoother integument than in Vermileo and Lampromyia. Although the crumpled last larval skin firmly envelops the two posterior segments as in those forms, there is no adherence of sandgrains to the surface. This seems, however, to have been covered during the last larval ecdysis with a whitish but non-sticky secretion. The body is long and narrow, the thoracic dorsum very convex and rounded, the abdominal segments somewhat flattened dorsoventrally. The head has a very broad face and the antennæ are widely separated, with long aristæ and enclosed in free sheaths directed downward along the inner borders of the eyes. The latter seem to be much smaller and less convex than in Vermileo and Lampromyia. The proboscis is short and stout and, therefore, more like that of Vermileo than Lampromyia. The caudal segment terminates in a pair of long, slender, curved, diverging appendages. There are no traces of tubercles or spines on the abdominal segments and only the spiracles of the second and third segments are borne on distinct tubercles.

The foregoing description of the larva and pupa of the Sumatran insect shows that it differs from both Vermileo and Lampromyia more than these genera differ from one another. Outstanding peculiarities of the larva are the character of the pseudopod and of the setal comb on the eighth abdominal segment, and of the pupa the structure of the antennæ, the small size of the eyes and failure to acquire an envelope of sandgrains. I believe, therefore, that the insect must represent an undescribed genus and species of Vermileoninæ, and propose to call it *Vermitigris fairchildi* after its discoverer.[1] I realize that many entomologists frown on the naming of insect larvæ or pupæ, but this case

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[1] Comstock (1924) has proposed the name "ant-tiger" for the Sierra wormlion, but since there is no evidence that the Sumatran larva feeds mainly on ants, I have given it a generic name expressive of its close relationship to Vermileo.

is exceptional since the Vermileoninæ are a very small and unusual group and since the species under discussion can be readily recognized by any future investigator who cares to collect and rear larvæ from the type-locality in Northern Sumatra. Shelford's larvæ, in my opinion, very probably belong to the same species. This may be inferred from his description of the pseudopodial papilla and its spines and also from the fact that most species of Indonesian insects are distributed over more than one of the larger islands of the archipelago. Furthermore, the locality in which Mr. Fairchild discovered the Vermitigris larvæ is so near the Malay Peninsula that we may confidently look forward to finding it also in the highlands of the Strait Settlements and therefore on the continent of Asia.

Note

Just as the greater portion of this volume was ready to go to press, one of my enthusiastic students, Mr. Richard P. Dow, brought me thirty living and several preserved Vermileo larvæ which he had discovered on August 28 and 29, 1930, at Mayarí (2800 feet) and San José (900 feet), in the Trinidad Mountains of Santa Clara Province, Cuba, thus greatly and most unexpectedly extending the range of the genus to the American tropics.

The specimens are clear pink or brownish pink and vary considerably in size. The largest are fully 19-20 mm. and are therefore even larger than *V. vermileo* larvæ. The head-capsule is very narrow, fully three times as long as broad, and therefore like the head-capsule of the Mediterranean species. The pseudopod is also much as in that species, the papilla being divided into two valves, the anterior of which is narrowly conical, projecting and covered with dense, fine hairs, the posterior flattened and armed with four stout, subequal spines. The comb on the posterior dorsal border of the seventh abdominal segment consists of rather short, stout setæ, of uneven length and not flattened at their bases.

Mr. Dow informs me that he found the larvæ in fine dust under overhanging limestone cliffs. In some places their pits were mingled with those of small ant-lions, a number of which he brought me in separate vials of sand. The Cubans in the Trinidad Mountains, according to Mr. Dow, are so well acquainted with these larvæ that they have given them a name, *caranganopito,* which, I suspect, is also applied to the ant-lion. The larvæ, owing to their careful transportation, arrived in Boston in excellent condition. On being placed on fresh sand they at once buried themselves and commenced making their pitfalls in broad daylight. A few hours later they were fed on termites which they greedily seized.[1]

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[1] During the latter part of October, 1930, three of the Cuban larvæ pupated and a single somewhat crippled male fly emerged November 5. This specimen, which proves to be a typical and very beautiful Vermileo, agrees closely with the description and figure of Walker's *Pheneus tibialis* (1851) from Jamaica, but differs in certain details of coloration. I therefore regard it as a variety (*V. tibialis* var. *dowi* var nov.). Williston in 1896 described a male Rhagionid fly, taken by H. H. Smith at Xucumanatlan, Guerrero, Mexico, as *Arthrostylum fascipennis,* but in the "Biologia Centrali-Americana" (1901) cited it as a synonym of Walker's *Ph. tibialis.* The description, however, shows that the Mexican form is quite different in coloration and other characters. There is, therefore, in Mexico yet another species of Vermileo, namely *V. fascipennis* (Williston). Xucumanatlan, the locality in which the type specimen was taken, has an elevation of 7,000 feet. Mr. Dow's finding the Cuban larvæ has led, therefore, to the rediscovery of Walker's *Ph. tibialis,* which had not been seen since 1851, the demonstration that Pheneus is merely another synonym of Vermileo, and the recognition of a fifth species of this genus in the mountains of southwestern Mexico.

CHAPTER IX

CONCLUSION

THE detailed account of the ant-lion and worm-lion in the preceding chapters, with the more or less relevant considerations that have been introduced, often, I fear, to the discomfiture of the reader, may have concealed, instead of bringing into striking relief the great dissimilarity of their structure and the extraordinary similarity of their behavior patterns. This concluding chapter is therefore devoted to some further remarks calculated to emphasize the peculiar convergent behavior of the two insects. This has impressed all observers since Degeer and Réaumur. As Redtenbacher (1884*a*) says: "A legless maggot and a six-legged Neuropteran larva equipped with powerful sucking mandibles, carry on, though by somewhat different methods, one and the same industry for the purpose of obtaining their food; truly, Nature nowhere shows us in a more beautiful and surprising manner how by the most diverse means the same purpose can be accomplished." The construction of the pitfall and the hurling of sand in the direction of the approaching or escaping prey by both ant-lion and worm-lion were naturally regarded as conspicuous instances of the use of tools by animals, and, as Ettlinger (1924) has shown, did not fail to suggest interpretations ranging from pure 'design' to crass 'mechanism'. Both of these extreme views are partial and, so far as we are able to see, can be reconciled only when we consider the behavior of each of the insects under discussion as a whole, that is as a configuration, or 'Gestalt', involving not only the insect but its specific environment as well. This should become clear as we proceed.

The striking parallelism or convergence to which I have so often alluded, can be detected both in the general and in the particular characteristics of the ant-lion and worm-lion. A consideration of their general convergence is best introduced by calling attention to a remarkable peculiarity of all holometabolous insects, which has often been noticed by entomologists in connection with special problems, as for example by Roubaud (1922). These insects have four very distinct ontogenetic stages, the embryonic, larval, pupal and imaginal, and for the purposes of discussion this series may be regarded as really comprising two widely separated embryonic stages, the embryo proper and the pupa, during both of which the insect is withdrawn, so to speak, from the environment and therefore exhibits scarcely any behavior. The two behavioristic, or effective stages, the larval and imaginal, are separated by the pupa, which represents a resumption of development after a prolonged period of growth. Accordingly, the life-cycle is much more complicated in the holometabolous insects than in most other animals. It is only to the latter that Woodger's (1929) valuable distinction of a developmental and a behavior period applies, in the simple form in which he states it: "Broadly speaking, we can distinguish (in Metazoa) two main (but partly overlapping) periods of the history — the developmental period, and a later period which we may call the 'behavior' period. If our slices are taken during the developmental period they will exhibit greater differences of a certain kind than if they are taken during the behavior period." We may say, therefore, that there are two developmental and two behavior periods in the Neuroptera and most of the higher insects (Coleoptera, Diptera, Hymenoptera, etc.), and it is clear that the two behavior periods, the larval and the imaginal, often differ greatly in the range and complexity of their particular patterns. In the ant-lion and worm-lion the behavior pattern, or configuration, is, as we have seen, unusually intricate and repetitious (polycyclic) during the prolonged larval stage, but in the imago restricted very largely to the single activities of mating and oviposition (monocyclic). In many Hymenoptera, on the other hand, the behavior of the larva is very monotonous and confined merely to feeding or imbibing, whereas that of the imago, as in the Parasitica, wasps, ants, bees, etc., may be very elaborate and highly specialized. This incidence of the main behavior pattern in the imaginal stage seems to be due to an increasingly selective ovipositional tendency on the part of the female insect. Simple oviposition in sand or water places the onus of behavior on the larva, which is left to shift for itself, while care in laying the eggs in or on some particular host or other special organic food, or actual mouth to mouth feeding of the larva by the mother or nurses as in the social insects, relieves the larva from all behavioristic effort. The larval behavior of the ant-lion and worm-lion, accordingly, may be said to be a consequence of oviposition in such a simple inorganic environment as sand or dust. We are not surprised, therefore, to find that in both insects the larva is tough, bristly and long-lived, and the imago frail, delicately pilose and short-lived, and that the one is a predominantly tactile denizen of a coarse terrestrial, the other an almost exclusively visual and olfactory dweller in an aërial medium.

It would be easy to make a long list of the detailed resemblances between the ant-lion and worm-lion, including the various taxes and sensory reactions of the larva, its normally biennal life-span, the excavation of the pitfall, lying in wait, the poisoning, burial and extraintestinal digestion of the prey, the occlusion of the posterior end of the stomach, death-feigning, the ability to remain for long months in asitotic stupor, pupation in the sand, the wriggling of the pupa up to the surface to permit eclosion of the imago, etc. On the other hand, certain striking differences are to be noticed between the two insects, especially those in locomotion (retrograde in the ant-lion, dorsigrade in the worm-lion), in pit-excavation (circuitous method absent in worm-lion), in the lying in wait posture and in the method of capturing prey, in ability to leap (absent in ant-lion), in the making of a cocoon (absent in worm-lion), etc. On the whole the ant-lion's behavior pattern, as the expression of a structurally more highly differentiated type of larva, is decidedly more elaborate than that of the worm-lion.

The behavior pattern of either insect, nevertheless, is so complicated that, according to any of the prevailing evolutionary hypotheses, it could have been built up only very gradually and therefore over a considerable period of time. In other words, it must have had a long and eventful history in space-time. This is indicated by such data as we possess in regard to the palæontological age of the Myrmeleontidæ and Rhagionidæ. In Chapter III, I traced the origin of the former family to Nymphid forms, which go back to the Jurassic, and assumed that this group in turn must have had an anterior phylogenetic development extending back perhaps to some Neuropteroid ancestor in the Permian. Our data do not permit a like assurance in tracing the phylogeny of the Rhagionidæ to so remote a period. It is possible, nevertheless, to follow this family back through a considerable portion of the Tertiary. In 1914 Cockerell found in the Miocene Florissant Shales of Colorado two fossil flies which he described as *Atrichops hesperius* and *Xylomyia moratula.* Atrichops is scarcely more than a synonym of Atherix. Several typical Rhagionids have been recorded from an even earlier formation, the Baltic Amber, which is of Lower Oligocene age. Handlirsch (1908) lists in addition to some unidentified forms, a species of Arthropeas, four of Atherix, seven of Rhagio, one of Chrysopilus, a species of Palæoschrysopila and one of Palæohilarimorpha. With the exception of the two last, which are extinct forms allied to Chrysopilus and Hilarimorpha, all these genera are well known components of our present Rhagionid fauna. It is certain, therefore, that the family may be traced back as far as the Early Tertiary at least, and paleoentomologists might be inclined to seek its hypothetical ancestor in the Mesozoic and perhaps as early as the Jurassic, though the family has probably had a more recent origin than the Nymphidæ. In our present classification of the Diptera, the suborder Brachycera, to which the Rhagionids belong, occupies an intermediate position between the very archaic Nematocera and the highly specialized modern Cyclorrhapha, but some of the genera, such as Xylomyia, Xylophagus, Rhachicerus, have a decidedly ancient habitus. The absence of any records of Vermileoninæ in the Tertiary shales is not surprising, because the imagines are such delicate insects. Nor should we expect to find them even in the amber because the existing forms do not frequent vegetation but, if we may judge from observations on Vermileo and Lampromyia, pass their brief lives in the sandy environment in which they lived as larvæ.

That the Vermileoninæ are an ancient group is also indicated by the living species, as shown in the maps (FIGS. 19 and 42). Though the three genera Vermileo, Lampromyia and Vermitigris are very closely related, their species exhibit a singularly discontinuous distribution, and this in all analogous cases is regarded as strong presumptive evidence of antiquity. The subfamily is obviously composed of relicts, or isolated remnants of a more extensive Vermileonine fauna which formerly occupied a much more considerable area of the globe's land-surface. It will be noticed that all of the species, except *Vermitigris fairchildi* and *Vermileo tibialis,* live only in sub-tropical or warm temperate regions and that these two species, though occurring in the tropics, are mountain forms. Moreover, all the species with the exception of Vermitigris, occur in semi-arid environments or such as have a long, dry period during the year, and where, owing to the occurrence of the larvæ under overhanging cliffs and boulders, the ecological conditions are really desertic. This is true also of Vermitigris in Sumatra and Borneo. Hence we are inclined to assume that both the worm-lions and the ant-lions developed their singular larval behavior during some semi-arid Mesozoic period and that their modern descendants are now precariously occupying circumscribed, sporadic areas in which the climatic and topographical conditions are essentially the same as those to which their remote ancestors had become adapted, millions of years ago.

There are certain peculiarities in the behavior of the ant-lion and worm-lion that require further elucidation. One of these is the retrogression of the former and the dorsigression of the latter. These methods of locomotion are certainly very diverse, but both agree in being quite unlike those of other animals. Their occurrence nevertheless in two unrelated insects with a very similar and highly specialized method of feeding might be taken to indicate a possible correlation with this behavior. The feeding cycle of both insects is a definitely organized configuration of which the exciting capture and overcoming of the prey is the center or goal. Now, in the case of the worm-lion, lying on its back in the funnel is an essential feature of the behavior organization and was, moreover, probably a necessary result of the structural organization of the larva at the time when it acquired the habit of encircling the prey. Indeed, the skeleton and musculature of Arthropods is of such a character as to admit readily of more or less ventral, but of no dorsal flexure of the body. It seems very probable, therefore, that the larva acquired the inverted posture of the body in the pitfall, because this was the only position in which it could quickly and efficiently encircle and overcome its prey. After this singular orientation had become established for this purpose, it was probably retained also during locomotion and gradually supplanted the original ventrigrade habit. I have shown that the very young larva is still ambigrade and therefore retains an evanescent vestige of the former ventrigression common to other Dipteran larvæ and to insects in general.

The retrogression of the ant-lion may, perhaps, be accounted for in a similar manner. It will be recalled that this peculiar form of locomotion is always employed by the insect immediately after it has grasped its prey, as the most expeditious means of smothering it in the sand. This essential and distinctly reflex act, always performed under very exciting circumstances, may then have completely superseded the original progressive mode of locomotion. Both modes, as we have seen, are still retained in some of the lower Myrmeleontids (Palpares, Acanthaclisis) and even in two much closer, pit-making allies of the ant-lion, namely *Myrmocælurus trigrammicus* and the Papuan ant-lion described by Biró. Unfortunately, we have no observations on the mode of locomotion of the just-hatched Myrmeleon. Perhaps it still retains feeble traces of progression comparable with the vestigial ventrigression of the just-hatched worm-lion.

The ant-lion and worm-lion, which we have been so long considering, appear in a new light when we compare their behavior with that of many other organisms that ambush instead of actively seeking their prey. These organisms are sufficiently numerous and remarkable to justify special designation. I shall therefore call them *lochētic* (from λοχητικός, lying in wait, entrapping). In this category we may even include such insectivorous plants as the sundews (Drosera), pitcher-plants (Sarracenia, Nepenthes) and the Venus' fly-trap (Dionæa). Among animals we have an extraordinary diversity of forms, ranging from the sea-anemones, Hydroids, corals, tube-dwelling Annelids, Crinoids and Polyzoa to many reptiles, such as the Anniella described on p. 70 and at least one group of mammals, the cats. The most remarkable examples, however, are found among the Arthropods, many of which exhibit an even more highly differentiated lochetic behavior than the ant-lion and worm-lion. At first sight there would seem to be two kinds of *lochēsis,* one exhibited by forms that merely lie in wait and one in which this behavior is supplemented by the making of a pitfall or snare, but I prefer to use the proposed designation as a blanket term, because the phenomena grade into one another in such a manner that the distinction is rather arbitrary, at least from the point of view which I wish to take in the concluding discussion.

Very simple cases of lochesis are common in certain groups of insects, such as the Mantids among the Orthoptera, the Mantispids among the Neuroptera, Ochthera and some Empidids among the Diptera and the Reduviids among the Heteroptera, all of which merely wait till their prey comes within striking distance and then suddenly seize it with their specially enlarged 'raptorial' fore legs. We may also include among these simple forms, which are sometimes protectively colored or disguise themselves with a covering of detritus, certain spiders (Misumena) that can make their color harmonize with that of the flowers on which they rest and waylay insect visitors. Another type and one more akin to the above-mentioned tubicolous Annelids is represented by the larvæ of our common blackflies (Simulium), which attach themselves by means of their posterior ends to the stones in torrents, stand quietly erect and with a pair of unfurled rake-shaped cephalic appendages collect the passing diatoms and other micro-plancton. Yet another and more specialized type of lochesis is seen in the larval tiger-beetles (Cicindelidæ) which live in cylindrical burrows and lie in wait, with body curved like an interrogation point and head occluding the entrance, ready to seize any small insect that happens to stroll over it. The burrows of all the species in temperate regions and of many of those in the tropics are always made in earth or sand. A number of these species have been described in detail by V. E. Shelford (1908) and others, but there are several genera represented especially in Brazil, by species that establish their burrows in dead twigs, as Zikan (1929) has recently demonstrated in an excellent paper. Shelford found that the larvæ of two of our North American species, *Cicindela lepida* and *generosa* make a pitfall somewhat like that of the ant-lion, but smaller, at the entrance to the burrow, and that the larva of the latter species actually cements the sandgrains of the structure with saliva to prevent its caving in.

More complicated and more interesting forms of lochesis are displayed by a considerable number of spiders, larval gnats (Mycetophilidæ) and caddis-flies (Trichoptera) that make snares of silk or mucus and therefore with substances secreted by their own bodies. The three groups not only form a series of increasing differentiation in the arrangement and use of the snare, but each presents a number of behavior patterns which may in turn be arranged in a similar series. In the following paragraphs the various cases are reviewed in this order of differentiation, with a more detailed description of those that have been least frequently discussed in the entomological literature.

(1) Most of the gnats of the family Mycetophilidæ, as suggested by the name, live in fungi and are vegetarian, but a small number of species have taken to feeding on small flying insects, which they capture by means of strands of mucus secreted by their salivary glands. They therefore lead a less concealed life, but owing to their inability to abandon the pronounced negative phototaxis, or 'photophobia' of their fungus-eating ancestors, seem to be able to survive only in dark places such as caves, cellars or deep ravines. Two of the species are steadily luminous, like larval fire-flies and glow-worms, a peculiarity that might be regarded as a lure, if it really has an adaptive significance. The earliest account of a web-spinning Mycetophilid is by Wahlberg (1849), who observed that the larva of *Ceroplatus sesioides* lives gregariously on the lower surfaces of mushrooms (Polyporus) beneath a glutinous web. The whole body of both larva and pupa is luminous, probably owing to the presence of phosphorescent bacteria in the tissues. Wahlberg says nothing about the capture of insects by means of the web and the case is cited merely as a simple form of behavior from which that of the following species may have evolved.

A more interesting insect is the New Zealand glow-worm (*Bolitophila luminosa*), which emits a beautiful blue-green light from the posterior end of its body and is not uncommon in the deep forested ravines of the North Island. In 1914 I found it abundant on the walls of a long dark tunnel near Auckland and with Dr. F. X. Williams published an account (1915) of its luminous organs, which are formed by the tips of the four Malpighian tubules (another instance of the singular functional plasticity of these organs!), with a reflector consisting of a ventral layer of adipose tissue, probably filled during life with fine vacuoles of fat. Hudson, who had written on this insect in 1886 and 1887, in his final paper (1891) describes its web as "suspended in a rocky or earthy niche in the banks of streams in the densest part of the forest. It consists of a thick glutinous thread stretched across the niche, and supported by several smaller threads running right and left, and attached to the sides and end of the cavity. On this the larva invariably rests, but when disturbed immediately glides along the main thread and retreats into a hole which he has provided at the end of it. From the lower side of this central thread numerous smaller threads hang down, and are always covered with little globules of water, resembling a number of minute silver-beaded necklaces, constituting a conspicuous, though apparently unimportant portion of the insect's web." My observations on the webs in the tunnel confirm this statement. Nevertheless, Hudson did not believe that the larva feeds on insects, but Williams and I, from examination of its stomach contents, were able to prove that it does.

The slender larvæ of another Mycetophilid, *Macrocera fasciata,* were discovered by Enslin (1906) on the walls of a cave in the Franconian Jura and later in a deep cellar where opportunity for observation was much more favorable. They were inhabiting small irregular webs, six centimeters long and three centimeters wide, consisting of mucous threads partly applied to the surface of the walls and partly spanning their crevices. The larva could glide back and forth on a stouter strand which ran through the center of the web. Enslin saw the insect devouring a small moth that happened to become entangled in the glutinous threads. He also demonstrated that these are secreted by the salivary glands of the larva. The pupa is described as suspended and as producing the imago in eight days. Even in its dark, cavernous environment the larva is not protected from enemies since it was found to be attacked by a minute Hymenopterous parasite. Owing probably to the constancy of the temperature and humidity of the environment, the generations of the fly succeed one another without interruption.

Finally, Cook (1913) has described the glutinous webs of an undetermined Mycetophilid larva which he and H. S. Barber observed in several caves in Guatemala. This insect makes a hanging web which is figured and described as resembling "the rope signals that are hung near bridges and railroad tunnels to avoid accidents to train-crews." It consists of single threads suspended from the roof of the cavern, with their tips connected by a horizontal strand, or cable a foot or two in length, from which depends a regular fringe of thicker glutinous threads two to three inches long and one to three millimeters apart. The larva was always found lying along the horizontal cable, along which it was able to glide back and forth with considerable speed. Cook found tangled in the slimy threads several insects such as small gnats and even a small beetle and regarded them as the captured prey of the larva. The web described and figured by Cook appears to be the most differentiated snare of any Mycetophilid larva and therefore represents, so far as known, the final evolutionary stage of a structure which may have had its origin in a simple protective web like that of the European *Ceroplatus sesioides*. The larvæ of *Macrocera fasciata, Bolitophila luminosa* and the unidentified species observed by Cook may be regarded as cavernicolous *lochētes,* which make glutinous snares to capture the rare aërial insect plancton of their dark abodes.

(2) In a very different order of insects, the caddis-flies (Trichoptera), we have a series of forms exhibiting a much higher stage of web-making. The material used is also a secretion of the salivary glands but has greater consistency and is in fact true silk like that employed by the larvæ of moths in making their cocoons. The first to observe the

nets made by caddis-fly larvæ in their aqueous habitat were Fritz Müller (1881), who described the nets of a Brazilian Rhyacophylax, and Miss Cora Clarke (1883), who published on a species of Hydropsyche from the streams of Brookline, near Boston. The nets of the latter insect were also studied by Howard (1886) and McCook (1907), and those of a Chinese species by Miss Adele M. Fielde (1887). In 1911 this early literature was reviewed by Wesenberg-Lund in a monograph containing an excellent illustrated account of the Danish net-making caddis-flies. Our North American caddis-fly larvæ have been more recently studied by Lloyd (1921) and their nets by Miss Noyes (1914).

Students of the Trichoptera recognize two divisions of the order, one having sluggish, caterpillar-like ('eruciform'), vegetarian larvæ that build the well-known cylindrical cases of pebbles, bits of leaf, moss, wood, etc., the other having more active and more slender ('suberuciform' or 'campodeoid'), insectivorous larvæ. It is only certain species of this latter predatory group that make nets. According to Wesenberg-Lund, the web-makers belong to four different families, the Philopotamidæ, the Polycentropodidæ, the Psychomyidæ and the Hydropsychidæ. His figures show much diversity in the structure of the nets. Some of them (Holocentropus, Neureclipsis) are curved, trumpet-shaped objects about four inches long, attached to the leaves and stems of water-plants. The funnel of the trumpet serves to capture the small insects borne by the current while the tubular portion serves as a lair for the larva. Other nets (Plectrocnemia) are flattened webs with a hole in the center leading to a tubular retreat hidden under a stone; still others (Polycentropus) are bag-shaped structures attached to stones or to the bottom. The net of *Plectrocnemia conspersa* was originally described by T. H. Taylor (in Miall 1895) as follows: "Plectrocnemia finds its home in streams where the water flows swiftly over a stony bed. If a stone be lifted out, the underside is often found to be covered with patches of mud from which brown larvæ emerge and begin to crawl over the surface. The muddy particles are evidently held together by some binding substance, and the whole forms the retreat of the Caddis-worms, corresponding to the cases of Phryganea. When a larva is placed in a vessel of clear water, it at once begins to explore its new quarters, and eventually selects a site for its dwelling. This is made of silken threads secreted by the large silk glands, and when completed the structure consists of a tube considerably longer and broader than its occupant, and open at both ends. It is supported and strengthened by a meshwork of silken threads, which spread out for a considerable distance and are attached to the surrounding objects. . . . From time to time the larva turns round in its case, and even leaves it for a short space. Generally, however, it remains quiet inside, apparently on the alert for prey. If a Chironomus or other small aquatic larva approaches, it is almost certain to get entangled in the network of silken threads. At once the Caddis in its retreat perceives the presence of a possible victim. The long hairs which cover the body are possibly tactile, and reveal slight disturbances of the silken network. The Plectrocnemia then proceeds warily to determine the cause of the disturbance. Should the Chironomus be entangled near the middle of the tube, the Caddis-worm does not hesitate to bite its way through the side, and its jaws very soon quiet the struggles of the prey." Miss Noyes has discovered the nets of *Cimarrha aterrima,* one of the Philopotamidæ, near Ithaca, N. Y. They usually occur in series, side by side on the undersides of stones in very rapid streams and have the form of a tubular pocket about 25 mm. long and 3 mm. wide, are open at both ends and made of a very fine web of silken threads. The broad anterior end is free and opens up stream, the posterior opening is very small.

The beautiful net with square meshes and the adjoining structures made by Hydropsychid larvæ are described by Lloyd as follows: "Hydropsychid larvæ dwell only in swift-flowing waters and on the wave-beaten shores of lakes. In these situations they occur in vast numbers. Miss Noyes seems to have found it not uncommon to find as many as 165 larvæ on a square of the stream's bottom measuring 8½ by 8½ inches. The larvæ are most abundant on the exposed surfaces of stones, ledges and even on the brinks of falls. In these situations they build the characteristic nets that are so well-known in the literature of entomology. The nets, typically, have a semicircular opening facing up stream. From this opening the net extends back in bag-like form. The front end is made of fine silk, strengthened by irregular coarse strands. Behind the fine-meshed front margin there is an area of coarser mesh that acts as a sieve. It is made of tough strands running in two directions, forming a mesh of minute squares, through which the water passes while straining out its burden of plancton of small insects. The larva lives in a silken tube at one end of the sieve. From this retreat it can freely enter the trap to feed upon its catch of aquatic organisms." Miss Noyes has described in interesting detail the construction of the Hydropsyche net under laboratory conditions. Wesenberg-Lund gives the following description of the *Hydropsyche angustipennis* dwellings which he often found built side by side in chain formation among duck-weed in the streams of Denmark: "The chains afford numerous dwellings, each consisting of a front compartment, the opening of which heads up stream; the opposite or back-side of the structure ends in a funnel-shaped tube directed towards the stream and is covered with particles of detritus. On one side next to the fore compartment is a round disk spun over with thick silken-threads, crossing each other with wonderful accuracy. Inside the tube the animal sits in wait for its prey, which the stream will conduct into its net." Wesenberg-Lund believes that the net-making habit has arisen independently in several different genera, perhaps from primitive conditions like those exhibited by the Rhyacophilidæ, the larvæ of which make neither cases nor nets, but lead an active predatory life, though they spin a silk thread like the 'drag-line' of the hunting spiders over the substratum.

(3) Since the spiders are lochetic animals *par excellence* it is not surprising that they have reached a much higher level in making webs than any other infrahuman organisms. Certainly there are no more exquisite and beautifully adapted snares than the orb-webs of the Epeirid and Uloborid spiders, in which all the diversified spinning and weaving activities of the Araneæ culminate. The employment of silk is such an ancient and universal institution in this order that several arachnologists have been tempted to speculate on the phylogenetic development of the web. Two of the most recent attempts are those of Savory (1928) and Bristowe (1930). The former traces the web to the simple thread or 'drag-line' which is emitted by the more primitive hunting spiders and which, he believes, gave rise to a nest very much like that of the caddis-fly larva *Plectrocnemia conspersa,* described above. The primitive spider may be assumed to have lived in a burrow or crevice. The drag-lines "laid down when the spider left or returned to its retreat, would run outwards in all directions from the mouth of the crevice; and the next assumption it is necessary to make is that the spider discovered that, as it rested at home, movement of these lines would imply the tripping up of some passer-by, who might be caught and eaten." Webs of this type are still made by certain spiders, for example *Segestria florentina.* From such a stage it is not difficult to pass by selection of types of web that might represent critical phylogenetic stages to the wonderful orb webs of the Epeirids and Uloborids. Bristowe, however, is

inclined to derive the spider's web from the use of silk in protecting the eggs and this in turn, perhaps, from the dragline. He then develops the snare web diphyletically, or along two diverging lines, according as the spider habitually assumed an inverted or an erect posture while guarding its eggs. The former line starts with Linyphiids and culminates in the Epeirids and Uloborids, the latter leads from burrowing Lycosids and terminates on the one hand in the trap-door spiders and on the other in such forms as Segestria and Cœlotes.

But spiders can use their silk also for lassoing and enswathing their prey after it has become more or less entangled among the strands of the web. One of the most beautiful examples of this behavior is seen in *Theridion riparium,* long ago observed by Henking (1886), and especially interesting because it preys largely on rather savage ants. Its web and nest are constructed under bushes a little above the bare ground and consist of a conical case, or retreat, made of earth-particles and food-refuse, with downwardly directed opening and suspended perpendicularly among a number of silken threads which are attached both to the vegetation and to the surface of the soil. Those attached to the soil are very sticky so that when a passing ant happens to touch one of them with a leg or antenna, the appendage is held fast and the struggling insect signals its presence to the spider lurking in its conical den, as if it were ringing a door bell. The spider cautiously descends to within a short distance from the ant and after throwing silk over it from the spinnerets, hoists it up by a thread to the nest. There, after throwing more silk over the captive, the spider warily approaches it, bites one of its appendages and then waits for the venom to take effect before sucking out its juices. As described by Henking, the whole procedure on the part of the feeble and vulnerable Theridion is much more subtle and elaborate than the crude ambushing of ants by the burly ant-lion or cowardly worm-lion.

The preceding review of lochetic animals was introduced not so much for the purpose of adequately exhibiting their diversity, for that would have required much more space, as for the purpose of emphasizing the rôle of the environment in their behavior. The cases presented are sufficient to admit of arrangement in a series like the following: (1) the tiger-beetle larvæ and Lycosid spiders, (2) the flower-spiders, (3) the ant-lion and worm-lion, (4) the net-making forms culminating in the orb-weaving spiders, (5) such forms as the blackfly larva and tube-dwelling Annelid. This series, of course, represents an artificial and selected and not a genetic or phylogenetic sequence. We notice that in (1) the environment is indefinitely conditioned with respect to the lochetic insect, which merely lies in wait at the orifice of its burrow, whereas in (2) a definite environmental object, the flower, or in the case of many protectively colored Mantids, leaves or twigs are used as traps, much as the water-hole is used by the leopard lying in wait for an antelope. In (3) the insect actually makes a portion of the immediate environment over into a pitfall; in (4) the materials employed in making the web or snare are secretions and hence exteriorized portions of the animal's own body, and in (5) the trap (rake of the blackfly larva, fringed tentacles of the Annelid) are actual organs of the lochete, with the function and approximate structure of nets. If the series be read in the opposite direction it illustrates the transfer of functions from the animal organ to some discrete portion or region of the environment, like the transfer of function from the human hand to the tool or machine.

Series analogous to the preceding confront us again and again in the study of insect behavior. They suggest that the interpretation of behavior as a configuration confined to the organism is incomplete without the implication and integration of environmental elements. The spider's silk, employed either as a web or as a lasso, and the pit of the ant-lion are really more than mere tools, without which these organisms are not only unable to secure their food but even unable to eat. In other words, the structures mentioned may be regarded as functionally true organs and therefore essential, internalized components of the organized behavior pattern, or configuration.

The ambushing, or lochetic, animals are also important as excellent examples of convergent evolution, a principle which, to my knowledge, has not been treated monographically since the publication of Willey's work in 1911. The principle has of late been little noticed among zoologists, though it has been much discussed by some ethnologists and archæologists in connection with the independent as opposed to the derivative sources of human cultures and institutions. The zoologist who is continually encountering so many convergent, or parallel developments in animal structures, industries and behavior patterns, like those we have been considering in the ant-lions, worm-lions and various web-spinning Arthropods, is naturally sceptical in regard to the inability of such gifted superorganisms as human societies to develop many of the features of their cultural patterns independently.

APPENDICES

APPENDIX A

REPORT ON THE WORM-LION

Composed and Handed to Her Majesty the Queen
by Carl De Geer
and by Her Majesty most graciously
presented to the Academy of Sciences.[1]

THE insect Formica-Leo, or the ant-lion, thus styled by Herr Pluche in his 'Spectacle de la Nature' and now sufficiently known, is one of the most remarkable insects of its kind that has ever been observed, especially in its cunning strategy of capturing for food other insects such as flies, ants, etc. Herr Réaumur has given its history in the sixth volume of his 'Mémoires pour Servir à l'Histoire des Insectes.'

Recently some worms were discovered in France, which though differing from the ant-lion in form, are nevertheless very similar in their mode of life and in the cunning they display in securing their food. They conceal themselves in the sand and make a pit in it like a funnel, on the floor of

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[1] Rön om Mask-Lyonet. Kongl. Svensk. Vetenskaps Acad. Handl. 13, 1752, pp. 180-192, 261-265, Pl. V. This Swedish article was republished by Degeer in French, with some additions and omissions and in a more fluent style in the sixth volume (1776) of his 'Mémoires pour Servir à l'Histoire des Insectes.' I have selected the original article for translation because it is so little known.

which they lie and wait till an insect comes and falls in. Last spring Herr Réaumur, who calls them *worm-lions,* sent some of them by post to Her Majesty in a small box filled with sand. Of the seven or eight worms which it contained, only one was still alive when the box was received; the others had died and were dried up. As soon as the worm arrived on the 8th of April, Her Majesty graciously condescended to present it to me with the command to describe it and observe its mode of life.

How inspiring it is to a lover of natural history to behold a great Queen not only delighting in the wonders of Nature but actually acquainting herself with the profoundest secrets of the sciences. It is easy to imagine, therefore, with what joy and diligence I set about observing this curiosity, especially since it seems not to be found in Sweden, because Herr Réaumur in his letter to the Queen asserts that it does not occur even in the neighborhood of Paris but only in the southern parts of France.

When I received the worm (Pl. V, Figs. 1, 2) from Her Majesty's gracious hands, it was enclosed in a small four-cornered box, Fig. 7, *abcdef,*[1] half filled with sand. During that very night it made a pit *gg, hh,* for itself and therefore seemed to indicate that it was hungry. Indeed, it was easy to believe that after a fast of some weeks it should demand food. As I had no insect to give it, I waited till the following morning, the 9th of April, when I obtained a small fly and presented it its first game. I thrust it into the small pit in which the worm was lying in wait, with half its body concealed under the sand, and the other half *m,* that is, the anterior half, projecting above the surface. It seized the fly at once, or rather threw itself upon it and like a little snake encircled its body. The fly was suddenly prevented from escaping and I saw that it was held fast by a sharp prong which the worm bore at the tip of its

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[1] Figure numbers in Appendix A refer to the small figures of Figure 48.

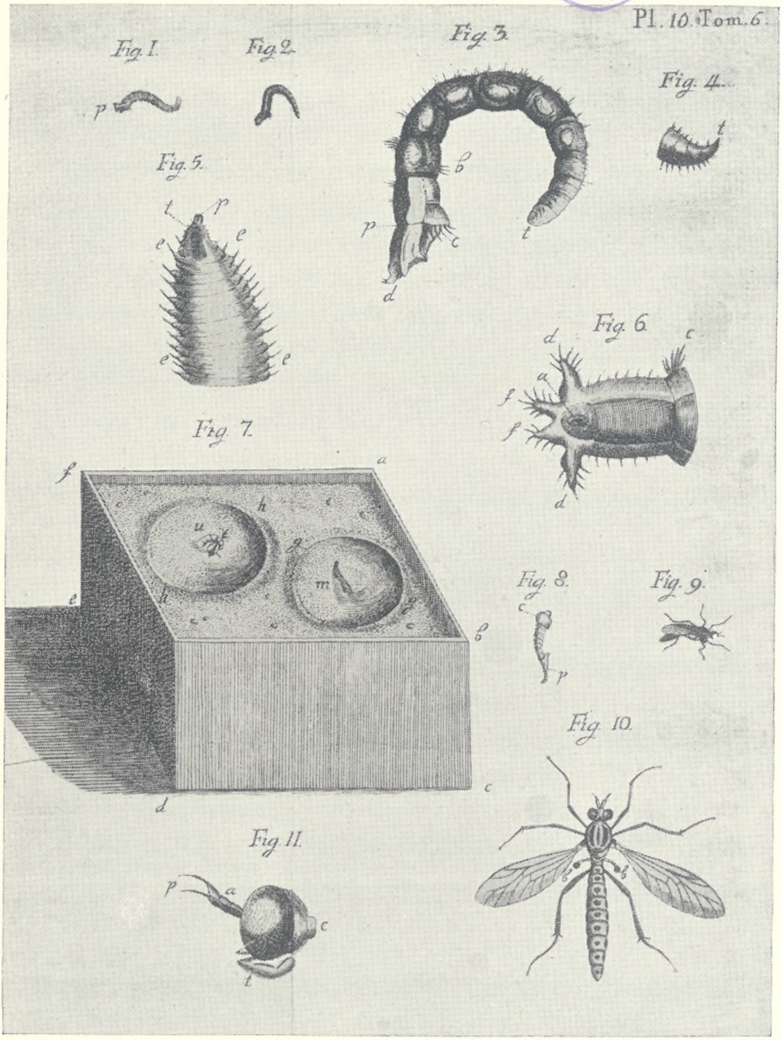

FIG. 48. Plate from Degeer's article on the Mediterranean worm-lion.

head and had fastened into its victim. Then it buried itself completely in the sand and drew the fly after it. In this situation it remained quiet for a long time and sucked at the fly, which soon died. From time to time, it stirred suddenly as if it were shaking itself. It thus passed the greater part of the day sucking at the fly, but towards evening I found that it had deserted its prey and had tossed it to a considerable distance beyond the margin of the pit. About 11 o'clock at night I noticed that it had repaired the pit, which, owing to its efforts to hold the fly fast and to suck out its contents, had become somewhat disarranged. The structure again had the form of a funnel as in the beginning.

On the morning of the tenth the worm was lying perfectly motionless on the floor of the funnel, with its hind part buried in the sand and its fore part stretched out over the floor and next to the wall of the pit. I observed, however, that it did not lie with this part exposed but gently moved it about in the sand and thus covered it with a thin layer of sand grains so that it was scarcely visible. Perhaps this is a bit of strategy to conceal itself from the insects it desires to capture? I am the more inclined to believe this, because on another occasion I found that it may readily remain completely exposed after it has secured its prey and is busy imbibing its juices.

When I saw it in this position I threw it a small black Tipula. It aroused itself instantly, threw itself on the prey, attached its mouth to the gnat's abdomen and held it so firmly that it remained motionless till it was sucked out. The gnat struggled, indeed, for a short time to free itself, but in vain, and was soon dead. At noon the worm deserted the fly, apparently only after it had sucked all the juices out of its body. Then I saw its method of ejecting the fly from the pit. It thrust its head somewhat under the sand beneath which the dead gnat was lying, lifted it quickly and vigorously and then threw the cadaver over the margin of the pit to a distance of two inches. On this occasion the worm's body acted like a compressed spring fixed at one end and at the other attached to some object. When such a spring is free to act, it will, according to its greater or lesser elasticity, throw the encumbrance to a greater or lesser distance. In precisely the same manner the worm also ejects the sand from its pit when it desires to clean or deepen it. It thrusts its head and the fore part of its body into the sand and then raises it suddenly, so that the sand is scattered through the air and falls on all sides like rain. And since the worm, while making these movements, describes as it were a semicircle with the fore part of its body, the sand is scattered about over the walls and whole circumference of the pit.

Later I gave the worm a large fly (one of our common house-flies) after tearing off its wings and four of its legs so that it might not be too vigorous for the worm and thus escape. But the worm seemed to fear this animal, which was rather large compared with its own bulk. It crept into the sand and refrained from reappearing as long as the fly remained in the pit. This, of course, was no evidence of the heroism implied by its name.[1]

As the movements of the fly had disturbed the pit, I extracted the worm from the sand for the purpose of drawing and describing it.

I then observed a rather extraordinary fact. As long as the worm is lying in its pit, it is very much alive. No matter how gently the box or the sand surrounding the pit

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[1] In the German translation of this article A. G. Kästner (1775) inserts the following footnote: "The so-called ant-lion is just as little deserving of its name, so far as courage is concerned. Moreover, the creature described by Herr De Geer is not called the 'worm-lion' for the same reason as the ant-lion is so called. The latter name is supposed to designate an animal as dangerous to ants as is the lion to higher animals; the former is supposed to apply to a worm that behaves like a lion. It would be more appropriate if the inventors of names observed the laws of language, even in natural history, as a special form of graphic illustration. Kästner."

be disturbed, it darts down into the sand with lightning rapidity. Its other movements, as, for example, when it digs up the sand, are also performed with great vehemence, but when it is withdrawn from its habitat and lies exposed, it becomes motionless and allows itself to be handled without exhibiting the slightest movement, as if it were dead. It remains in this condition for some time, till it perceives that all is quiet, when it again begins to move, searching with its head on all sides for sand in which to conceal itself. Sand is its element, just as water is the fish's element; when it gets out of it, it is ill at ease and unable to continue the movements essential to its existence.

I again placed it on the sand, where it lay motionless for some time but then began to creep into it head foremost. This penetration requires some labor and the task is accomplished with some slight effort. Its head is the instrument with which it opens its path. I have noticed that it does not descend deeply but stays only a short distance beneath the surface. After it has first pushed its head down perpendicularly it progresses horizontally under the sand and continues in this direction parallel with the surface. This can be easily observed, because the sand where the worm is advancing moves and is somewhat elevated over its body, but subsides on either side after the worm has passed on, so that the path it pursues beneath the sand is clearly visible from above. After it had moved about an inch, it stood still and lay as if in deep sleep for the half hour it was under observation.

Three hours later, at about 11 o'clock in the morning, when I again visited the worm, it was still motionless and had not yet made its pit. It may have had to rest because it had been disturbed so much and for so long a time while I was drawing it. By the following day it had already made a shallow pit and was lying in it with half its body exposed, according to its wont when waiting for prey. In the afternoon it abandoned this pit and made another a short distance away. Before proceeding I shall describe the insect itself.

The worm, FIGS. 1 and 2, is half an inch long and very slender. Its body is cylindrical but its fore part is narrower than the hinder. At first sight it resembles a small caterpillar of the kind known as a measuring worm (*chenille arpenteuse*). The shape of the body is very similar, and when extracted from the sand it also possesses a rigidity like that of the so-called *"chenilles arpenteuses en bâton"*, for it then commonly maintains a stiff and immobile posture. But on other occasions it is quite able to bend itself in all sorts of ways, sometimes in the form of a semicircle or of some other curve, sometimes like an *S*, (FIG. 1) and not infrequently with the fore part of the body almost like a more or less incomplete ring (FIG. 3). It resembles the caterpillars above mentioned even in these curved and varied postures of its body.

But when observed under a magnifying glass (FIG. 3) it is seen to be in other respects very unlike the caterpillars. It possesses no feet, nor does it need them, because it lives only in the sand. It creeps about in the sand like other earthworms and performs all its movements merely by the contraction and expansion of the segments of which its body consists. Its color is gray or grayish, with a slight yellowish or whitish tinge. This color rather closely approaches that of the sand itself, and the worm has presumably acquired the same hue for better concealment of itself from the eyes of the insects on which it preys. After it has fed well on the juices of some insect, the imbibed liquid is visible through its transparent skin and the worm then appears black.

The body, as in the caterpillars, is divided into segments. I have counted eleven, but the foremost of them are not so clearly distinguishable as the hinder, so that I am not perfectly certain that there may not be more than eleven. The head is conical, pointed at the tip (FIG. 4 *t* and 5 *t.p.*) and not unlike the head of the common flesh maggots that transform into blue flies. It seems also to vary in form as in these same flesh maggots, which are not covered with a hard cartilaginous or bony skin, that would render their form stable and unchangeable as in various other insects, but soft, so that the worm can expand and contract its head. At the tip of the head a prick or sting is visible, which is shelly or bony [chitinous] of a brown color and sometimes, it seemed to me, cleft (FIG. 5 *p.*). This is the instrument with which it seizes, holds and pierces the captured insects and is also to all appearances the tube with which it sucks. At any rate, the mouth cannot be situated very far from it. The tip of the head in the worms that devour plant-lice and become two-winged flies [Syrphidæ] is very similar in shape to the tip of the wormlion's head.

In order, however, to investigate this head adequately more worms would be needed, since it would have to be compressed for the purpose of extruding its parts. I was unable to do this with my specimen because I was desirous of keeping it alive in order to witness its transformation. When resting it withdraws its head into the first segment so that none of it is to be seen, and then the fore end of the body is rounded (FIG. 3 *t*). I have seen it using its head in locomotion beneath the sand; at such times the head serves as a foot and acts as a support on which it rests and with which it fixes itself in the sand when it desires to contract its segments. The plant-louse-devouring maggots just mentioned use their heads in the same manner.

I have said that the worm's fore part is more slender than the hinder. The thickness of the body increases gradually and rather uniformly from head to tail. Besides the constrictions separating the segments, it has a number of wrinkles across the body, especially on the fore part. These hindered me from distinguishing the segments. On each side and along the whole body there is a raised border, not everywhere of the same width, but broader in the middle of each segment than elsewhere. The last segment (FIG. 1, *p* and FIG. 3 *p.d.*) is longer than the others and somewhat flattened. Its natural position in relation to the other parts of the body is erect and somewhat curved, forming an obtuse angle with the preceding segment. It also forms a projecting hook on the worm and may perhaps enable it to retain its hold in the sand. The same purpose is perhaps served by a row of hard, stiff tines, like scales or rather long hooks (FIGS. 3 and 4), bent forward towards the head and inserted between the tenth and eleventh segments, on a ridge across the belly of the worm and half way up the sides. On the underside of the ninth segment there are also a few hooks (FIG. 3 *b*) like the preceding, but shorter and less numerous. Besides these hooks the worm has in various situations stiff hairs that form tufts here and there, but these are most numerous on both sides of the first five segments (FIG. 5). Each of these hairs arises from a small, elongate, conical outgrowth. They resemble tubercles or claws (FIG. 5 *eeee*) and cause the forepart of the head to appear toothed and uneven on the sides. They are invisible, except when the worm is viewed from the back or belly, for when it lies on its side (FIG. 3), they are not to be seen.

The last segment ends in four rather long conical, fleshy processes (FIG. 6) not unlike horns. The median pair *f.f.* lie in a straight line with the body itself, but the lateral pair are at right angles to its length. The former are somewhat smaller than the latter. All of them are covered with stiff, stout hairs. I have not observed that the worm can move these processes and it is difficult to say to what use they may be put. They seemed to me to be bent somewhat upward. Do they not, perhaps, aid the worm in keeping its hind end fast in the sand? I am inclined to believe that this is their function.

Above, on the last segment, nearest the middle and between the lateral processes there is a small elongate organ, lying lengthwise against the body and resembling an orifice or slit (FIG. 6*a*). Perhaps this is the exit for the natural excrement and lies above at the anal end. I have sought this organ below on the belly but have there found nothing like an orifice. Herr Réaumur has already found the anal opening on the dorsal side in the lily worms (*vers de lis*), which cover their bodies with their own excrement and transform into red beetles. Had I dared to compress this worm I should have been able, perhaps, to make some discovery in this regard, but the question now remains unanswered. At times I believed that the opening resembled a spiracle, or breathing pore, such as one finds on the sides of the caterpillars that produce butterflies, but it seems to me more probable that it is the anal opening.

I continued daily to feed the worm flies. Sometimes it seized them instantly, at others it seemed not to care for them, and if it failed to secure the fly with the first grasp, it at once hid itself in the sand as if frightened and did not reappear as long as the fly remained in the pit. It is unable to hold the insects that have fallen into the pit, save by coiling round them and, while doing this, piercing them with the prongs on its head, but as this often takes some time, the insects frequently manage to free themselves from its clutches and escape. It is not, therefore, as good a hunter as the ant-lion, which instantly seizes its prey with its two huge moveable horns [mandibles], so that it is never able to escape. Our worm, on the contrary, is often unsuccessful. Had Nature not taught it to capture insects by subterfuge, it would have to die of starvation, precisely like the ant-lion, for I have observed that it is quite unable to move about except in the sand. We know that the ant-lion can only walk backward and is unable to take a single forward step, and it also lives, like our worm-lion, on captured prey. Can we contemplate, without the deepest admiration of the Creator's wisdom, the manifold ways in which these creatures nourish themselves? Could we have believed that an animal, scarcely capable of walking and then only backward, would nevertheless be able to capture insects and devour living prey? We learn this and an infinite number of other wonders from the study of insects. Can we say, therefore, that they deserve no attention? It seems to me that the man who fails to find delight in contemplating such marvels, must be utterly devoid of feeling.

I have not yet witnessed the behavior of the worm when it is beginning to make a fresh pit, but from the manner already described, whereby it deepens and widens one already made, we can easily imagine that the whole excavation is carried out by similar movements. I have described how it tosses the sand out of the pit, which thus becomes deeper and deeper. After it has made a few tosses, it goes round the walls and presses its body against them, thereby smoothing out their whole circumference. The sand thus detached is eventually tossed out. Thus the pit keeps increasing in depth and its orifice continually widens.

The remainder of this report will be printed in the Handlingar during the next quarter.[1]

Further Observations on the Sand-worm, or Worm-lion.[2]

Since this worm seemed to have nothing more of particular interest to show me, I awaited the period of its transformation with impatience, but this was not to occur

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[1] The concluding portion of the article is here inserted before the description of the plate. W. M. W.

[2] See the foregoing number of the Acad. Handl. for July, August, September, beginning at p. 180 *et seq.*

for some time. I had to feed it during the whole month of May and the first half of June, but during the middle of the latter month I noticed that it had remained inactive for two days. I did not fail to examine it and to take it out of the sand. I found that it had changed color and had become somewhat reddish and transparent. Previously, what it had devoured showed through its skin as a black mass, but all this had now disappeared. The worm had evacuated it and was now of a uniform color. I at once inferred that it was probably about to transform and was not deceived, for on the fifteenth of June it assumed the pupal form (Pl. 5, FIG. 8). It had laid aside its larval skin, but not altogether. The skin (*p.*) was attached to and still covered a portion of the posterior end, but it was wrinkled and contracted. The worm had made no preparation for this change, that is to say, it had made no envelope or covering for itself, but lay naked in the midst of the sand. Since the pupa was everywhere covered with sandgrains, which adhered firmly to its surface, it was impossible for me to distinguish all its component parts, for I did not wish to remove the sand, for fear of injuring the animal. I did not therefore make an enlarged drawing of the pupa, since I could have figured nothing but a mass of sandgrains. Yet the head, thorax and abdomen were distinguishable. The head is small and roundish, the thorax (*c*) which also has a rounded form, is stout and hunchbacked; the abdomen, however, is long and extended. The sand also prevented me from ascertaining its true color, but it seemed to me to resemble the former hue of the worm, though the head and thorax are darker. I laid the pupa gently on the sand and permitted it to complete its transformation.

Fourteen days later, or on the twenty-ninth of the same month, the insect abandoned its pupal envelope and revealed itself as a fly (FIGS. 9 and 10), with two wings and a long cylindrical body like that of the crane-flies, which the Swedes call *harkrank*.[1] The pupa skin ruptures over the head and thorax and permits the animal to escape.

At first sight this fly might be mistaken for such a crane-fly. It closely resembles certain of them in the appearance and form of its body, which is cylindrical and elongate, as also in having the thorax rather stout and convex so that the animal appears to be hunchbacked. This, as is well-known, is the typical form of the true flies which possess two wings, and are called by the Latin name *Musca* in Herr Linnaeus' system, because the mouth is snout-like, with fleshy lips.

The length of this fly is about four and a half lines. The two wings are nearly as long as the abdomen, and when it is resting (FIG. 9) are held parallel over the abdomen so that one of them covers the other. The sides of the thorax and abdomen are pale yellow, but the upper portions of these regions are deep yellow, like ochre. On the uppermost portion of the thorax there is a pair of shining, black stripes running lengthwise (FIG. 10) and on each side there is a similar spot, also shining and apparently shelly [chitinous]. Along the abdomen there is a row of black spots, one to each segment and on each side two rows of elongated spots of the same color. The ventral surface of the abdomen is dark yellow. It should be noted that the abdomen is covered above and below with shelly [chitinous] plates held together by membranes and forming the segments. The sides, however, are membranous and only in these regions do we see contracting and expanding movements which seem to be respiratory. The head seems to be covered almost entirely by the two lozenge-shaped eyes, which are very large and of a brown color shading into dark green, the color varying according to the position

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[1] "In Linnaeus Faun. Suec. the *Tipula alis exalbidis maculis albis sparsis obsoletis*, 1125, is called in Swedish *harkrank*, but apparently Herr De Geer gives this name to all crane-flies. (Kästner.)"

from which it is viewed. The space between the eyes is gray; above it there are three smooth black eyes [ocelli]. The snout [proboscis] is pale yellow and the antennæ are partly yellow and partly brown. The first two pairs of feet are yellow, but the hind feet are brown and much stouter and longer than the others. The wings are transparent and slightly suffused with brown; they are somewhat iridescent.

The antennæ (FIG. 11 *a*) of this fly are short and constructed like those of various two-winged flies of the kind called by Herr Réaumur 'shovel-feelers' (*antennes à palettes*). They consist of three articulated particles, of which the one at the end of the antennæ is not unlike the two others but bears at its tip a long, somewhat curved hair [arista] (*p*). These antennæ are somewhat like those depicted by Herr Réaumur on PLATE 9, FIG. 18, in the fourth volume of his 'Mémoires' as belonging to the fly represented on PLATE 10, FIGS. 5 and 6. I find considerable resemblance both in form and color pattern between this fly and the present one.[1] Furthermore, the antennæ are yellow and the hairs [aristæ] at their tips dark brown.

The snout (FIG. 11 *t*) has fleshy lips like those of the fly just mentioned, or nearly as in the common flies found in apartments. It is rather stout and somewhat roughened beneath. The legs are rather long, especially the hind pair, and like those of the crane flies in having their connections [coxæ] with the thorax rather long and conical. These connections greatly increase the height of the thorax and cause it to appear very stout from above downward. The neck, which unites the head with the thorax is very thin (*c*). The two balancers [halteres] (FIG. 10 *bb*) are rather long and stout, and brown in color. The abdomen is not as bulky at the base as behind, and its tip is rounded. I have noticed that the fly generally carries its abdomen bent like a bow.

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[1] The fly figured by Réaumur is a species of Rhagio and therefore closely related to Vermileo. W. M. W.

It is very agile and flies very lightly. When completely at rest, it holds its wings away from the body as shown in FIG. 10.

Explanation of Plate V (FIG. 48)

FIGURES 1 and 2 represent the worm of the natural size and with its body in two different postures. In FIG. 1 it is curved like an S, *p* being its hind part. In FIG. 2 it forms a semicircle.

FIG. 3 shows the worm on its side as seen through the microscope; *t,* the head, which is invisible and withdrawn into the first segment; *p.d.* the last segment of the hind part; *c.b.* the chitinous prongs constructed like hooks.

FIG. 4. The foremost portions of the body seen from above; *t,* the pointed head.

FIG. 5. The head and some of the forepart seen from above under the microscope, but more highly magnified; *t.p.,* the head, which seems to be cleft at the tip, *p; eeee,* the tooth-like processes along the sides of the body.

FIG. 6. The hind part seen under the same magnifying glass as FIG. 5; *a,* the opening which I regard as the anus; *d.d. f.f.* the four fleshy outgrowths in which the body terminates; *c,* the stiff hairs on the hooks also indicated at *c* in FIG. 3.

FIG. 7. *abcdef* represents a small four-cornered box, filled with sand and serving the worm-lion as a habitation; *gghh,* the funnel-shaped pit which it makes in the sand; *m,* the worm in the extended posture which it assumes in the pit while lying in wait for its prey; *u,* its posture after seizing an insect and while enveloping and piercing it with the hooks on its head.

FIG. 8. Shows the pupa of the sand-worm from the side (*c*). The thorax, *p,* which is stout and hunched; *r,* the worm's shrivelled skin, which is firmly attached to and partly envelops its hind end.

Fig. 9. Is the fly after escaping from the pupa. It is resting and holding its wings parallel over its body.

Fig. 10. Shows the fly more enlarged and from above, holding its wings off from its body. It is yellow, with black spots; *bb*, the two balancers.

In Fig. 11 the head of the fly is shown more enlarged and from the side, in order that the large proboscis with its fleshy lips at *t* may be seen; *a*, the antennæ, which end in a hair *p*; *c*, the neck which was attached to the thorax. It will be seen that the large lozenge-shaped eyes occupy nearly the whole surface of the head.

APPENDIX B

THE HISTORY OF THE WORM-LION FLY

By R. A. F. de Réaumur[1]

THE ANT-LION, unknown for so many centuries and not even mentioned by the ancients, at least, is today one of the most famous of insects; one, indeed, always cited by those who wish to produce examples of the singular activities in which small animals show themselves worthy of our attention. Writers always expatiate on the art with which it forms in the sand, or in fine, mobile soil the funnel at the bottom of which it lurks in ambush to seize any insects imprudent enough to fall into the trap and then sucks out their juices. It is not, however, the only insect that knows how to employ such strategy and is compelled to resort to it to avoid dying of hunger. There is one differing greatly in shape from the ant-lion which likewise hollows out a pit in the sand or in friable earth and lurks at the bottom for the same purpose. It is a worm, belonging to that legless class that eventually transform themselves into flies with only two wings, whereas the ant-lion is furnished with six legs and transforms itself into a fly with four wings. This worm is rarer than the ant-lion, at least in the Kingdom of France and, unlike the latter, has had no historians

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[1] Histoire du ver lion mouche. Mém. Acad. Sc. Paris, 1753, pp. 402-419, 1 pl.

to recount in sufficient detail the round of its vital activities. It was mentioned for the first time in the "History of the Academy" for 1706, page 8, but what is there set forth is not very accurate and makes it desirable that a more circumstantial account should be written, together with an engraved figure of the worm and the fly into which it transforms. It has been called the ant-fox (*formica-vulpes*) to distinguish it from the ant-lion (*formica-leo*), but the latter is no less foxy in its strategy than the former, which is no less a lion in strength and voracity than is the ant-lion. I prefer therefore to call the new insect the *worm-lion*. This name accurately describes it in its first stage and its redoubtable attitude towards other insects.

Two years ago I secured for the worm-lion a historian who would have made my efforts superfluous had he not recorded his observations in a language less widely used than French. A single one of these worms, which Monsieur De Geer had in his possession for several months, but was obliged to be more careful with than he might have wished, enabled him to witness its more remarkable activities. Perhaps he would have detected particulars that have escaped me, had he, like myself, possessed a large number of specimens so that he could have observed them and experimented with them at all seasons of the year.

Although the ant-lions have often reminded me of these worms, which are likewise carnivorous, attack the same prey and in order to secure it resort to the same cunning, I sought for them in vain in the environs of Paris and elsewhere, in places where it seemed to me they would be inclined to establish themselves. I abandoned all hope of observing them till I received a letter on February 11th, 1751, from Monsieur Rebory, then curate of the Palud, in the diocese of Riez, in Provence. During his walks he bestows his attention on meritorious objects and delights in sharing with me his interest in those that are most singular.

In the letter I have mentioned, there was a question that interested me. He asked whether *I was acquainted with a little white worm, always bent on itself, which digs a pit like that of the ant-lion, lies in ambush in it and throws dust into the air for the purpose of making its prey fall into the hole.* I had no doubt that this was the worm I had for so many years longed to see. The great number of other insects which I have successfully sent on long travels in a living condition, gave me ground to hope that several worms of this species might be sent without injury from Provence to Paris if due precautions were observed. Knowing M. Rebory's desire to please me I was sure that he would make such arrangements as I might suggest in order to insure the arrival of the worms in good condition. I begged him to fill a small box with powdered earth or with the fine sand in which they were living, to place in this pulverized earth a goodly number of the worm-lions and to send me the box by post. Of a dozen or more which the box contained only three or four were alive on their arrival. Though sufficient to satisfy my desire to see them, I felt that I needed a greater supply for a study of their activities and an investigation of their whole life-history. The box in which they came, had opened on the way; a part of the sand had fallen out and the worm-lions had been subjected to a shaking that had proved fatal to most of them and might have been avoided, had the box remained full of sand.

As Monsieur Rebory had informed me that these worms were not uncommon in his parish, I begged him to send me a fresh and more abundant supply and to take the necessary and easy precautions to prevent the sand from escaping from the box while on the way. He readily complied with my request, so that three or four additional packages, each of which contained at least fifty specimens, reached me in excellent condition and without more than three or four having perished during the journey.

These worm-lions have another peculiarity which they share with the ant-lion and which makes it easy to send them very long distances without injury. They are able to endure the severest and most prolonged fasts; they can spend weeks or even several months without taking food and without dying of hunger. It is a general rule that predaceous animals have to be able to endure long deprivations of food.

I have since learned by experience that worm-lions can endure much longer voyages, even by post, than that from Provence to Paris. There is every reason to suppose that they are not found in northern regions, or, at any rate, they are unknown there, since Monsieur Linnaeus makes no mention of them in his "System of Nature." In Sweden reigns a Queen whose most agreeable relaxation is the observation and admiration of the works of Nature. Her taste has led her to assemble all kinds of such objects in cabinets which she herself arranges and to which she resorts for study in such moments as she can spare from the arduous occupations of state. The worm-lions seemed to me worthy to engage the attention of one, who, I was sure, would not despise them on account of their insignificant dimensions, and of one who beholds in the minutest of animated beings the limitless power and supreme intelligence of the Creator of the Universe. I was therefore emboldened to send twelve of the worms to this enlightened Queen. Owing to circumstances which might have been avoided, only a single specimen reached the palace in Stockholm alive. It was graciously welcomed by the Sovereign who turned it over to Monsieur De Geer to care for and observe. For either purpose it could not have been entrusted to a more competent person. Obeying these enlightened instructions he was able to publish in the mémoirs of the Swedish Academy, his curious observations on that single worm.

The specimens mentioned in the "History of the

Academy" in 1706 were observed in the environs of Lyons, but the Lyonnais and the Provence are not the only provinces of the Kingdom where they flourish and where they are at present known to occur, for they have also been found in Auvergne. Monsieur Ozy, apothecary at Clermont, posted some, taken in the environs of the latter town, to Monsieur de Malesherbes, first president of the Cours des Aides, who courteously forwarded them to me on the day of their arrival. They were all, or nearly all, in very good condition. During the very first night they were under my roof some of them made funnels and the remainder had excavated theirs by the evening of the following day.

The worm-lions inhabit localities similar to and often the very same as those inhabited by the ant-lions. Though the latter have no dealings with the former, both are very often found together. Both have the same purpose in life — to make funnels in the loose sand or in powdery earth, and both appear to know that the funnels thus excavated will, if not sheltered, be exposed to destruction by the rain, and that if the rain, falling into their funnels, does not destroy their form, it will at any rate impair the mobility of their component earth particles. The water, by compacting these particles would rob the funnel walls of their tendency to crumble and thus afford a solid support for the insects attempting to escape from the trap into which they have fallen. The worm-lions and ant-lions therefore establish themselves at the foundations of old walls or at the base of certain rocks where they have overhanging or almost horizontal projections. Such spots afford a kind of extensive shelter which protects the sand or loose earth from the rain. The ant-lion pits commonly occupy the first situations, that is, the outer portions of these little caves, whereas the pits of the worm-lions are in the recesses. The conical burrows of the worm-lions are distinguished by having a greater depth than those of the ant-lion, with the same diameter. The apertures of the largest worm-lion pits, however, scarcely attain the diameter of those made by half-grown ant-lions.

Though so much like the ant-lion in its wiles and proclivities the worm-lion nevertheless has a very different structure. The former has six legs, a short, slightly flattened body, and a head of invariable form, which bears two horns, [mandibles] the perforated tips of which take the place of the mouth. The worm-lion has absolutely no legs (FIGS. 4, 5, 7 and 8); its body is long in proportion to its width and terminates in a head (FIGS. 1 to 5 *a*) of the type which I have designated elsewhere as of variable form. It is fleshy, so that it can be stretched out and contracted by the insect, thus becoming thicker or more attenuated, though it is always more slender than the remainder of the body. From its anterior end, which may be regarded as the mouth, the worm-lion can extrude, when thus inclined, the tips of two chitinous darts(FIGS. 5 and 8*a*), placed parallel to each other like those of the worms that feed on plant-lice [Syrphidæ]. Each of the darts has a chitinous sheath and the brown color and volume of the two sheaths render them visible if they be sought for in the skin which the insect sloughs when it transforms into the nymph, or during preceding moults. The sheaths are rounded and oblong, and are broader at their posterior than at their anterior end.

The worm's body is of a dirty white color, sometimes with a reddish tinge. Its substance is sufficiently transparent to reveal a brown matter filling the interior of the posterior portion. It is rarely found extended in a straight line in such a way that its length can be measured, for it does not assume this posture (FIG. 5), when removed from the sand, till after it has rested for some time on a body which it is unable to penetrate, such as a sheet of paper or a book. Hence this posture is one of constraint for the insect, for it is assumed only under compulsion. If the largest individuals

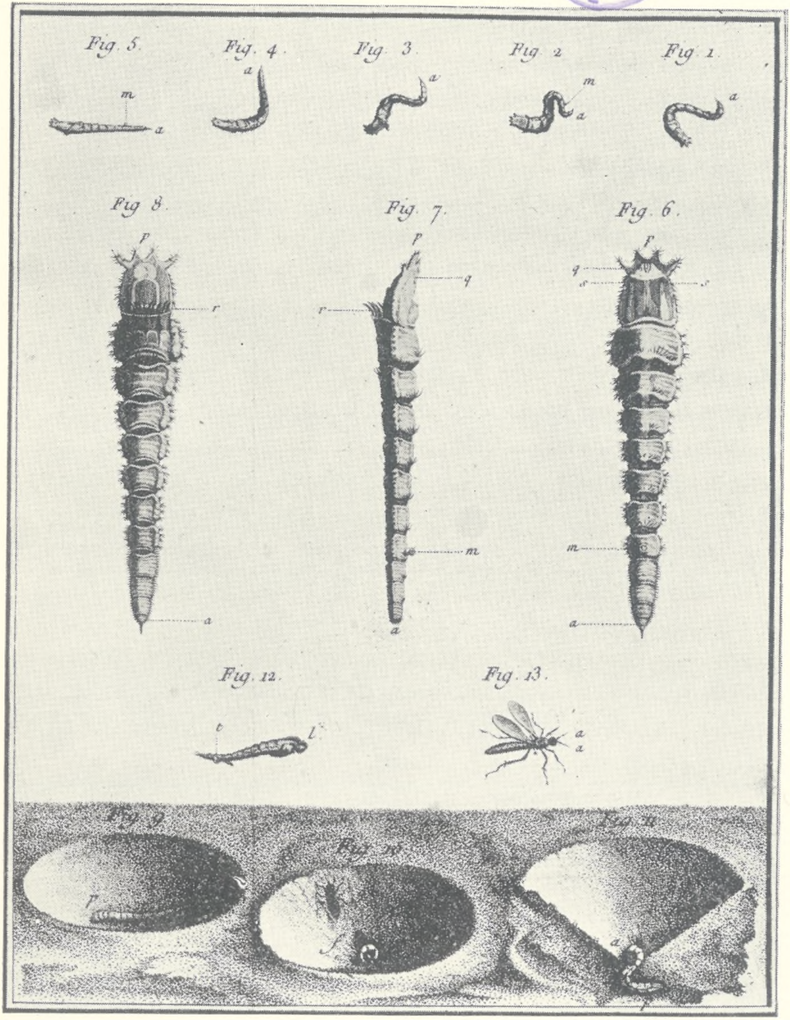

FIG. 49. Plate from Réaumur's article on the Mediterranean worm-lion.

are then measured, they will be found to be at most eight to nine lines long. Their posterior portion (FIGS. 6 to 8 *p.*), comprising at least one third of their length, is the region in which they are thickest; their segments lying nearer to the head gradually diminish in diameter, the head being the slenderest portion and terminating almost in a point.

Immediately after removal from the bottom of its funnel, the worm usually assumes the form of the letter S (FIGS. 1, 2 and 3), the head terminating the upper end (*a*), the abdomen corresponding to the greater convexity of the letter; but different individuals of the species when taken from their burrows, or the same worm unearthed at different times, give their bodies different S-shaped flexures. Sometimes they merely fold the body in such a manner as to form two limbs parallel with each, sometimes they bend it at a right angle. While lying undisturbed in their funnels, their anterior portion is exposed (FIG. 9) and stretched out in a straight line, forming with the more posterior portion an angle with a dorsal concavity. This angle is not always the same, but is sometimes obtuse, sometimes a right angle and rarely acute. When we come to observe it in the act of overpowering some insect that has fallen into its pit we shall see why the worm-lion is always compelled to keep its body folded in this fashion.

The last segment constitutes the thickest part of the body. It is slightly depressed dorsally, obliquely truncated and terminates in four conical but flattened lobes, each of which bears at its tip a stiff hair or kind of spinule. This portion of the body resembles an open hand with only four fingers and with these more spreading than in the human hand. The preceding segment has its posterior circumference above bristling with eight to ten small red hooks, which stand out at an angle with the body and have their concavity turned towards the head.

On the upper surface of the last segment and towards the middle of its length, the lens reveals two red dots (FIG. 6.*s.s.*) which one is inclined to regard as the two principal spiracles, serving for respiration, for these dots are situated like the spiracles of the majority of worms that transform into two-winged flies. There will be no hesitation in ascribing the same function to the two red dots, for when the attempt is made to ascertain in the interior of the body whatever may be revealed by the transparency of its substance, two white tubes are seen, each terminating in one of the yellowish dots. We can only regard these tubes as the tracheæ.

The slit-shaped anus, more easily seen than the two stigmata just mentioned, is on the middle of the same segment and nearer the end of the body, with the long axis of which it is parallel (FIG. 5*q*). It is oblong and appears to have a raised border. The position of the anus on the dorsal surface is a peculiarity of which we have already given an example in the history of that filthy worm, which is always covered with its excrement, but which eventually becomes the beautiful scarabæus of the lily.

If the crawling of the worm-lion had not been observed the position of the anus might suggest a doubt as to whether the side which we take to be the back of the insect, may not be the belly instead, for when the side on which the anus is situated is below, the worm tries to reverse its position and only after having succeeded, does it proceed at ease. The ventral is a little more flattened than the dorsal surface.

Although to the unaided vision the worm seems to have no hairs, examination with a strong lens shows that it is amply provided with these structures. Its segments are bordered on each side, some with more, some with fewer hairs. At its base each hair is borne on the tip of a triangular tubercle. Some of these hairs are much longer and stouter than others. On the ventral side at the end of the penultimate segment there is a series of them so coarse and stiff as to resemble spines (FIG. 8.*r*).

On the dorsal surface of the fifth segment there is an organ which might escape the unaided eye of a moderately attentive observer. Though not larger than a sand grain (FIGS. 6 and 7,*m*) [1] it is of such a structure when examined under a strong lens as to lead one to suspect that it has important functions. It then appears like one of those caterpillar legs which we have called "membranous" and which bear a crown of complete hooks, for it too is encircled by small, curved, and very short spines. It is a tubercle more or less capable of opening and closing; and in its center there is a cavity in which I believed that I could detect a dark brown, conical body, evidently corneous and apparently constructed like a dart with a rather blunt point. This organ seems to me to be of no service to the worm while it is crawling, but there is a time when it seems to have considerable importance, namely, when the worm is endeavoring to subdue an insect that is making every effort to escape. Then the organ assists in holding the prey more securely and might also serve to deal it fatal blows if it be really armed with the dart of whose existence I was unable to satisfy myself completely. The position of this tubercle is such that it cannot be seen when in action, for at such times it is hidden from the observer by the whole thickness of the body.

If the worm, just extracted from its burrow, be placed on a plane surface into which it is unable to burrow, it remains for some time flexed like an S or bent near the middle to form a kind of hook. Then it sometimes reveals the fact that it is able to leap like the cheese-maggots by suddenly straightening the posterior portion of its body, i.e. by thrusting this portion back suddenly so that it forms a more or less open angle with the anterior portion. It thrusts itself

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[1] Figure numbers in Appendix B refer to FIGURE 49.

obliquely upward, leaps into the air, sometimes to a height of half an inch or even of an inch and may fall at a distance of about seven or eight lines from its former position. A gentle touch with a hard point like that of a pin or penknife will often induce it to take such a leap; but there are times when it will remain motionless, no matter how much it may be annoyed. It more readily resorts to crawling. Then it smooths out all the flexures of its body (FIG. 5), and not content with having righted itself, reaches out in order to bring its head as far forward as possible. It thereupon extrudes from the orifice at the end those two little darts, or hooks (FIG. 6*a*) of which we have already spoken, and strikes them into the surface on which it is lying. They give the worm a fixed point towards which it drags its body and thus it takes a single step, though never a very long one, and after that it can take another and many others in succession.

Should the worm, on removal from its pit, be placed on the very sand in which it was made, or on similar sand, it loses no time in burrowing into it. It rights its body, thrusts its head under the sand and drags itself beneath the surface. Then it descends perpendicularly in the same manner as we saw it progressing horizontally. After each step, another portion of its body is concealed and soon the whole insect is buried in the sand.

Ordinarily it is not till several hours have elapsed after the worm-lion has burrowed into the sand or friable earth, that it thinks of making a funnel (FIGS. 8 and 10). Some individuals undertake the task earlier, others later, apparently according to whether they are more or less stimulated by a craving for food, but generally the evening is their favorite time for work. They do not willingly give themselves up to it during the day. If one approaches to observe them when night is coming on, or better still, after it has already set in, in some spot where a goodly number of the worms has been assembled, and if one or several candles be used for illumination, nearly all the insects will be found to be in full activity. Those that had no funnels are digging them and others are repairing such breaches as may have been made in their walls. They enlarge the funnels, make them deeper, broader and more regular. The ant-lion always begins by tracing the circumference of the hollow cone it intends to make in the sand, but the worm-lion does not thus lay out the plan of the burrow it intends to excavate; all it does is to toss the sand into the air obliquely so that it falls at some distance from the spot from which it was taken and beyond the upper border of the pit, if the latter has been already started. The worm, when beginning a burrow, is hidden under the sand, a very thin layer of which covers its dorsal surface. By suddenly raising its anterior end it throws a jet of the overlying grains into the air. Similar movements often repeated at very short intervals soon expose a large portion of the worm-lion's body to view, and the center of the pit, which will be made both deeper and broader, is marked out. The insect soon manages to draw a larger portion of the remainder of its body from beneath the sand, for the body is nearly always visible during the strenuous part of the work. It is extremely flexible and the insect has need of such suppleness, for it is solely by means of the inflections imparted to its body that the latter can serve as a kind of shovel for taking up the sand and throwing it beyond the margin of the pit. Sometimes the worm bends its anterior portion in such a manner that the back, or upper surface is almost underneath while the remainder of the dorsal surface of the body retains its natural position. Then the part of the abdomen adjoining the anterior region functions as a shovel to take up the sand and toss it into the air. Sometimes, and this is the most usual method of working, the dorsal surface of the anterior segments is thrust into the sand, takes a load and tosses it out. I shall not undertake to describe all the diverse contortions which the insect can impart at will to its cylindrical body in order to make it execute what would seem to require a flat implement; I shall merely say that the contortions are varied in manifold ways. I have sometimes seen worms which, after having given their body the form of a pair of dividers with two unequal legs, kept turning around the shorter, represented by the posterior portion of the body, without ceasing to toss the sand with their anterior portion. This manner of excavating is well adapted to forming a hollow cone. As I have already said, the pit made by the worm-lion is proportionally deeper than that of the ant-lion and its slope is therefore steeper, so that the incautious insect that steps over the rim of the precipice can secure even less of a foothold to prevent its falling to the bottom.

When the funnel has become sufficiently deep to suit the worm-lion, it lies in wait without making the slightest movement, till prey comes to repay it for the pains it has taken in making its trap. Ordinarily a large part of the worm's body, though exposed (FIG. 9, *a,p.*), is not for that reason more visible, or to speak more accurately, more easily recognized as what it really is. It looks like a small fragment of wood, placed transversely at a very short distance from the bottom of the funnel. Although I knew that the small body I saw must be that of the worm, its straightened form, its immobility and seeming rigidity, sometimes impelled me to resort to a lens in order to dissipate the doubts nevertheless engendered by these appearances. At such times the worm's posterior portion and the summit of the angle which it helps to form, lie in the sand, while the head is plunged into it at the diametrically opposite side of the funnel.

The moment thus awaited by the worm-lion and the most interesting for the observer, arrives when the ill-fortune of some little fly or worm leads it beyond the edge of the declivity. There it finds nothing but a steep slope made of sandgrains, which give way beneath it, and when it seeks a foot-hold it falls to the bottom of the diminutive precipice. What was to all appearances a splinter of wood, the motionless worm-lion, instantly makes very rapid movements to seize its prey. Not being furnished, like the ant-lion, with two horns forming wonderful forceps for seizing and piercing the unfortunate insect and being deprived of legs and hooks, how can the worm-lion hold and overpower its prey? With its own body, which is more flexible than a serpent's, it tries to encircle the body of the insect (FIGS. 10 and 11) and if successful, to grip it tightly in order to deprive it of all power of escape and then disposes of it as seems best, that is, it at once pierces its body and sucks out its juices with the tip of the head which remains free and is armed with suitable instruments in the form of the two darts previously described. Then it is that the hollow tubercle situated on the fifth segment is of use in gripping the prey more tightly. The position of this tubercle, which cannot be seen while the worm-lion is encircling the seized insect, shows that it is the dorsal surface that is in immediate contact with the surface of the prey.

It is at the very moment when the insect to be overcome is still free to exert its powers of resistance that it is of importance to our worm to have the posterior portion of its body form an angle with the anterior portion (FIGS. 6 and 7 *m.*). The efforts made by the unfortunate insect to escape would drag the voracious worm out of the sand, if it were unable to secure a good purchase. The sand in which the posterior portion is embedded acts as such a mechanical support, for the worm-lion could not be dragged out without bringing with it a thick mass of sand as long as its posterior portion, whereas if the latter lay in a straight line with the remainder of the body, the sand would offer little resistance, apart from some slight friction, to the displacement of the worm.

But not all insects that fall into the worm-lion's funnel become victims; for some are its superiors in strength. I have occasionally seen flies, whose wings I had removed, and large species of ants escape, and sometimes even insects that are not its superiors in strength have this good fortune. Notwithstanding all its cleverness, the worm-lion is not always quick enough to encircle the body of the little animal it desires to capture. The insect, aware of the great peril that threatens it, struggles with all its might, and sometimes successfully. It frees itself from the worm-lion's clutches and tries to scale the walls of the funnel. The difficulties it has to overcome in ascending the steep slope are increased by a hail of sand continually falling on its body, for the worm-lion, in desperation, so to speak, because its prey is escaping, employs every sand-tossing artifice at its command. On such occasions it executes movements like those it employs in excavating its funnel, directing the jets of sand as adroitly as it can towards the insect struggling to climb the funnel wall. Again the latter drops to the bottom of the precipice and this second fall is sometimes more unfortunate than the first, for it is seized and loses its life. If the insect is strong enough to escape from the spot in which the worm-lion intends to grasp it, it renews its attempts to mount the walls and though it may fall back repeatedly, nevertheless, if it is too superior in strength, the worm-lion desists from its unsuccessful attacks, the prey escapes and makes off and the worm-lion finds itself in a badly damaged funnel, for the sand that has slid down from its walls has made the slopes too gradual and too easily surmounted. But all this disorder is repaired not later than toward the end of the day.

If the worm-lion succeeds in embracing the body of another insect, it at once administers a mortal thrust by piercing the abdomen or back and sucking out the body juices. The instruments employed in accomplishing this are the darts to which we have repeatedly referred. They seemed to me to be very much like those with which the larvæ that feed on plant-lice are armed. Both of these voracious larvæ seem to employ in the same manner the instruments which have been given for the same purpose; their function is not merely to pierce, but also to act like pistons.

If one have only a supply of ants and flies too large to offer to the worm-lions that are being kept for the amusement of seeing them display all their manœuvres, it is best to enfeeble the too vigorous insect before throwing it into the funnel. The ant may be rolled and pressed between the fingers, and some of its legs may be torn off; all but one or two of the legs and especially the wings of the fly should be removed, but under no circumstances should the insect be killed outright, if the worm-lion is to accept it as food. These worms are as sensitive as the ant-lions and never attempt to feed on an insect completely deprived of life, though it may die in an instant after seizure. But if the insect placed in the funnel is still able to make a few weak movements, it will stimulate the worm to attack. If the body of the prey is too robust to be completely encircled by the worm-lion, the latter will embrace only a portion of it. Then it soon extrudes the darts from its head at the end of the coil and plunges them into the interior of its victim. It will devote several hours to pumping out the contents of a large fly's body.

Our worm-lions do not have to pass their entire life in the form in which we have so far studied them; they are to become flies and they cannot undergo this transformation till they have passed through a stage, known as the nymph, which renders them incapable of crawling. Having reached the last stage of their growth, they therefore transform themselves into nymphs and that often without leaving their funnels. In order to prepare themselves for this change of condition. they do not, like the ant-lions and so many other insects, construct and enclose themselves in cocoons. It is sufficient for them to shed their skins. This also suffices in the case of the worms that produce the crane-flies, especially the species most abundant in our meadows. The worm-lion nymph (FIG. 12) also closely resembles the nymphs into which the crane-fly worms are transformed. The anterior which is the most slender portion of the body in the larva, is the stoutest in the nymph; within it and behind the head the wings and legs are usually assembled, all the rest of the body being slender and of rather uniform thickness. At the posterior end there is usually a dry flaccid membrane (FIG. 12 *t*), the skin from which it withdrew, in order to appear in its proper form.

My observations have not permitted me to ascertain very precisely the number of days passed by the insect in the nymphal stage. I believe that the period never exceeds fifteen and I have reason to believe that it is often only ten to twelve days, perhaps even less. I placed the nymphs which I sought and found in the sand in pounce-boxes, in order that the emerging flies might not escape me. Some of them I saw ready to fly at the end of three or four days, others at the end of five or six. It remained for me to ascertain the number of days that had elapsed between the first transformation and the day they were placed in the pounce-boxes. From investigations made at various times to find the nymphs, I was led to believe that some of them taken from the sand had not been in the pupal stage longer than five or six days.

The fly (FIG. 13) which arises from so small a worm, cannot, of course, be of considerable dimensions. If what was established as a rule in the *"Mémoires pour servir à l'Histoire des Insectes"* be recalled, we might surmise in advance that the worm, being of the type with the head of variable form, would produce a fly with only two wings. At first sight it closely resembles the crane-flies; like them it has rather long legs and a long body, but when examined with some attention, it is found to have more fundamental and characteristic resemblances to the flies arising from the worms that prey on plant-lice. Although these usually have a short body, there are some species in which it is elongate. The body of the flies arising from these latter worms is round, sometimes almost cylindrical, and that of our new fly has the same shape. It does not have the kind of a mouth surrounded by several barbels, so characteristic of the crane-flies. The latter are sometimes adorned with very elegant antennæ, beset with plumose hairs; but the antennæ of the worm-lion fly (FIG. 13 *a a*) resemble those of the flies arising from the worms that prey on plant-lice; they are short, consist of an almost cylindrical stem to which is articulated a button only about a third as large and united in turn with a kind of oblong palette, from the tip of which projects a very long bristle [arista].

The prevailing color of this fly is pale chestnut brown; at any rate this is the color of the head and thorax, but the segments of its abdomen are not exclusively of that tint, but are bordered with yellow. The abdomen has no yellow, but is reddish brown throughout. The four anterior legs are entirely very pale yellow, the hind pair, much larger than the others, are more reddish and are tinged with brown in some places.

It was near the end of June when the first flies were born from the worms which I received at the end of August of the preceding year. At that time many of the larvæ were very small and several were of more than medium size. It seems very probable therefore that there is each year only a single generation of these flies, and then only if the worms are well nourished. But if they be subjected to too severe and too protracted starvation during the months when the temperature of the air is at least mild, and if their need of food be not so great as to prove fatal, their transformation into nymphs is probably delayed till the following year, and if they be treated as badly during this second year, their transformations may be postponed till the third year.

Explanation of the Figures

Figures 1, 2, 3 and 4 represent the worm-lion about natural size, and each shows it with a different flexure of the body. These are the postures it ordinarily assumes. It takes on a great number of other curvatures intermediate between the preceding.

Figure 5 shows it in dorsal view, stretched out in a straight line, an attitude which it does not assume when taken from its funnel till after it has remained for some time on a plane surface into which it is unable to burrow.

In FIGURES 6, 7 and 8 the larva is represented under the magnification of the microscope and extended in a straight line as in FIG. 5. In FIG. 6 the dorsal surface is presented; it is seen from the side, or in profile in FIG. 7 and the lower surface or venter is represented in FIG. 8.

The same parts are designated in the different figures by the same letters.

a. the head.

In FIGURES 6 and 8 the two darts with which the insect pierces its prey and which serve to draw it forward when crawling, are carried at the anterior end of the head.

In FIGURE 7 the darts, the head itself and the first segment are withdrawn into the second.

p. the posterior portion, terminated by four appendages which have somewhat the appearance of an open hand with only four outspread fingers.

q. (FIGURES 6 and 7) the anus.

s.s. (FIGURE 6) the two posterior spiracles.

r. (FIGURES 7 and 8) long, stiff, hairs.

m (FIGURES 6 and 7) is the hollow tubercle with its periphery beset with short, stiff hairs, which may perform the function of little spines in assisting the larva to hold its prey. Even the posterior borders of the tubercle may have the same function, being able to hold the seized part very firmly. This was proved by the considerable resistance experienced in trying to remove a small sand-grain that had entered its cavity.

FIG. 9 shows a funnel excavated in the sand; the worm-lion *a.p.* appears like a small rod in this funnel, with its anterior portion *a,* and its posterior portion *p,* concealed under the sand.

FIGURE 10 represents another funnel into which an ant has fallen and has been overpowered by the worm-lion; *f,* the ant; the worm-lion *u* makes a coil of its body and is busy sucking; *g,* an ant attempting to scale the wall of the funnel.

FIGURE 11 is a section of a funnel similar to that in the preceding figure but giving a better view of the way the anterior portion *a* of the worm is coiled around the ant *f,* and the posterior portion *p* of the former is placed under the sand, where, owing to its flexure, it gives the worm such a purchase that the efforts of the ant are unable to pull it out without lifting a too considerable mass of sand.

FIGURE 12 depicts the nymphal skin of the worm-lion and represents the nymph. It also shows at *l* the opening through which the fly has emerged; in *t* we see the skin the larva quitted when it transformed itself into the nymph; it is much wrinkled.

FIGURE 13 shows the fly in the form in which the worm-lion appears after its last transformation. *a.a.* antennæ of the fly.

BIBLIOGRAPHY

BIBLIOGRAPHY

Adlerz, G., 1890, Om digestionssekretionen jemte några dermed sammenhängande fenomen hos Insekter och Myriopoder. Bihang. K. Svensk. Vet. Akad. Handl. 16: 3-57, 5 pls.

Albertus Magnus, 1478, De animalibus libri XXVI. Roma, Simon Nicolai de Luca., 1478; Venetus, 1519; Germ. trans. by W. Ryff, Frankfurt, 1544. New ed. after the Cologne manuscript edited by H. Stadler, Münster, 1, W. vol. 1, 1916, vol. 2, 1920, being vols. 15 and 16 of the 'Beiträge zur Geschichte des Mittelalters.'

Aldrich, J. M., 1905, A catalogue of North American Diptera. Smithson. Miscell. Coll. vol. 44, No. 1444, Washington.

1912, Flies of the Leptid genus Atherix used as food by California Indians. Ent. News 23: 159-163.

1915, The Dipterous genus Symphoromyia in North America. Proc. U. S. Nat. Mus. 49: 113-142, 11 figs.

Aldrovandus, U., 1602, De animalibis insectis libri septem. Bononiæ.

Andrews, C. W., 1915, A description of the skull and skeleton of a peculiarly modified Rupicaprine Antelope (*Myotragus balearicus,* Bate), with a notice of a new variety, *M. balearicus* var. *major.* Trans. Roy. Soc. London, B 206: 281-305, pl. 12-22.

Arnheim, F., 1888, Die Memoiren der Königin von Schweden, Ulrike Luise, Schwester Friedrichs des Grossen. (Heft 22 of G. Droysen's Hallesche Abhandlungen zur neueren Geschichte.) Halle, M. Niemeyer.

1909-'10, Luise Ulrike, die Schwedische Schwester Friedrichs des Grossen. 2 vols. Gotha, F. A. Perthes.

Austen, E. E., 1899, On the preliminary stages and mode of escape of the imago of the Dipterous genus Xylomyia, Rond. (Subula, Mg. et auct.), with special reference to *Xylomyia maculata* F. and on the systematic position of the genus. Ann. Mag. Nat. Hist. (7) 3, 1899: 181-192.

Autenrieth, J. H. F., 1802, Bemerkungen über die psychologische Gleichheit des ganzen Thierreichs. Wied. Arch., Vol. 2: 225-229.

Averim, V. G., 1909, Beiträge zur Biologie der Larve des Ameisenlöwen (In Russian). Sborn. Stud. Kruž. lĭnb. prir. Chark. Univ. Charĭkov 1: 34-52.

Bachmann, M., 1918, Biologische Beobachtungen über die Käsefliege. Entom. Zeitschr. 31: 93-94, 101-102; 32: 1-2, 5-6, 10-11, 14-15, 19-20, 23-24, 27, 30-32.

Bailey, V., 1923, Sources of water supply for desert animals. Scient. Month. 27: 66-86.

Baker, C. F., 1904, Reports on Californian and Nevadan Diptera. I. Invertebrata Pacifica 1: 17-39 (description of *Phineus opacus,* etc., by D. W. Coquillett).

Banks, N., 1927, Revision of the Nearctic Myrmeleonidæ. Bull. Mus. Comp. Zool. 68: 3-84, 4 pls.

Barber, G. W., 1929, Heat and time of exposure necessary to kill larvæ of the European corn borer in ear corn. Circ. No. 71. U. S. Dept. Agric. 13 pp.

Barbour, T., 1926, Reptiles and Amphibians, their habits and adaptations. Boston and N. Y. Houghton, Mifflin Co.

Bate, Miss D. M. A., 1909, A new Artiodactyle from Majorca, *Myotragus balearicus* gen. et sp. nov. Geol. Mag. 6: 385-388.

1914, On the Pleistocene ossiferous deposits of the Balearic Islands. Geol. Mag. 1: 337-345, 1 pl. 2 figs.

de Beauvieu, G. G., 1764, Abrégé de l'histoire des insectes, dédié aux jeunes personnes, orné de figures en tailledouce. 2 vols. Paris, C. J. Panckoucke.

Becker, R., 1910, Zur Kenntnis der Mundteile und des Kopfes der Dipteren-Larven. Zool. Jahrb. Abt. Anat. 29: 281-314, 3 pls. 4 figs.

Becker, T., 1900, Die Leptiden im Gebiete der Europäisch-Asiatischen und Mittelmeer-Fauna. Ent. Nachricht. 26: 97-116.

1906-'07, Die Ergebnisse meiner dipterologischen Frühjahrsreise nach Algier und Tunis. Zeitschr. f. Hymenopt. u. Dipterol. 1906: 1-16, 97-158, 273-287, 353-367; 1907: 33-61, 97-128, 225-256, 369-407.

1908, Dipteren der Kanarischen Inseln und der Insel Madeira. Mitt. Zool. Mus. Berlin 4: 3-206, 4 pls.

1921-'22, Neue Dipteren meiner Sammlung. Zeitschr. wiss. Insektenbiol.: 41-48, 54-64, 69-72.

Beling, T., 1875, Beitrag zur Metamorphose der zweiflügeligen Insekten. Arch. f. Naturg. 41: 31-57.

1880, Die Metamorphose von *Cœnomyia ferruginea* Scop. Verh. zool. bot. Ges. Wien 30: 343.

1882, Beitrag zur Metamorphose zweiflügliger Insekten aus den Familien Tabanidæ, Leptidæ, Asilidæ, Empidæ, Dolichopodidæ, und Syrphidæ. Arch. f. Naturg. 48: 187-240.

Bequaert, J., 1921, *Atherix braunsi* nov. sp., a South African Leptid with gregarious habits. Psyche 28: 1-7.

1922, The predaceous enemies of Ants. Bull. Amer. Mus. Nat. Hist. 45: 271-331, 2 pls.

1929, A new Pseudomasaris from California, with some considerations on the Masarid wasps. Psyche, 36: 61-88, 2 figs.

Berce, E., 1865, [Note on Myrmeleon] Ann. Soc. Ent. France (4) 5, Bull: xlvi.

Bergmann, E., and *Leuckart, R.*, 1855, Anatomisch-Physiologische Uebersicht des Tierreichs. Neue Ausg. Stuttgart, I. B. Müller.

Berlese, A., 1902, Osservazioni su fenomeni che avvengono durante la ninfosi (Lepidotteri, Imenotteri, Neurotteri, Coleotteri), I. Riv. Patol. Veg. 9: 177-344, 8 pls. II. Tessuto muscolare. *op.cit.* 10: 1-120.

Bezzi, M., 1898, Contribuzioni alla fauna Ditterologia Italiana II. Ditteri delle marche e degli Abruzzi. Bull. Soc. Ent. Ital. 30: 19-50.

1900, Zur Synonymie und Verbreitung des *Psammorycter vermileo* Deg. Wiener Ent. Zeitung 19: 56, 57.

1905, Ditteri Eritrei raccolti dal Dott. Andreini e dal Prof. Tellini. Bull. Soc. Ent. Ital. 37: 195-304.

1926, South African Rhagionidæ (Diptera) in the South African Museum. Ann. South Afric. Mus. 23: 297-324.

Bierens de Haan, J. A., 1925, Reflex und Instinkt bei dem Ameisenlöwen. Biol. Zentralbl. 44: 657-667.

Bigot, J., 1879 *a*, [Caractères du genre Vermileo.] Ann. Soc. Ent. France (5) 9 Bull: xx-xxi.

1879 *b*, [Classification des Diptères.] Ann. Soc. Ent. France (5) 9 Bull: cxxii-cxxiii.

1881, [Caractères du genre Vermileo.] Ann. Soc. Ent. France (6) I Bull: liii.

1885, [*Lampromyia argentata* sp. n.] Ann. Soc. Ent. France (6) 5 Bull: lxvii-lxviii.

Billups, T. R., 1889, Note upon *Atherix ibis,* Fabricius. Entomologist 22: 193-194, 1 pl.

Bingley, W., 1805, Animal biography. 3 vols. London, R. Phillips. Vol. 3: 342-348 on ant-lion.

Birge, E. A. 1873, The ant-lion. Amer. Nat. 7: 432.

Biró, L., 1897, Biologische Mittheilungen aus Neu Guinea. 1. Die Ameisen-Löwen in Neu Guinea. Berl. Ent. Zeitschr. 42: 129-138.

Blaisdell, F. E., 1925, Expedition of the California Academy of Sciences to the Gulf of California in 1921 (The Tenebrionidæ). Proc. Calif. Acad. Sci. 4: 201-288.

Blair, K. G., 1920-'21, [Larva of a Nemoptera sp.] Proc. S. London Ent. Nat. Hist. Soc. p. 85.

Blanchard, E., 1840, Histoire Naturelle des Insectes 3: 65.

1868, Métamorphoses, mœurs et instincts des insectes. Paris, Baillière.

Bodenheimer, F. S., 1928, Materialien zur Geschichte der Entomologie Bd. I. Berlin, W. Junk.

Bonnet, C., 1743, An abstract of some new observations upon insects (Erucæ, Formicaleo, Aphids), Phil. Trans. Vol. 42: 458-488.

1773, Abhandlungen aus der Insectologie. Trans. by J. A. E. Goeze. Halle.

1779 *a,* Sur le Fourmilion, et en particulier sur sa structure. Vol. I of his "Collection Complète des Oeuvres." Neuchatel. S. Fauche.

1779, *b,* Sur le procédé industrieux au moyen duquel le Fourmilion transporte hors de sa fosse les corps trop pesans pour être lancés au loin avec sa tête. Vol. I of his "Collection Complète des Oeuvres.": 511-515.

1779, Sur une nouvelle espèce de Fourmilion découverte par l'auteur. Vol. I of his "Collection Complète des Oeuvres.": 516-534.

Boudier, H. P., 1834, Observations sur divers parasites. Ann. Soc. Ent. France, 3: 327-336, 1 pl.

Brauer, F., 1853, Beschreibung der Larven von *Myrmeleon formicarius* und *formicalynx.* Verh. zool. bot. Ges. Wien 3: 144-145.

1854, Beiträge zur Kenntniss des inneren Baues und der Uerwandlung der Neuropteren (*Ascalaphus macaronius; Myrmeleon tetragrammicus*). Verh. zool. bot. Ges. Wien 4: 463-472, 3 pls.

1855, Beiträge zur Kenntniss der Verwandlung der Neuropteren (*Acanthaclisis occitanea*). Verh. zool bot. Ges. Wien 5: 777-786, 1 pl.

1869, Beschreibung der Verwandlungsgeschichte der *Mantispa styriaca*. Verh. zool. bot. Ges. Wien 9: 831-840, 1 pl.

1883 *a,* Die Zweiflügler des Kaiserlichen Museums zu Wien. III Systematische Studien auf Grundlage der Dipteren-Larven nebst einer Zusammenstellung von Beispielen aus der Literatur über dieselben und Beschreibung neuer Formen. Denkschr. K. Akad. Wiss. Wien. Math. naturw. Cl. 47: 1-100, 5 pls.

1883, *b, Vermileo Degeeri* Macq. Wien. Ent. Zeitg. 2: 114.

1887, Beitrag zur Kenntnis der Verwandlung der Mantispiden-Gattung Symphrasis Hg. Zool. Anzeig.: 212-218, 4 figs.

Brischke, C., 1879, Ueber die Eier von Myrmeleon. Ent. Nachr. 5: 29.

Bristowe, W. S., 1930, Notes on the biology of spiders. I. The evolution of spiders' snares. Ann. Mag. Nat. Hist. 6: 334-342, 2 figs.

Brown, John, 1895, Original memoirs of the sovereigns of Sweden and Denmark from 1766 to 1818. 2 vols. London, H. S. Nichols & Co. 1895.

Brues, C. T., 1924, Observations on animal life in the thermal waters of Yellowstone Park, with a consideration of the thermal environment. Proc. Amer. Acad. Arts. Sci. 59; 371-437, 1 pl. 5 figs.

1927, Animal life in Hot Springs. Quart. Review Biol. 2: 181-203, 19 figs.

1928, Studies on the fauna of Hot Springs in the western United States and the biology of thermophilous animals. Proc. Amer. Acad. Arts Sci. 63: 139-228, 6 pls. 7 figs.

Buchner, P., 1917, Der Ameisenlöwe (Review of Doflein, 1916) Biol. Zentralbl. 37: 46-48.

Bugnion, E., 1922, Etudes relatives à l'anatomie et à l'embryologie des vers luisants ou Lampyrides. Bull. Biol. France Belg. 56: 1-53, 36 figs.

1929, Le ver-luisant Provençal et la Luciole Niçoise. Riviera Scientifique. Suppl. 1929: 3-131, 61 figs.

Burmeister, H., 1839, Handbuch der Entomologie Bd. 2. Berlin, T. E. F. Enslin.

Buxton, P. A., 1923, Animal life in deserts. London, Edw. Arnold Co.

1924 *a,* Moisture and animal life in deserts. Proc. Roy. Soc. Ser. B, vol. 96, no B-673: 123-131, 3 figs.

1924 *b,* Physical factors controlling harvesting in an ant. Trans. Ent. Soc. London: 538-543.

Cameron, A. E., 1913, General survey of the insect fauna of the soil within a limited area near Manchester, a consideration of the relationships between soil insects and the physical conditions of their habitat. Journ. Econ. Biol. 8: 159-204, 2 pls. 2 figs.

de Caraman, Duc V. A. C. R., 1859, Charles Bonnet, philosopher et naturaliste, sa vie et ses œuvres. Paris, A. Vaton.

Cardanus, G., 1553, De rerum varietate. Basileæ per Sebastianum Henric Petri.

Carpenter, F. M., 1929, A Jurassic Neuropteran from the lithographic limestone of Bavaria. Psyche, 36: 190-194, 1 fig.

Catteau-Calleville and *Walckenaer* 1816, [Life of Baron Charles Degeer] Biographie Universelle 17: 19.

Chanvallon, J. B., 1761, Voyage à la Martinique, p. 185.

Chapman, R. N., 1926, Animal ecology with special reference to insects. Minneapolis, Burgess Roseberry.

Chapman, R. N.; Mickel, C. E.; Parker, J. R.; Miller, G. E.; and *Kelly, E. G.* 1926, Studies on the ecology of sand dune insects. Ecology 7: 416-426, 2 figs.

Claparède, E., 1909, La psychologie de Charles Bonnet, Genève et Bâle.

Clarke, Miss C. H., 1882, Description of two interesting houses made by native caddis-fly larvæ. Proc. Boston Soc. Nat. Hist. 22: 67-71, 6 figs.

Cockerell, T. D. A., 1907, Some Old-World types of insects in the Miocene of Colorado. Science n.s. 36: 446-447.

1914, Three Diptera from the Biocene of Colorado. Canad. Ent. 46: 101-102.

Coe, W. R., and *Kunkel, B. W.,* 1906, Studies on the California limbless lizard, Anniella. Trans. Conn. Acad. 12: 1-55, 8 pls. 15 figs.

Coinde, J. P., 1855, Description scientifique de la vie du Myrmeleon sous ses trois états de larve, de nymphe et d'insecte parfait. Lyon, Rey et Sezanne, 29 pp.

Cole, F. R., 1923, A revision of the North American two-winged flies of the family Therevidæ. Proc. U. S. Nat. Mus. No. 2450, 62: 1-140, 13 pls.

Comes, S., 1909, Stereotropismo, geotropismo e termotropismo nella larva de *Myrmeleon formicarius* L. Atti Accad. Gioen. Sc. Nat. Catania, 86: mem. 4: 1-14.

Comstock, Mrs. A. B., 1913, Handbook of nature study, pp. 395-397.

Comstock, J. H., 1924, An introduction to entomology. Ithaca, Comstock Publ. Co., 1924.

Cook, O. F., 1913, Webspinning fly-larvæ in Guatemalan caves. Journ. Wash. Acad. Sci. 3: 190-193, 1 fig.

Costa, A., 1855, Fauna del Regno di Napoli. Myrmeleontidea, pp. 20, 2 pls.

Costa, O. G., 1844, Descrizione di dodici specie nuove dell'ordine dei ditteri ed illustrazione di altre quattordici meno ovvie raccolte nella state del 1834. Atti Real. Accad. Scienze, sez. Soc. Real. Borbonica, 5, parte 2, Napoli, pp. 81-107.

Coucke, L., 1893, Matériaux pour une étude des Leptides de Belgique, y compris les genres Xylophagus et Cœnomyia. Ann. Soc. Ent. Belg. 37: 123-137.

Courtiller, A., 1867, *Leptis vermileo* (Fabricius). Ann. Soc. Linnéenne du Dép. Maine-et-Loire, 9: 72-75, 1 pl.

Daecke, E., 1905, Notes on *Prionapteryx nebulifera* Steph. Ent. News 16: 12-14, 1 pl. 1 fig.

Darwin, C., 1860, Journal of researches into the natural history and geology of the countries visited during the voyage of H. M. S. *Beagle* round the world. London, John Murray.

Degeer, C., 1752, Rön om Mask-Lejonet. Vetensk. Akad. Handl. 1752: 180-192, 261-265, 1 pl.

1755, Nachricht vom Wurmlöwen (Mask-Lejonet) aufgesetzt und Ihre Majestät der Königin überreichet, und von Ihre Majestät der Akademie der Wissenschaften, allergnädigst gegeben. Abhand. Schwed. Akad. Wiss. (A. G. Kästner transl.). 14: 187-198, 266-270, pl. V.

1776, Mémoires pour servir à l'histoire des Insectes. 6: 168-183, pl. 10.

Delarouzée, C., 1858 [Note on *Myrmeleo libelluloides.*]Ann. Soc. Ent. France (3) 6: 152.

Dewitz, H., 1881, Die Mundteile der Larve von Myrmeleon. Sitzb. Ges. Naturf. Freunde, Berlin 1881, pp. 163-166.

1882, Ueber die Führung an den Körperanhängen der Insekten, speciell betrachtet an der Legescheide der Acridier, dem Stachel der Meliponen und den Mundteilen der Larve von

Myrmeleon nebst Beschreibung dieser Organe. Berlin. Ent. Zeitschr. 26: 51-68.

Dice, L. R., 1930, Mammal distribution in the Alamagordo Region, New Mexico. Occas. Pap. Mus. Zool. Univ. Mich. No. 213: 32 pp., 2 pls.

Disderi, S., 1809, Observationes entomologicæ. Mem. Acad. Sc. Turin, 15: 60-94.

Doflein, F., 1914, Das Tier als Glied des Naturganzen. Vol. II of Hesse and Doflein's "Tierbau und Tierleben." Leipzig u. Berlin, Teubner.

1916, Der Ameisenlöwe, eine biologische, tierpsychologische und reflexbiologische Untersuchung. Jena, Fischer, 138 pp., 10 pls., 43 text-figs.

Dohrn, C. A., 1866, [On Degeer.] Stettin. Ent. Zeitg. 27: 248-249.

Dufour, L., 1848, Recherches sur l'anatomie et l'histoire naturelle de l'*Osmylus maculatus.* Ann. Sc. Nat. (3) 9: 349-356.

1850, Description et iconographie de quelques Diptères de l'Espagne. Ann. Soc. Ent. France (2) 8: 131-155, 2 pls.

1862, Notices entomologiques. I. Consultation sur une larve aquatique. Ann. Soc. Ent. France (4) 2: 131-138, 2 figs.

Duncan, J., 1840, Introduction to entomology. Vol. I, in Sir Wm. Jardine's "Naturalists' Library."

Duncan, P. M., 1871, The transformations or metamorphoses of insects. Phila., Claxton, Remsen & Haffelfinger.

Dutrochet, R. J. H., 1818, Mémoire sur les métamorphoses du canal alimentaire dans les insectes. Journ. Physique 86: 130-135, 189-204.

Elditt, H. L., 1852, Zur Geschichte der Ameisenlöwe nach Réaumur und Rösel. Königsberg.

Eltringham, H., 1923, On the larva of *Pterocroce storyi* With. (Nemopteridæ) with additional notes by E. N. Willmer and C. B. Williams. Trans. Ent. Soc. London, 1923, pp. 263-268, 1 fig., 1 pl.

1926, On the structure of an organ in the hind-wing of *Myrmeleon nostras,* Fourc. Trans. Ent. Soc. London 74: 267-268, 1 pl.

Emerton, J. H., 1871, The ant-lion. Amer. Nat., 4: 705-708.

1912, Four burrowing Lycosa (Geolycosa Montg. Scaptocosa Banks) including one new species. Psyche 19: 25-36, 1 pl. 6 figs.

Engel, E. O., 1929, Notes on two larvæ of South African Diptera belonging to the families Leptidæ and Asilidæ. Trans. Roy. Soc. South Africa 18: 147-162, 20 figs.

Enslin, E., 1906, Die Lebensweise der Larve von *Macrocera fasciata* Meig. Zeitschr. f. wiss. Insektenbiol. 2: 251-253.

Ettlinger, M., 1924, Ueber Werkzeuggebrauch bei Tieren. Philos. Jahrb. 37, 1924, 20 pp.

Fabre, H., 1907, Souvenirs Entomologiques Sér. 10. Paris, Delagrave p. 241.

Fabricius, J. C., 1794, Entomologia systematica. Tome IV, Hafniæ. 1805, Systema antliatorum. Brunsvigæ.

Fairchild, D., 1930, Exploring for plants. New York, Macmillan Co.

Falcoz, L., 1927, Observations biologiques sur divers insectes des environs de Vienne en Dauphiné. Bull. Soc. Ent. France, pp. 226-232.

Ferrari, A., 1863, Ergebnisse weniger Sammelstunden in Venedig und am Lido in September, 1862. Wien. Ent. Monatschr. 7: 80-85.

Fielde, Miss A. M., 1887, On an aquatic larva and its case. Proc. Acad. Nat. Sci. Phila. 1887, pp. 293-294.

Flournoy, T., 1901, Le cas de Charles Bonnet. Arch. Psych. 1.

Fourcroy, A. F., 1785, Entomologia Parisiensis II: 360.

Froggatt, W. W., 1902-'03, Notes on Australian Neuroptera and their life-histories. Proc. Linn. Soc. N. S. Wales, 27: 358-369.

Gaullier, E. H., 1859, Charles Bonnet considéré comme homme politique. Musée Suisse. Vol. II, Genève: 20-25, 35-39.

Geoffroy, J., 1761, Histoire abrégée des insectes qui se trouvent aux environs de Paris. Vol. 2: 257.

Gerstaecker, A., 1873, Ueber zwei eigentümliche bei *Gastropacha neustria* und *Myrmeleon formicarius* beobachtete Modifikationen der Harnsäureabsonderung. Ber. Ges. Naturf. Freunde. Berlin.

Geubel, H. K., 1852, Zoologische Notizen. Enthaltend eine Reihe v. Beobachtungen nebst philosophische und chemisch-physiologische Bemerkungen über mehrere Wiech- und Gliederthiere, p. 38.

Ghosh, C. C., 1910, *Croce filipennis* Westw., Journ. Bombay Nat. Hist. Soc. 20: 530-532, 1 pl.

1913, Life-history of *Helicomitus dicax* Walk. Journ. Bombay Nat. Hist. Soc. 22: 643-648, 1 pl.

Giard, A., 1893, Sur le *Myrmeleo europæus*. Ann. Soc. Ent. France, 63, Bull: ccciv.

1894, [Sur les prétendus œufs de Fourmilions.] Ann. Soc. Ent. France, 43 Bull: viii.

1902, Note sur la larve de *l'Atherix ibis* Fabr. Bull. Soc. Ent. France: 220-222.

Girard, M., 1866, Les métamorphoses des insectes. Paris, Hachette et C^e.

1875, Remarques relatives aux Myrméleonides du sud-ouest de la France. Ann. Soc. Ent. France, 5 Bull: ccxxi-ccxxii.

Goeze, J. A. E., 1796, Belehrung über Natur und Lebenssachen. Leipzig, Weidmann, 326 pp. (p. 207-212 on Vermileo).

Goldsmith, O., 1774, History of the earth and animated nature. 8 vols. London.

Görnitz, K., 1923, Ueber die Wirkung klimatischer Faktoren auf die Pigmentfarben der Vogelfedern. Journ. f. Ornithol. 71: 456-511, 1 pl.

Gosse, P. H., 1851, A naturalist's sojourn in Jamaica. London, Longman, Brown, etc.

Graenicher, S., 1930, Bee-fauna and vegetation of the Miami Region of Florida. Ann. Ent. Soc. Amer. 23: 153-174.

Graham, S. A., 1921, Factors influencing the subcortical temperature of logs. 18th Rep. State Ent. Minnesota. pp. 26-42, 5 pls.

1923, Effect of physical factors in the ecology of certain insects in logs. 19th Rep. State Ent. Minnesota. pp. 22-40.

1924, Temperature as a limiting factor in the life of subcortical insects. Journ. Econ. Ent. 17: 377-383.

Grasse, P. P., 1929, Etude écologique et biogéographique sur les Orthoptères Français. Bull. Biol. France Belg. 63: 489-537.

Gravely, F. H., and *Maulik, S.*, 1911, Notes on the development of some Indian Ascalaphidæ and Myrmeleonidæ. Rec. Ind. Mus. Calcutta 6: 101-110, 1 pl.

Greene, C. T., 1926, Descriptions of larvæ and pupæ of two-winged flies belonging to the family Leptidæ. Proc. U. S. Nat. Mus. 70: 1-20, 3 pls.

Gregory the Great (*ca.* 580), In Jobum, lib. V. cap. 16.

Griffini, A., 1895, Sopra alcuni Leptidi e Tabanidi del Piemonte. Boll. Mus. Zool. Anat. Comp. Torino 10: No. 218, 9 pp.

Guérin-Méneville, F. E., 1846, Note sur la larve de *l'Ascalaphus longicornis*. Ann. Soc. Ent. France (2) 4, Bull.: cxv-cxvi.

Guilding, L., 1827, On *Ascalaphus macleyanus*. Trans. Linn. Soc. 15, 1824-25 (1827): 509-512.

1833, The generic characters of Formicaleo. Trans. Linn. Soc. London 16: 47-51.

Hagen, H., 1854, Ueber die Neuropteren der Bernsteinfauna. Verh. zool. bot. Ver. Wien. 4: 221-232.

1860, Beitrag zur Kenntniss der Myrmeleon-Arten. Stettin. Ent. Zeitg.: 359-369.

1872-'73, On the larva of the Hemerobina. Proc. Boston Soc. Nat. Hist. 15: 243-248.

1873 *a,* Die Larven von Ascalaphus. Stettin. Ent. Zeitg. 34: 33-62.

1873 *b,* Die Larven von Myrmeleon. Stettin. Ent. Zeitg: 249-295, 377-398.

1888, Monograph of the Hemerobiidæ. Part I, Nemopteridæ. Proc. Boston Soc. Nat. Hist. 23: 250-269.

Handlirsch, A., 1908, Die fossilen Insekten und die Phylogenie der rezenten Formen. 2 vols. Leipzig, W. Engelmann.

1924, Systematische Uebersicht der Neuroptera in Schröder's "Handbuch der Entomologie". Bd. III: 829-839.

Hart, C. A. and *Gleason, H. A.*, 1907, On the biology of the sand areas of Illinois. Bull. Ill. Lab. Nat. Hist. 7: 137-272, 17 pls.

Haycraft, J. B., 1898, Upon the production of rapid voluntary movements. Journ. Physiol. 23: 1-9, 8 figs.

Henking, H., 1886, Nahrungserwerb und Nestbau von *Theridium riparium* (Blackw.) Thor. Kosmos 1: 1-11, 4 figs.

Henneguy, L. F., 1904, Les insectes, morphologie, reproduction, embryogénie. Paris, Masson & Co.

Herbst, I. F. W., 1784, Des Hrn. v. Réaumur Bemerkungen über den Wurm-Löwen. (Verlion). Neues Mag. für die Liebhaber der Entomologie (Fuessly), 2, 2:1-5.

Hesse, R., 1901, Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren. VII Von den Arthropoden-Augen. Zeitschr. f. wiss. Zool. 7: 347-473, 6 pls., 2 figs.

Hingston, R. W. G., 1925, Nature at the Desert's edge, studies and observations in the Bagdad oasis. Boston, Small, Maynard & Co.

Holmes, S. J., 1903, Death-feigning in terrestrial Amphipods. Biol. Bull. 4: 191-196.

Holmgren, N., 1904, Zur Morphologie des Insektenkopfes. 2. Einiges über die Reduktion des Kopfes der Dipterenlarven. Zool. Anzeig. 27: 343-354, 12 figs.

Höppner, H., 1901, Die Bienenfauna der Dünen und Weserabhänge zwischen Uesen und Baden. Abhandl. Nat. Ver. Bremen. 15: 231-255.

Howard, L. O., 1887, Enemies of the Buffalo gnat (in Report of the Entomologist). Rep. Commiss. Agric. Washington (1886), p. 510.

Hudson, G. V., 1891, The habits and life-history of the New Zealand glow-worm. Trans. Proc. New Zeal. Inst. 23: 43-47, 1 pl.

Hughes, G., 1750, The natural history of Barbados in ten books. London.

Humbert, E., 1858, Ch. Bonnet, disciple de Montesquieu. Bibl. Universelle I. Genève.

Imms, A. D., 1911, Contributions to a knowledge of the structure and biology of some insects. I, On the life-history of *Croce filipennis* Westw. Trans. Linn. Soc. London Zool. (2) 11: 151-160, 1 pl.

1925, A general textbook of entomology. London: Methuen & Co.

Isidorus Hispalensis, 1911, Etymologiarum sive originum libri XX. 2 vols. Recogn. W. M. Lindsay, Oxford, Clarendon Press.

Ives, J. E., 1890, An interesting method of egg deposition. Ent. News 1: 39.

Jacobson, E., 1912, Biological notes on some Planipennia from Java. Tijdschr. Ent. 55: 97-103.

1926, Supplement to P. Esben-Petersen, Fauna Sumatrensis. Neuroptera and Megaloptera. Entom. Mitteil. 15: 29-30.

Johnson, C. W., 1929, Meeting place of the insects. Nature Mag. May: 333-335, 9 figs.

Jordan, H., 1913, Vergleichende Physiologie wirbelloser Tiere. 1. Band. Die Ernährung. Jena, G. Fischer.

Jordans, A. von, 1928, Die Ergebnisse meiner dritten Reise nach den Balearen. Novitat. Zool. Tring 34: 262-336, 1 fig.

1924-'25, Die Ergebnisse meiner zweiten Reise nach Mallorca. I, Journ. Ornithol. 72: 145-170; II, *ibid:* 381-410; III, *ibid:* 518-536; IV, *ibid:* 73: 194-207.

Kashkarov, D. and *Kurbatov, V.,* 1930, Preliminary ecological survey of the vertebrate fauna of the central Kara-kum Desert in West Turkestan. Ecology 11: 35-60, 11 figs.

Keferstein, G. A., 1825, Ueber die goldgrabenden Ameisen der Alten. Isis, 2: 105-114.

Kertész, C., 1908, Catalogus Dipterorum hucusque descriptorum 3: 297, 298.

Kieffer, J. J., 1913, Diptera. Fam. Cecidomyidæ. In Wytsman's 'Genera Insectorum.' Fasc. 152. Tervueren, Belgium.

King, F. H., 1914, A textbook of the physics of agriculture. Madison, Wisconsin.

Klapálek, F., 1901, Neuropteroiden in 'Zoologische Ergebnisse der dritten Asiatischen Forschungsreise des Grafen Eugen. Zichy.' 2: 205-221, 1 pl.

Klinckowström, 1867-'72 (The Memoirs of Queen Ulrica). In Riksradet och Fältmarskalken Grefve Fredrik Axel v. Fersens Historiska Skrifter. 8 vols. Stockholm.

Knab, F., 1912, Blood-sucking and supposedly blood-sucking Leptidæ. Proc. Ent. Soc. Washington 14: 108-110.

1915, Dipterological miscellany. Evolution of the blood-sucking habit in Symphoromyia. Proc. Ent. Soc. Washington 17: 38-40.

Knab, F. and *Cooley, R. A.*, 1912, Symphoromyia as a blood-sucker. Proc. Ent. Soc. Washington 17: 38-40.

Knauer, F., 1879, Der Ameisenlöwe und sein Trichterbau. Naturhistoriker, Vienna 1, No. 2.

Krausse, A. H., 1909, Ueber die Maden der Käsefliege *Piophila casei* L. Zeitschr. wiss. Insektenbiol. 5: 394-398, 1 fig.

1915, Beiträge zur Biologie von *Myrmeleon europæus* M' Lachl. Arch. Naturg. Berlin A. 81, Heft 7: 125-128.

Kusnezov-Ugamsky, N., 1927, On the marriage flight of ants. (In Russian.) Rev. zool. Russe. 7: 77-104.

1929, The ants of the genus Messor in the fauna of Middle Asia. (In Russian.) Act. Univ. Asiæ Mediæ ser. 8*a*, 25 pp., 3 pls.

Lameere, A., 1902, Note sur les mœurs des fourmis du Sahara. Ann. Soc. Ent. Belg. 46: 160-169.

de La Mettrie, J. O., 1912, Man a machine. Chicago, Open Court Publ. Co.

Ledermüller, M. F., 1762, Mikroscopische Gemüts- und Augenergötzung. p. 83.

Lefebure, A., 1842, Communication sur la larve d'Ascalaphus. Ann. Soc. Ent. France (1) 11, Bull.: xvii-xix.

Leiberg, G., 1924, Der Ameisenlöwe Myrmeleon, dessen Lebensweise und Entwicklung, Ent. Anzeig. Vienna 4: 125-127.

Lemoine, A., 1850, Charles Bonnet de Genève philosophe et naturaliste, Paris, A. Durand.

Leonard, M. D., 1930, A revision of the Dipterous family Rhagionidæ (Leptidæ) in the United States and Canada. Mem. Amer. Ent. Soc. No. 7: 181 pp., 3 pls.

Leydig, F., 1855, Zum feineren Bau der Arthropoden. Müller's Arch. Anat. Phys. Med.: 376-480, 4 pls.

1878, Herpetologische Zeichnungen aus dem Nachlass Rösels von Rosenhof. Verh. naturh. Ver. preuss. Rheinlande u. Westfalens (4) 5: 1-41.

Lindner, E., 1924, Die Fliegen der palæarktischen Region. Lieferung I: 1-16, 2 pls.

Linnaeus, C., 1758, Systema naturæ. Ed. X, 1758, p. 590; Ed. XII, 2, 1767, p. 982: Ed. XIII, 1, 1770, p. 982.

Lloyd, J. T., 1921, The biology of North American caddis-fly larvæ. Bull. Lloyd Library No. 21. Ent. Ser. 1, 1921, pp. 1-124.

Loew, H., 1874, Neue nordamerikanische Dipteren. Berliner Ent. Zeitschr. 18: 378-384.

Lozinski, P., 1908, Beitrag zur Anatomie und Histologie der Mundwerkzeuge der Myrmeleoniden-larven. Zool. Anzeig. 33: 473-484, 9 figs.

1910, Zur Histologie der borstenartigen Bildungen am Hinterleibe der Myrmeleoniden-larven. Zool. Anzeig. 35: 526-530, 2 figs.

1911, Ueber die Malpighischen Gefässe der Myrmeleonidenlarven als Spinndrüsen. Zool. Anzeig. 38: 401-417, 12 figs.

1921 *a*, Untersuchungen über die Histologie und Cytologie der Malpighischen Gefässe der Myrmeleoniden-larven. Bull. intern. Acad. polon. Sci. Cracow B. (1921) 1922, pp. 5-29, 1 pl.

1921 *b*, Cytologische Untersuchungen über die Umwandlung der Malpighischen Gefässe der Myrmeleoniden-larven in Spinndrüsen und über die Spinnstoffsekretion. Bull. intern. Acad. polon. Sci. Cracow B. (1921) 1922, pp. 61-86, 2 pls.

1921 *c*, Histologische Untersuchungen über den Darm der Myrmeleoniden-larve. Bull. intern. Acad. polon. Sci. Cracow B. (1921) 1922, pp. 199-222, 1 pl.

Lucas, W. J., 1906, On the emergence of *Myrmeleon formicarius* from the pupa. Trans. Ent. Soc. London: 53-57, fig.

Lundbeck, W., 1907, Diptera Danica. Part I. Copenhagen, Gad.

McClendon, J. F., 1902 *a*, The life-history of *Ulula hyalina*. Amer. Natural. 36: 421-429, 15 figs.

1902 *b*, The larvæ of *Myrmeleon texanus* Banks and *M. rusticus* Hagen. Ent. News 13: 209-213. Pl. 11.

1906, Notes on the true Neuroptera. Ent. News 17: 116.

McCook, H. C., 1882, On the habits of the ant-lion. Proc. Acad. Nat. Sc. Phila. 3: 258-260.

1907, Nature's craftsmen. Popular studies of ants and other insects. New York & London, Harper & Bros.

McDunnough, J., 1909, Ueber den Bau des Darmes und seiner Anhänge von *Chrysopa perla* L. Arch. f. Naturgesch. 75: 313-360, 5 pls.

MacLachlan, B., 1865, Habits of *Myrmeleon formicarius* L. Ent. Mag. 2: 73-75.

1866, Note sur les œufs de *Myrmeleon formicarius*. Ann. Soc. Ent. France (4) 6, Bull.: xv-xvi.

1873, An attempt towards the systematic classification of the family Ascalaphidæ. Journ. Linn. Soc. 11: 219-276.

Macquart, J., 1827, Insectes Diptères du Nord de la France. Lille.

1834, Suites à Buffon. Histoire Naturelle des insectes. Diptères. I, II. Paris.

1836-1844, Diptera. In Barker-Webb and Sabine Berthelot 'Histoire naturelle des Isles Canaries.' Vol. II. Pl. 4, fig. 7.

1840, Diptères exotiques nouveaux ou peu connus. 2, 1. Paris.

Malebranche, N., 1711, Entretiens, sur la métaphysique, sur la religion, et sur la mort. Nouv. éd. revue, corrigée et augmentée. 2 vols. Paris, M. David. (First ed. 1688.)

1923, Dialogues on metaphysics and on religion. Trans. by Ginsberg. London, Allen and Unwin.

Malloch, J. R., 1917, A preliminary classification of Diptera exclusive of Pupipara, based upon larval and pupal characters, with keys to imagines in certain families. Part I. Bull. Ill. State Lab. Nat. Hist. 12: 161-407, 57 pls.

Marchal, P., 1896, Sur les mœurs d'un Lampromyia. Bull. Soc. Ent. France: 343.

1897, Notes d'entomologie biologique sur une excursion en Algérie et en Tunisie. Mém. Soc. Zool. France, 10: 5-25, 1 pl.

Maxwell-Lefroy, H., 1909, Indian insect life. Calcutta & Simla, Thacker Spink & Co.

1910, Entomological notes (b). The Indian Nemapterid and its food. Journ. Bombay Nat. Hist. Soc. 19: 1005-1007, 1 fig.

de Meijere, J. C. H., 1895, Ueber zusammengesetzte Stigmen bei Dipteren-larven. Tijdschr. Ent. 38: 65-100, 33 figs.

1917, Beiträge zur Kenntnis der Dipteren-Larven und Puppen. Zool. Jahrb. Abt. Syst. 40: 177-322, 11 pls.

Meinert, F., 1879, Om Mundens Bygning hos Larverne af Myrmeleontiderne, Hermerobierne og Dytiscerne. Vid. Medd. Nat. Foren: 69-72.

1880, Sur la conformation de la tête et sur l'interprétation des organes buccaux chez les insectes, ainsi que sur la systématique de cet ordre. Ent. Tidskr. 1: 147-150.

1889, Contribution à l'anatomie des Fourmilions. Overs. K. Dansk. Vidensk. Selsk. Forh.: 43-66, 2 pls.

Meissner, O., 1906 *a*, Die Lebensdauer von *Myrmecoleon formicarius*. Insektenbörse 23: 131-132.

1906 *b*, Weiteres zur Biologie von *Myrmecoleon formicarius*. Insektenbörse 23: 168.

1907, Ueberwinterung von Myrmecoleonlarven. Insektenbörse, 24: 2 pp.

1908 *a*, Entwicklung zweier Exemplare von *Myrmecoleon formicarius*. Insektenbörse 25: 96.

1908 *b*, Kleine Notizen über die Neuropteren der Umgegend von Potsdam. Wiener Ent. Zeitg. 27: 99-100.

1908 *c*, Zur Biologie von *Myrmecoleon formicarius* L. Ent. Wochenbl. 25: 169.

1909, *Myrmeleon formicarius* L. Ent. Jahrb. 18, (1908): 177-187.

1911, Ameisen und Ameisenlöwen. Ein Beitrag zur Ameisenpsychologie. Soc. Entomologica 26: 59-60.

1917, Review of Frz. Doflein: Der Ameisenlöwe. Ent. Zeitschr. 31: Nov. 24, p. 68.

1919 *a*, Zur Psychologie der Ameisenlöwen. Ent. Zeitschr. 33: 25-26, 30-31.

1919 *b*, Nachtrag zur Psychologie des Ameisenlöwen. Ent. Zeitschr. 33: 38.

Melander, A. L., 1927, Diptera, family Empididæ in P. Wytsman's 'Genera Insectorum.' 434 pp. 8 pls.

Melin, D., 1923, Contributions to the knowledge of the biology, metamorphosis and distribution of the Swedish Asilids. Zoolog. Bidrag från Uppsala, 8: 1-307, 305 figs.

Metcalf, Z. P. and *Osborn, H.*, 1920, Some observations on insects of the between-tide zone of the North Carolina coast. Ann. Ent. Soc. Amer. 13: 108-117, 3 pls.

Miall, L. C., 1895, The natural history of aquatic insects. London and N. Y., Macmillan & Co.

1912, The early naturalists. Their lives and work (1530-1789) London, Macmillan & Co.

Mickel, C. E., 1928, Biological and taxonomic investigations on the Mutillid wasps. Bull. 143, Smithson. Inst. U. S. Nat. Mus. 351 pp. 5 pls.

Mik, J., 1887, Ueber *Apogon Dufourii* Perr. Wien. Ent. Zeitg. 6: 311-313.

1894, Dipterologische Miscellen 2. Ser. Wiener Ent. Zeitg. 13: 164-168.

Millet, 1926 [Habits of the ant-lion.] Nature, Paris No. 2751: 415-416.

Moffat, J. A., 1884, Notes on Ant-lions. Canad. Ent. 16: 121-122.

Moody, H. L., 1873, Habits of *Myrmeleon immaculatus.* Canad. Ent. 5: 63-65.

Morley, J., 1923, Diderot and the encyclopædists. Vol. I, Macmillan, p. 28.

Morse, A. P., 1904, Researches on North American Acridiidæ. Pub. Carnegie Inst. Washington, 55 pp., 8 pls.

Müller, F., 1880, Ueber die von den Trichopterenlarven der Provinz Santa Catharina verfertigten Gehäuse. Zeitschr. wiss. Zool. 35: 47-87, 2 pls.

Myers, J. G., 1929, Insect singers, a natural history of the Cicadas. London, George Routledge & Sons.

Nagel, W. A., 1896, Ueber eiweissverdauenden Speichel bei Insekten-larven. Biol. Centralbl. 16: 51-57, 103-112, 1 fig.

Navás, L., 1900, Algunas costumbres de las Hormigas y Hormigaleones. Act. Soc. Espan: 219-222.

1910, Monografia de los Nemoptéridos (Insectos Neurópteros). Mem. Real. Acad. Ciencias y Artes Barcelona (3) 8: 341-408, 24 figs. 1 pl.

1912, Notas sobre Mirmeleonidæ. Broteria 10: 29-75.

1912-1913, Biologische Beobachtungen zur Lebensweise der Ameisenlöwen. Ent. Mittheil. 1: 300; 2: 81.

1915, Mirmelionidas de Europa. Revista Real Acad. Cienc. Exact. Fisic. y Natur. Madrid, 12 figs.

Needham, J. G., 1903, Some new life histories of Diptera, in "Aquatic insects of New York State." Bull. 68. New York State Mus. Aug. p. 26, pl. 10, figs. 1 & 2.

Noire, L., 1880, Das Werkzeug und seine Bedeutung für die Entwicklungsgeschichte der Menschheit.

von Nolcken, J. H. W., 1847, Langsame Entwickelung der Flügel von *Myrmeleon formicarius*. Stett. Ent. Zeitschr. 8: 224.

Noyes, Miss A. A., 1914, The biology of the net-spinning Trichoptera of Cascadilla Creek. Ann. Ent. Soc. Amer. 7: 251-272, 3 pls. 2 figs.

Offner, M., 1893, Die Psychologie Charles Bonnet's.

Oken, L., 1836, Allgemeine Naturgeschichte für alle Stände. 5: 3. Abth. p. 1450.

d'Orbigny, A., 1859, Naturhistorische Schilderung des nördlichen Patagonien. Arch. f. Naturg.: 47-61.

Osborn, H. and *Metcalf, Z. P.*, 1920, Notes on the life-history of the salt marsh Cicada (*Tibicen viridifasciata* Walk.) Ent. News 31: 248-252, 1 pl. 5 figs.

Osten Sacken, Baron C. R., 1883, Synonymica concerning exotic Dipterology No. 2. Berlin. Ent. Zeitschr. 27: 295-300.

Palm, J., 1869, Beitrag zur Dipterenfauna Tirols. Verh. zool. bot. Ges. Wien 19: 395-454.

Papillon, F., 1876, Histoire de la philosophie moderne. II: 242-259. Paris.

Park, O., 1929, *Reticulitermes tibialis* Banks in the Chicago area. Proc. Ent. Soc. Washington 31: 121-126.

Parker, J. R., 1930, Some effects of temperature and moisture upon *Melanoplus mexicanus mexicanus* Saussure and *Camnula pellucida* Scudder. Bull. No. 223, Univ. Montana Agric. Exper. Stat. 132 pp., 25 figs.

Percheron, A. R., 1833, Note sur la larve du *Myrmeleon libelluloides*. Guérin's Mag. Zool. No. 59, 6 pp. 1 pl.

Perrier, E., 1884, La philosophie zoologique avant Darwin. Paris: 39-47.

Perris, E., 1852, Seconde excursion dans les Grandes-Landes. Ann. Soc. Linn. Lyon 5: 199.

1857, Nouvelles excursions dans les Grandes-Landes. Ann. Soc. Linn. Lyon 4: 83-180.

Petersen, P. E., 1917, Australian Neuroptera III, Proc. Linn. Soc. N.S. Wales: 203-209, 6 pls.

1918, Help-notes towards the determination and the classification of the European Myrmeleonidæ. Entom. Meddelelser 12: 97-127, 10 pls.

Pillsbury, W. B., 1929, The history of psychology. New York, W. W. Norton.

Pluche, N. A., 1732-1750, Le spectacle de la nature ou entretiens sur les particularités d'histoire naturelle, qui ont paru les plus propres à rendre les jeunes gens curieux, et à leur former l'esprit. 8 vol., 192 pl. Paris, Estienne.

1743, Spectacle de la nature or nature delineated, being philosophical conversations. Transl. by J. Kelly, D. Bellamy and J. Sparrow. 7 vols. 3rd ed. Vol. I, London, James Hodges.

Portier, P., 1909, Recherches physiologiques sur les insectes aquatiques. C. R. Soc. Biol. 66: 343-344, 379-382.

1911, Recherches physiologiques sur les insectes aquatiques. Arch. Zool. Expér. (5) 8: 89-379, 4 pls. 67 figs.

De Pouilly, 1794, Eloge de Bonnet. Lausanne.

Poupart, F., 1704, Histoire du Formica-Leo. Mémoires de l'Académie Roy. des Sciences. Année 1704 (1745): 235-244, 1 pl.

Rabaud, E., 1919, L'immobilisation réflexe et l'activité normale des Arthropodes. Bull. Biol. France Belg. 53: 1-149.

1927, Etude biologique des larves de quelques Planipennes. Bull. Biol. France Belg. 61: 433-499, 5 figs.

Ragonot, E. L., 1878 [Larva of *Ascalaphus longicornis*]. Ann. Soc. Ent. France (5) 8 Bull: cxx.

Rambur, P., 1842, Histoire naturelle des insectes Neuroptères. Paris, Libr. Encycl. Roret. pp. 365-411.

Ramdohr, K. A., 1811, Abhandlungen über die Verdauungswerkzeuge der Insekten. Halle, Hendel.

Ratzeburg, J. T. C., 1844, Die Ichneumoniden der Forstinsekten in entomologischer und forstlicher Beziehung. 224 pp., 4 pls.

Rau, P., 1926, The ecology of a sheltered clay bank; a study in insect sociology. Trans. Acad. Sc. St. Louis, 25: 157-276, 8 pls.

de Réaumur, R. A. F., 1742, Dixième mémoire. Histoire des Formica-leo. In 'Mémoires pour Servir à l'Histoire des Insectes', Vol. 6: 333-386, pl. 32-34.

1753, Histoire du ver lion mouche. Mém. Acad. Sc. Paris 1753: 402-419. 1 pl. Ed. 1762: 604-631.

Redtenbacher, J., 1883, Zur Kenntniss der Myrmeleoniden-Larven. Wien. Ent. Zeitschr. 2: 289-296.

1884 *a*, Die Lebensweise der Ameisenlöwe. Progr. Commun. Ober-Realschule Wien. pp. 1-27, 1 pl.

1884 *b*, Uebersicht der Myrmeleoniden-Larven. Denkschr. Akad. Wien 48: 335-368, 7 pls.

R (egensberg), F., 1911, Der "listige und geschickte Ameis-Rauber" Kosmos 8: 167-171, 2 figs.

Reimarus, H. S., 1798, Allgemeine Betrachtungen über die Triebe der Thiere hauptsächlich über ihre Kunsttriebe. 4. Aufl. Hamburg, C. E. Bohn 1798 (first ed. 1760, 2nd 1762, 3rd after author's death, 1773). (On Myrmeleon pp. 164, 165, 239, 331.)

Rengel, C., 1908, Ueber *Myrmeleon formicarius* L. Sitzb. Ges. Naturf. Freunde Berlin: 140-149, 1 pl.

Rennie, J., 1830, Insect architecture. 2nd ed.: 209-214. London, Chas. Knight.

Rensch, B., 1929, Das Prinzip geographischer Rassen-Kreise und das Problem der Artbildung. Berlin, Gebr. Bornträger.

Reuter, O. M., 1913, Lebensgewohnheiten und Instinkte der Insekten bis zum Erwachen der sozialen Instinkte. Trans. by A. U. M. Buch, Berlin, R. Friedlander u. Sohn.

Rey, E., 1895, Ueber die Ameisenlöwen. Sitzb. Naturf. Ges. Leipzig. 29, 1892-1894: 35-36.

Richards, O. W., 1927, Sexual selection and allied problems in insects. Biol. Reviews 2: 298-364, 7 figs.

Riley, C. V., 1890, The eggs of Atherix. Insect Life 2: 386-387.

von Röder, V., 1892, Ueber *Apogon Dufourii* Perr. nebst einer Berichtigung zu Schiner's Fauna (die Fliegen). Ent. Nachrichten 18: 248, 249.

de Romand, B. E., 1833, Note sur la larve du *Leptis vermileo*. Ann. Soc. Ent. France, 2 Bull.: 498-499, 6 figs.

1850, Note sur la métamorphose de *Myrmeleo formicarius*. Ann. Soc. Ent. France (2) 8, Bull.: XLV.

Romanes, G. J., 1883, Animal intelligence. N. Y. Appleton & Co. pp. 235, 236.

Romier, L., 1929, L'homme nouveau. Paris, Libr. Hachette.

Rösel von Rosenhof, 1755, Insektenbelustigungen. Bd. 3: 101-132, pls. 17-21.

Roubaud, E., 1922, Etudes sur le sommeil d'hiver pré-imaginal des Muscides. Le cycle d'asthénie et l'athermobiose réactivante spécifique. Bull. Biol. France Belg. 56: 455-544, 5 figs.

Rousseau, E., 1921, Les larves et nymphes aquatiques des insectes d'Europe. Vol. 1, Bruxelles.

Roux, P., 1833, Lettre relative à divers coquilles, crustacés, insectes, reptiles et oiseaux, observés en Egypte, addressée par M. Roux à M. le baron Férussac. Ann. Soc. Nat. 28: 72-78, 4 figs.

Rudow, D., 1878, *Myrmecoleon formicalynx*. Ent. Nachr. 4: 272.

Sanders, N. J. and *Shelford, V. E.*, 1922, A quantitative and seasonal study of a pine dune community. Ecology 3: 306.

Santschi, F., 1909, Sur la signification de la barbe des fourmis arénicoles. Rev. Suisse Zool. 17: 449-458, 9 figs.

de Saussure, H. B., 1793, Eloge historique de Charles Bonnet. Genève.

Savory, T. H., 1928, The biology of spiders. N. Y. Macmillan Co.

Sayous, A., 1861, Le dix-huitième siècle à l'étranger. Paris, I: 157-205.

Scharff, R. F., 1907, European animals, their geological history and geographical distribution. New York, E. P. Dutton.

Schaum, H. R., 1857, *Necrophilus arenarius* Roux, die muthmassliche Larve von Nemoptera. Berlin. Ent. Zeitschr.: 1-9, pl. 1, fig. 1.

Schenck, C. F., 1877, Die Myrmeleon-Arten Nassau's und der angränzenden Gegenden. Ent. Nachrichten, p. 93.

Scheuchzer, J. J., 1733, Physica sacra, vol. III: 322 and vol. IV: 787.

Schiner, J. R., 1862, Fauna Austriaca. Die Fliegen (Diptera) 1. Theil. Wien.

Schröder, E., 1862, Der gemeine Ameisenlöwe. Aus d. Heimath: 821-830, 6 figs.

Shannon, R. C., 1915, Eastern Symphoromyia attacking man. Proc. Ent. Soc. Washington, 17: 188-189.

Sharp, D., 1895, Insects, Part. I, Cambridge Natural History, Vol. 5: 454-459, London, Macmillan & Co.

Shelford, R. S., 1900, On a remarkable Dipterous larva. Journ. Straits Branch Roy. Asiatic Soc. 1900, No. 33: 256-257.

1901, Notes on some Bornean insects. Rep. Brit. Assoc. Section D. Glasgow, pp. 689-691.

Shelford, V. E., 1908, Life histories and larval habits of the tiger beetles (Cicindelidæ). Linnean Soc. Journ. Zool. 30: 157-184, 4 pl.

1913, The life-history of a bee-fly (*Spogostylum anale* Say) parasite of the larva of a tiger beetle (*Cicindela scutellaris* Say var. *lecontei* Hald.) Ann. Ent. Soc. Amer. 6: 213-225.

1914, The significance of evaporation in animal geography. Ann. Assoc. Amer. Geogr. 3: 29-42.

1915, Principles and problems of ecology, as illustrated by animals. Journ. Ecol. 3: 1-23.

Shinoda, O., 1927, Contributions to the knowledge of intestinal secretion in insects. II. A comparative histo-cytology of the mid-intestine in various orders of insects. Zeitschr. Zellforsch. mikr. Anat. 5: 278-292, 21 figs.

Shipley, M., 1920, A forerunner of evolution. Science 61: 315-316.

von Siebold, C. T. E., 1861, Ueber die Larve von *Leptis vermileo.* Amtl. Ber. 35. Versam. Deutsch. Naturf. u. Aerzte in Königsberg (1860), pp. 105-107.

von Siebold, C. T. E. and *Stannius, F. H.*, 1846-'48, Lehrbuch der vergleichenden Anatomie. 2 Theile, Berlin.

Sinclair, J. G., 1922, Temperatures of the soil and air in a desert. Month. Weath. Rev. 50: 142-144.

Speck, J., 1897, Bonnet's Einwirkung auf die deutsche Psychologie des vorigen Jahrhunderts. Arch. f. Geschichte u. Philos. 10: 504-519; 11: 58-72, 181-211.

Stäger, R., 1924 *a,* Ist der Ameisenlöwe eine Reflexmaschine? Schweiz. entom. Anzeiger 3. No. 1.

1924 *b,* Andere Beobachtungen am Ameisenlöwen. Schweiz. entom. Anzeig. 3. No. 3.

1925, Studien am Ameisenlöwen. Biol. Centralbl. 45: 65-93.

Stavenow, L., 1908, Geschichte Schwedens 1708-1772. In Heeren, Ukert, von Giesebrecht and Lamprecht's "Geschichte der Europäischen Staaten." 7 vols. Gotha, F. A. Perthes.

Steck, T., 1920, Die Myrmeleoniden der Schweiz. Mitteil. Schweiz. Ent. Ges. 13: 102-105.

Stephens, F., 1906, California mammals. San Diego.

Steudel, A., 1913, Absorption und Secretion im Darm von Insekten. Zool. Jahrb. Abt. Physiol. 33: 165-224, 3 pls. 3 figs.

Strobl, G., 1906, Spanische Dipteren. 2. Beitrag. Mem. Sos. Españ. Hist. Nat. 3: 271-422.

Sulzer, D., 1776, Allgemeine Geschichte der Insekten I: 175.

Sumner, F. B., 1925, Some biological problems of our southwestern deserts. Ecology 6: 352-371.

Taschenberg, E. L., 1880, Praktische Insektenkunde. 4. Teil. Zweiflügler, Netzflügler und Kaukerfe. Berlin, Heinsius.

Thomson, J. A., 1920, The system of animate nature. 2 vols. New York, Holt & Co.

Thorndyke, L., 1923, A history of magic and experimental science. 2 vols. New York, Macmillan, 1923.

Tillyard, R. J., 1915, Studies in Australian Neuroptera. 1. The wing-venation of the Myrmeleonidæ. Proc. Linn. Soc. N.S. Wales 40: 734-751, 1 pl. 10 figs.

1916, Studies in Australian Neuroptera. 2. Descriptions of new genera and species of the families Osmylidæ, Myrmeleontidæ and Ascalaphidæ. Proc. Linn. Soc. N.S. Wales 41: 41-70, 6 pls. 3 figs.

1917, Phylogeny of ant-lions. Ent. News 28: 42.

1918, Studies in Australian Neuroptera. 7. The life-history of *Psychopsis elegans* (Guérin). Proc. Linn. Soc. N.S. Wales 63: 787-818, 1 pl.

1922, The life-history of the Australian moth lace-wing, *Ithone fusca,* Newman. Bull. Ent. Res. 13: 205-223, 2 pls., 11 figs.

1926, The insects of Australia and New Zealand. Sydney, Angus & Robertson.

Tobias, R. O., 1851, Der Ameisenlöwe, *Myrmeleon formicarius.* Abhand. naturf. Gesell. Görlitz. 6: 15-21.

Tournier, H. and *Preudhomme de Borre, A.,* 1874 [On clustering *Atherix ibis*]. Ann. Soc. Ent. Belg. 17: C.R. p. lxxxix-xci.

Townsend, C. H. T., 1893, The puparium and pupa of *Subula pallipes* L. Ent. News 4: 163-165.

Trautmann, 1927, Der Ameisenlöwe. Ent. Anzeig. Vienna 7: 244-247, 259-260, 263-268.

Trembley, J., 1794, Mémoire pour servir à l'histoire de la vie et des ouvrages de Ch. Bonnet. Berne.

Trost, P., 1801, Kleiner Beitrag zur Entomologie. Erlangen, Palm.

Turner, C. H., 1915, Notes on the behavior of the ant-lion with emphasis on the feeding activities and letisimulation. Biol. Bull. 29: 277-307, 13 figs.

Vallisnieri, A., 1700, Dialoghi (fra Malpighi e Plinio intorno la curiosa origine de molti insetti). Venezia, Albrizzi 8: 268. 1st. ed. Patavii 1700, 8. First published in 1697 in Galeria di Minerva Tom. III, part 9. Dialog. 2: 302.

Van Dyke, E. C., 1928, A reclassification of the genera of North American Meloidæ and a revision of the genera and species formerly placed in the tribe Meloini, found in America north of Mexico, together with descriptions of new species. Univ. Cala. Publ. Ent. 4: 395-474, 5 pls.

Van Dyke, J. C., 1902, The desert. Scribner's, New York.

Van Gehuchten, A., 1890, Recherches histologiques sur l'appareil digestif de la *Ptychoptera contaminata.* I. Etude du revêtement epithélial et recherches sur la sécrétion. Cellule 6: 183-289, 6 pls.

Van Someren, V. G. L., 1924, Notes on the life-history and insect food preferences of a lichen-like Ascalaphid larva. Trans. Ent. Soc. London: lix-lxv.

Van der Weele, H. W., 1908, Ascalaphiden monographisch bearbeitet. In. Coll. Zool. du Baron Edm. de Sélys Longchamps. Cat. systém. et descript. Fasc. 8. Bruxelles, 326 pp. 253 figs. 2 pls.

1909, Mecoptera and Planipennia of Insulinde, with biological notes from Edw. Jacobson. Leiden Notes Mus. Jentink 31: 1-100, 5 pls.

Verrall, G. H., 1909, British flies, vol. 5. London, Gurney & Jackson.

Vincentius Bellovacensis, 1264, Speculum Doctrinæ, lib. 16 cap. 117.

Voigt, G., 1925, Notiz zu Dr. Robert Stäger's "Studien am Ameisenlöwen." Biol. Zentralbl. 45: 381, 382.

Vorhies, C. T. and *Taylor, W. P.,* 1922, Life-history of the kangaroo rat (*Dipodomys spectabilis spectabilis* Merriam). U. S. Dept. Agric. Bull. No. 1901.

Wahlberg, P., 1849, Merkwürdiger Instinkt und Lichtentwicklung bei einer schwedischen Mückenart. Stettin. Ent. Zeitg. 10: 120-123.

Walker, F., 1854, List of the specimens of dipterous insects in the collection of the British Museum. Part 6, Suppl. 2: 413.

Walsh, G. B., 1925, The coast Coleoptera of the British Isles. Ent. Month. Mag. 61: 137-151.

Welch, P. S., 1914, The early stages of the life-history of *Polystœchotes punctatus* Fabr. Bull. Brooklyn Ent. Soc. 9: 1-6, 1 pl.

Wesché, W., 1912, The phylogeny of the Nemocera, with notes on the leg bristles, hairs and certain mouth glands of Diptera. Biol. Bull. 22: 250-270, 1 pl.

Wesenberg-Lund, E. von, 1911, Biologische Studien über netzspinnende campodeoide Trichopterenlarven. Internat. Rev. f. Hydrobiologie, pp. 1-64, 6 pls. 6 figs.

Westwood, J. O., 1838, Notes on the natural history of the ant-lion (*Myrmeleon formicarium* Linn.) Mag. Nat. Hist. pp. 601-604, 1 fig.

1842, Description of some insects which inhabit the tissue of *Spongilla fluviatilis*. Trans. Ent. Soc. London 3: 105-108, 1 pl.

1876, Notæ dipterologicæ No. 3. Descriptions of new genera and species of the family Acroceridæ. Trans. Ent. Soc. London, pp. 507-518, 2 pls.

1888, Notes on the life-history of various species of the Neuropterous genus Ascalaphus. Trans. Ent. Soc. London, pp. 1-12, 2 pls.

Wheeler, R. H., 1929, The science of psychology, an introductory study. New York, Crowell Co.

Wheeler, W. M., 1893, A contribution to insect embryology. Journ. Morph. 8: 1-160, 6 pls. 4 figs.

1907, On certain modified hairs peculiar to the ants of arid regions. Biol. Bull. 13: 185-202, 14 figs.

1926, Réaumur's "Natural History of Ants". New York, Knopf.

Wheeler, W. M. and *Williams, F. X.,* 1915, The luminous organ of the New Zealand glow-worm. Psyche 22: 36-43, 1 pl.

White, A., 1915, The Diptera-Brachycera of Tasmania. Pap. and Proc. Roy. Soc. Tasmania (1914) pp. 35-72, 11 figs.

Whitman, C. O., 1895 *a,* Evolution and epigenesis. Biol. Lectures Woods Hole (1894) Boston, Ginn & Co. pp. 205-224.

1895 *b,* Bonnet's theory of evolution a system of negations. Biol. Lectures Woods Hole. Boston, Ginn & Co. (1894) pp. 225-240.

1895 *c,* The palingenesia and the germ doctrine of Bonnet. Biol. Lectures Woods Hole. Boston, Ginn. & Co. (1894) pp. 241-272.

Wiedemann, C. R. W., 1830, Aussereuropäische zweiflügelige Insekten. 2. Theil. Hamm.

Wille, J., 1923, Biologische und physiologische Beobachtungen und Versuche an der Käsefliegenlarve (*Piophila casei* L.). Zool. Jahrb. Abt. Allgem. Zool. u. Physiol. Tiere 39: 301-320, 4 figs.

Willey, A., 1911, Convergence in evolution. New York. E. P. Dutton & Co.

Williams, C. B., 1923, A short bio-climatic study of the Egyptian desert. Bull. 29 Tech. Sci. Service. Ministry of Agric. Egypt. pp. 1-20, 9 pls.

Williams, F. X., 1928, The natural history of a Philippine Nipa house with descriptions of new wasps. Philip. Journ. Sc. 35: 53-118, 8 pls.

Williston, S. W., 1886, On two interesting new Genera of Leptidæ, Ent. Americana 2: 105-108.

1908, Manual of North American Diptera, 3rd ed. New Haven, J. T. Hathaway.

Wilm, E. C., 1925, The theories of instinct, a study in the history of psychology. New Haven, Yale Univ. Press.

Winkler, B., 1910, Vom Ameisenlöwen. Kosmos 7: 465.

Withycombe, C. L., 1923 *a,* A new Egyptian Nemopterid (Neuroptera). The Entomologist 56: 141.

1923 *b,* Systematic notes on the Crocini (Nemopteridæ) with descriptions of new genera and species. Trans. Ent. Soc. London, pp. 269-287, 2 pls.

1923 *c,* Notes on the biology of some British Neuroptera (Planipennia). Trans. Ent. Soc. London, pp. 501-594, 6 pls.

1924, Some aspects of the biology and morphology of the Neuroptera with special reference to the immature stages and their possible phylogenetic significance. Trans. Ent. Soc. London, pp. 303-411, 6 pls.

Woglum, R. S., 1929, The Mediterranean fruit-fly. Bull. Cal. Fruit Grow. Exch. 6: 33-48, 7 figs., 2 pls.

Woodger, J. H., 1929, Biological Principles. N. Y. Harcourt, Brace & Co.

Woods, F. A., 1906, Mental and moral heredity in Royalty. New York, H. Holt & Co.

Zaki, M., 1917, Bull. Soc. Ent. Egypt. 10: 21-22.

Zàvadsky, K., 1922, Zur Frage der Verpuppungszeit des Ameisenlöwen (*Myrmeleo formicarius* L.) Zeitschr. wiss. Insektenbiol. 17: 130-132.

Zikan, J. J., 1929, Zur Biologie der Cicindeliden Brasiliens. Zool. Anzeig. 82. (Wasmann-Festband) pp. 269-414, 133 figs.

Anonymous, 1706 [On Vermileo] under "Diverses observations de physique générale." Hist. de l'Acad. Roy. Sciences. Observation VI, p. 7.

Anonymous, 1742-'45, Philosophische Untersuchungen von dem Seyn und Wesen der Seelen der Thiere von einigen Liebhabern der Weltweisheit in sechs verschiedenen Abhandlungen ausgeführt und mit einer Vorrede ans Licht gestellt von J. H. Winkler. See Reimarus p. 331.

Anonymous, 1924 [Biology of ant-lions]. Bols Levende Natuur. Amsterdam 28: 268-276, 12 figs.

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