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Studies in tropisms and ecology of the bed bug (*Cimex lectularius* L.)

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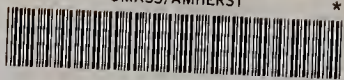
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**Studies in Tropisms and Ecology of the
Bed Bug - *Cimex Lectularius* L.**

Ezekiel Rivnay

STUDIES IN TROPISMS AND ECOLOGY
OF THE
BED BUG - CIMEX LECTULARIUS L.

By
Ezekiel Rivnay

Thesis submitted in partial fulfillment
for the degree of Doctor of Philosophy
Massachusetts State College.

Amherst, Massachusetts

April 1931.

C O N T E N T S

	<u>Page</u>
A. FOREWORD	I
B. ACKNOWLEDGMENT	II
C. STUDIES IN TROPISMS OF THE BED BUG	
I. Introduction	1
II. Thermotaxis	
(1) Literature	3
(2) Observations and Experiments	5
(a) Thermotactic reactions associated with feeding	5
(b) Factors of light, humidity and nutrition on thermotaxis	7
(c) Factors of time and distance in relation to thermotaxis	8
(d) Differential temperature required to produce a thermotactic reaction.	12
(e) Discussion	14
III. Chemotaxis	
(1) Literature	17
(2) Observations and Experiments	
(a) Experiment on the odor of blood . .	22
(b) Experiment on the odor of animal tissue	23
(c) Experiment on skin odor	25
(d) Experiment on odor of perspiration.	28
(e) Experiment on odor of sebum	33
(f) Influence of distance and time on olfactory reaction	36
(g) Experiment on sense of taste in the bed bug	38
(h) General discussion	39

C O N T E N T S (Con'd.)

	<u>Page</u>
IV. Hydrotaxis and Hygrotaxis	
(1) Definition and Literature	42
(2) Observations and Experiments	43
V. Stereotaxis vs. Phototaxis	
(1) Literature	45
(2) Experiments and Observations	48
(a) Discussion	52
VI. Interrelationship of Tropisms	53
VII. Literature	58
VIII. Explanation of Plates	62
IX. Plates	63
D. HOST SELECTION AND CANNIBALISM	
(1) Feeding experiment on warm-blooded animals . .	67
(2) Feeding experiment on cold-blooded vertebrates	68
(3) Cannibalism	72
(4) Literature	75
E. TECHNIQUE IN ARTIFICIAL FEEDING OF THE BED BUG . .	76
(1) Experiment	78
(2) Summary	82
F. TROPISMS EFFECTING COPULATION IN THE BED BUG . . .	84
G. RATE OF GROWTH OF THE BED BUG AND SOME FACTORS AFFECTING IT	
(1) Literature discussion	95
(2) Methods	
(a) Ecologic condition	98
(b) Obtaining data	99

C O N T E N T S (Con'd.)

	<u>Page</u>
(3) Experiment	101
(a) Effect of humidity	102
(b) Influence of quantity of nutrition . . .	105
(c) The Pre-feeding period	107
(d) Effect of temperature on rate of metabolism	108
(4) Literature	111
(5) Plates	113

FOREWORD

The study of Cimex has not been entirely neglected. So frequently an uninvited guest, and often a regular undesired occupant of human dwellings, could not be forgotten. As a matter of fact, hundreds of papers have been published on this blood-thirsty insect. Girault (1907) lists over 600 papers published up to 1906. Since then, because of its importance in medical studies as a potential disease carrier, more attention has been given to this creature and more papers have been published in recent years. Some of the problems discussed herewith by the present writer have never been discussed in any of the published works, while others have been treated by previous observers. However, in the present treatise, other methods have been applied; the studies were made from different points of view; and in several cases, entirely new conclusions were reached.

ACKNOWLEDGMENTS.

The studies presented herewith were carried out partly in Washington, D. C. in connection with the George Washington University, partly in Orlando, Florida and Amherst, Mass. in connection with the Massachusetts Agricultural College. The writer wishes to express his indebtedness to Mr. C. H. Popenoe of George Washington University for several suggestions and advice in connection with this study; to Dr. H. L. Sweetman of Massachusetts Agricultural College for reading the manuscript and offering important criticisms which led to the revision of a great part of the thesis as originally presented, and especially for suggestions in connection with the studies of heat and humidity; and to Dr. J. L. Finck, physicist in the Bureau of Standards, Washington, D. C. for suggestions in heat measuring and the loan of his valuable apparatus in this connection. To my wife, Edith, extreme appreciation is herewith expressed for her continuous effort in assisting me in every way in bringing the manuscript to its present form.

STUDIES IN TROPISMS OF THE BED BUG.

INTRODUCTION.

One of the problems discussed in the present paper is, how does a bed bug find its host? It is understood that the internal physiologic conditions, which are summed up in the term "hunger", force the bed bug to search for food. But how does it find its victim? What stimulus attracts the bug? and what guides it to its prey? Is it guided to the host by sight, odor, or what other agency? If it is assumed that the odor of man is the attractant, as most writers are inclined to believe, the question is, what particular odor in man exerts such an influence upon this insect?

Furthermore, in the literature (Kemper, 1929 a), the idea is brought forth that bugs discriminate between different individuals - that is, they will feed upon some, but refuse to feed upon others. The present writer was also told of a case wherein two persons, a father and a son, were sleeping in one bed in a bug-infested hotel, and while one of them was very much annoyed by the blood-

thirsty insects, the other was not touched. Many cases of this nature are related upon one occasion or another. How is it possible to explain this fact? This particular problem is rendered more complicated when one learns that the same insects which seem to be so discriminating in discerning between human individuals, feed readily, without discrimination, on rodents, fowls and other animals. An analysis of this problem involves the study of tropisms and it is with the intention of throwing light upon these matters that the writer undertook the study, the results of which are presented in this paper.

THERMOTAXIS.

Definition and Literature.

The term thermotaxis or thermotropism is used to designate the reactions of an organism toward heat. As pointed out by Marchand (1920), there are two kinds of reactions to heat. One reaction, the more common, is the aggregation of organisms in their specific temperature-optimum. It is a well established fact that every organism has a definite specific temperature-optimum in which its physiologic activities are best carried out. Therefore, if an organism is found in a temperature lower than its optimum, it will tend to move, if it is not hindered, toward a higher temperature and vice versa. Thus Herter (1923) found that the Heteropterous Pyrrhocoris apterus L. aggregated in a temperature of about 28° C. When placed at a temperature below this, or above it, the insects invariably moved toward this optimum. The same bugs experienced heat fright at $32\frac{1}{2}^{\circ}$ C and did not venture beyond this temperature. Such reactions are common in most insects. In a few groups of insects, however, there is in addition another kind of reaction to heat

and it is this type of reaction which is discussed hereafter.

Under certain physiologic conditions, few insects move toward a source of heat regardless of whether it is higher than their optimum-temperature and exhibit some definite reflex action associated with feeding. Naturally we would expect the same organism to move away from this heat when the particular physiologic conditions which brought forth the reactions have changed. To illustrate this type of reaction, the experiments of Howlett (1910 and 1917) and Marchand (1918) may be quoted. These observers independently discovered that mosquitoes are not stimulated to "bite" the person by the odor of blood, nor by the odor of perspiration, but by the heat of the body. Mosquitoes extended their probosces and tried to "bite" a test tube filled with hot water. Some lice react in the same way. Howlett (1917) states that Phthirus pubis L, while feeding, shows no reactions to a heated test tube placed over its back but "otherwise becomes greatly excited and moves with remarkable eagerness and rapidity" and "shows wild efforts to reach it." Also, Frickinger (1921), who experimented on the body louse for olfactory reactions, came to the conclusion that the louse has a sense of heat or "Wärmesinn."

To the present writer's knowledge, no one has made a special study of thermotaxis with reference to the bed bug. Occasionally, however, reference is made here and there regarding the effect of heat upon this insect. Hase (1917),

for instance, in speaking of presumptive attracting stimuli of the bed bug mentions first the smell of the skin and then heat, as follows: "Der Hautgeruch wohl auch die Wärmestrahlung der Haut." Klingmüller, according to Kemper (1929) believes that this insect, in search of food, will select the warmer areas on the human body. Kemper (1929) states that from a short distance the warmth radiating from the human body might act as an enticement for the insect. But none of these writers made a study of the subject.

Observations and Experiments.

Thermotropic Reactions Associated with Feeding:

The writer had the opportunity to observe the thermotropic reactions in the bed bug before he began experimenting on this subject. A male and a female of Cimex lectularius were placed together in a small, tightly-stopped vial for the purpose of observing courting and mating under a binocular microscope. The vial was held between the thumb and finger and the two were facing each other in an apparently quiet state. Suddenly the two raised and stretched their antennae toward the point where the finger touched the glass. Soon they advanced toward that point with probosces outstretched, stroking the surface of the glass as though seeking a suitable place for piercing. This casual observation led to a series of experiments, the object being to determine whether or not heat was an important stimulant which called forth feeding reactions.

A test tube 10 mm. in diameter, containing an adult female, was placed over the metal shade of a desk lamp so that the tube was slightly heated at one end. In a short while the female, which had been in a quiescent state, "woke up" and raised her antennae toward the direction from which the heat radiated. After stroking the antennae with the forelegs for a moment, she moved toward the source of the heat with proboscis extended, ready for piercing.

A petri dish was lined with paper to provide a foothold for an adult female bug which was placed therein. A dissecting needle was slightly heated over a lamp and placed near the bug. Soon she awoke, raised her antennae, stroked one, then the other, with her forelegs and started toward the needle with proboscis extended. Upon reaching the needle, she made futile attempts to pierce it. When the needle was moved, the bug followed it in every direction. The same needle was cooled and the procedure repeated, but none of the above reactions occurred. This experiment was repeated with other specimens, both adult and young.

A test tube, 10 mm. in diameter, filled with warm water, was placed in a dish wherein there were several hungry, adult bugs. Immediately upon detecting the heat, most of them advanced toward the glass with extended probosces and upon coming close to it, stroked with their tips, the surface of the tube as if searching for a suitable piercing point.

From the foregoing observations and experiments, it appears obvious that heat is an important factor in stimulating

the insect to obtain food. Under its influence, reflex actions associated with blood-sucking, take place regardless of whether there is a host available or not.

Factors of Light, Humidity and Nutrition on Thermotropism:

The question may be raised, what conditions influence these tropic reactions? would light, humidity, or state of nutrition affect it to any great extent? Contrary to the accepted opinion, as discussed in a later chapter, light, when not too intense, does not seem to interfere very much with the activities of the bug. All of the experiments on thermotropism were conducted during the day or in the evening at the light of a desk lamp; the light factor in this case was of little importance.

In order to determine whether relative humidity has any effect on these reactions, the writer tested thermotropism under different relative humidities as follows: By means of water, concentrated sulphuric acid and various saturated salt solutions, relative humidities of different ranges were obtained. The acid, or the solution, as the case may have been, was poured into a small dish, which in turn, was placed in an air-tight jar and left there for an hour or two and in some instances for several hours. The humidity was measured by means of a dew-point apparatus, which could be introduced into the jar by a special opening made for this purpose in its cover. Through the same opening, a thermometer could also be placed therein, as could likewise a rod to stir the solution

whenever the case required. When the desired humidity was obtained, the bugs were introduced through a very small hole on the side of the jar especially provided for this purpose. This opening served also for the introduction of the warm rod by means of which the thermotactic reactions were tested. This procedure was carried out several times under various conditions of humidity and it was found that the insects reacted positively to heat at a range of relative humidities from about 15% to 95%. However, when the object, which radiates the heat, is humid, the reactions are negative as shown in a later chapter.

Conditions of nutrition may interfere more with thermotropism than any of the other above-mentioned factors. Bugs, which had a full meal, do not react to heat as hungry bugs do. Nevertheless, the writer observed, on many occasions, that some individuals, after having gorged themselves with blood, and after crawling around for a few seconds, returned to feed anew. It is not exceptional for a bed bug to manifest reactions associated with feeding on the day following its consumption of a good meal. Lack of any such reactions was noticed during the pre-molting period and a day or two after molting. The bugs which show the greatest sensitivity to heat are those which have been starved for some time.

Factors of Time and Distance in Relation to Thermotropism:

It is of interest to learn whether heat radiation

also serves as a guide for the insect in locating the host from afar. For that purpose, it is important to establish at what distance a bug is capable of detecting heat and how quickly a response to heat takes place. The following experiments were conducted with a view to answering these questions.

A bed bug was put on a small piece of paper inside of a vial two cm. in diameter. The vial was placed horizontally and the paper, holding the insect, about four cm. from the bottom of the vial. The latter was permitted to remain undisturbed for from 20 to 30 minutes. The finger was then placed against the bottom of the vial without displacing or disturbing the insect. The object was to measure the lapse of time required for the first response to heat from the moment the finger was placed against the vial. The indication of this heat detection was based on a sudden awakening-like reaction, and an extension of the antennae. This test was repeated with several adult individuals at two different room temperatures. Of ten individuals tried at a room temperature of from 22° - 25° C., on an average, a minute and a half elapsed before a detection of heat was indicated. As mentioned above, the source of heat was the finger which, upon measurement, proved to be about 28° C, located at a distance of about four cm. from the bug. The minimum time was about one minute, while two individuals did not display any heat perception before the expiration of two minutes and a half. At a room temperature of 18° - 19° C, individuals, under the same condition, required on

the average approximately three minutes or more before they perceived the heat.

All other conditions remaining the same, there seemed to be no marked change in the time of reaction when the finger was placed at the opening of the vial instead of at the bottom. Naturally, olfactory responses might have interfered with heat reaction in this case; nevertheless, there still seemed to be no difference. On the other hand, when the vial was placed vertically on the finger, all other conditions remaining the same, the time of reaction was reduced to about a third.

A vial, filled with hot water of about 45° - 48° C, was placed in the center of a petri dish. Along the margins of the dish, there were about a dozen bugs in an apparently quiescent state. The purpose of this was again to test how long a time would elapse before the bugs detected the heat at this temperature and under these conditions. The experiment was repeated with several groups of bugs on various occasions. It was found that at a room temperature of 22° C, from one to two and a half minutes were required; at a room temperature of 19° C, at a distance of five cm., more than 3.5 minutes were required for their detection of this heat.

From the above, we learn, therefore, that bugs are not very quick in discerning the stimulation of heat, the source of which is at a distance beyond two or three centimeters. When the heat source is very close, or when heat is made to travel faster, the reaction takes place more rapidly - in other words, it depends upon the rate of heat conduction.

Upon the detection of heat, the bug does not necessarily crawl immediately to the source of heat. Often several minutes pass before it starts to move and then it may crawl aimlessly. The paths of a few bugs, which were very inactive and which were stimulated to crawl by heat, are presented in figure 1 .

The procedure described in the foregoing was applied, also, for the purpose of establishing the distance from whence the bugs crawl directly to the source of heat without wandering about. The paths of individuals verging about the source of heat are produced in figures 2 and 3 . It should be noticed that at a room temperature of 22° C, some bugs crawled directly to the temperature of 45° C from a distance of five cm. (Fig. 2). In this case, they did not advance nearer than 3.5 cm. because that temperature was too high. When the source of heat is of a lower temperature, the distance is shorter.

Figure 4 represents the paths of three bugs moving about in a petri dish, indicating the distance at which they finally detected the finger of the writer, the external heat of which is about 28° C.

Will a bed bug, under natural conditions, detect a host from a distance? In order to create such conditions, the following preliminary test was performed by the writer before going to bed. On a summer night, with the room temperature at about 24° C, the writer, in his pajamas, lay uncovered on the bed for five minutes. He then released one hungry, adult bug at a distance of about 50 cm. from his body and lay motionless

and watched carefully every movement of the bug. Immediately upon her release, she began to move away. When she came near the edge of the bed, she was brought back and placed at half the distance mentioned before. This time she moved in a direction parallel to the length of the body and then turned away. She was then placed at a distance of 3-4 cm. from him, whereupon she moved straight toward his direction with proboscis extended, ready to attack.

Differential Temperature Required to Produce a Thermotactic Reaction:

The experiments discussed above indicate that at a distance of four cm., in a closed vial, at a room temperature of 23° C, from one to two and a half minutes were required before hungry, adult bugs reacted to the heat radiating from the human body. Upon measurement, the external heat of the same person proved to be 28° C. By means of these records, it was possible to obtain some data as to how high the temperature in the environments of a bug must rise before it manifests positive reactions to heat. The experiments below were carried out for this purpose.

Two vials of the same size as those used in the experiments above were employed. A thermometer was placed in one of the vials "A", together with one junction of a thermocouple of copper and constantan. The other junction was placed in the other vial, "B". The readings were made with the aid of a

Leeds & Northrop portable potentiometer. At the beginning of the experiment, the temperature in both vials proved to be identical. The finger was then placed at the bottom of vial "B", about four cm. from the junction, while vial "A" was not touched. The differences in temperature were recorded at the end of thirty seconds, one minute, two minutes and three minutes. The reading was in millivolts and the temperature differences were obtained by dividing these numbers by .038, the number of millivolts per degree centigrade. The experiment was carried out at room temperatures of 23° C and 27° C. The readings at the mentioned time intervals with respective temperatures in both vials are given in the tables below.

Time from start of experiment in minutes	Difference of temperature in Millivolts	Difference of temperature in degrees C.	Temperature in vial "A" in degrees C.	Temperature in vial "B" in degrees C.
0	.00	0.0	23	23.0
0.5	.05	1.3	23	24.3
1	.068	1.8	23	24.8
2	.10	2.6	23	25.6
3	.10	2.6	23	25.6
0	.00	0.0	27	27.0
0.5	.05	1.3	27	28.3
1	.075	2.0	27	29.0
2	.075	2.0	27	29.0
3	.10	2.6	27	29.6

A short study of these data indicate that in either case, at the end of one minute and a half the difference in the temperatures in the two vials was approximately 2° C. It has been previously mentioned that under duplicate circumstances, at about this same lapse of time, the bugs, on an average, manifested thermotropic reactions. In other words, a rise in the temperature of about 2° brought forth these reactions.

It is a known fact that a nocturnal moth, under phototactic conditions, is liable to fly into a flame and be killed. Will a bed bug, likewise, under proper conditions, because of positive thermotropism, attempt to attack any warm object even though its temperature may prove to be detrimental to its life? From all indications, the case with the bed bug seems to be different. High temperatures may attract the bug at first but upon approaching it, it changes its course of direction. In the experiments described above, a temperature of 43° - 45° C. causes a change of direction at a distance of 25 or 30 mm., while a temperature of 39° - 40° C. caused the retreat at a shorter distance as figure indicates. Under the latter conditions, bed bugs are often quite active, advancing and retreating, attempting each time to touch the glass but retreating because of the high temperature.

Discussion:

Summarizing the foregoing, it may be stated that under certain conditions, the bed bug shows positive thermo-

tropism and that radiating heat is an important factor in its obtaining food. Thermotropism is greatly dependent upon the state of nutrition of the bug and its stage of molting. The strength of reaction is influenced by the distance of the object radiating the heat, its temperature, as well as the temperature of the environments.

Howlett (1910) states that the strength of reaction to heat in mosquitoes is "within certain limits proportional to the differential temperature," - that is, the difference between the air temperature and the temperature of the object. This difference must also be positive - that is, the temperature of the object higher than that of the air. The present writer finds the case with bed bugs slightly different, unless the term "within certain limits" provides for this difference. Quoting an example, an object of 28° C, at a room temperature of 23° C, will give a lesser differential temperature than a room temperature of 19° C. Therefore, the reaction in the latter instance should be, according to Howlett, stronger than in the former instance. The reverse was the result of the experiment on the bed bug conducted by the writer. In general, he found that at a cool room temperature, when the insects are less active, the reactions are weaker. However, with an optimum room temperature, Howlett's theory holds. Then the bed bugs are fairly active and the slightest heat radiation from an object causes positive thermotropism. Thus, at a room temperature of 23° C, an object of 24° or

25° C. will call forth positive reactions. The same object, however, will not affect the behavior of bugs at a room temperature of 26° C. Then a higher temperature is necessary to call forth any reactions. At a room temperature of 33° C. only an object of a still higher temperature will call forth positive thermotropic reactions associated with feeding.

CHEMOTAXIS.

Review of Literature.

There is no doubt that the olfactory sense plays a very important part in guiding insects to their food plants. It has been demonstrated that insects feeding on plants find their food by means of the odors emanating therefrom. The most plausible explanation, for instance, for the fact that the Harlequin bug, Murgantia histrionica Hn. attacks several plants belonging to the family Crucifera, is that some volatile oils, probably mustard oils, which are present in all the plants of this family, act as the attractant. Likewise, a special odor characteristic to all cucurbit plants, may guide the squash bug, Anasa tristis De G. to its food. Similarly, Blissus leucopterus Say, selects members of the grass family because of some common odor found in all these plants. No experiments have verified this assumption but with our present knowledge, it is the best explanation.

In the literature on the subject, it is commonly believed that blood-sucking insects also are attracted to their prey by the odor emanating from the animal. Weiss (1913), for instance, assumed that "when emerging from their winter quarters, females of Culex pipiens are at first positively chemotropic---." Howlett (1910), who experimented on the

olfactory response of the mosquito, believed that neither sweat nor blood attracted them. The medical entomologists, who made a study of the olfactory reactions of the body louse, generally obtained negative results. Frickinger (1916), in reviewing the literature on the subject, states that most authors find that the louse does not react to odors and that they question whether the insect possesses a sense of smell. His own experiments would support this view but for one exception - wherein a body louse was attracted to a piece of cotton soaked in sweat. Hase, according to Frickinger, also claims to have demonstrated that the louse can smell because he succeeded in making one of these parasites follow his finger in all directions.

The first one to pursue a scientific study on olfactory responses of *Cimex lectularius* was De Geer (1773), who tried the influence of turpentine upon this creature. Since then, to the knowledge of the present writer, no investigation has been carried on in this line until very recently. It has been commonly assumed by many authors, without facts to support their idea, that the bug is guided to its host by its sense of smell. Bohn (1905) for instance, states that during the night "il semble guidé presque uniquement par les odeurs." Hase (1917) in every case wherein he wished to refer to any reactions of the bug toward his hand spoke of the "Handgeruch."

Kemper (1929) made a more complete study of the olfactory responses of the bed bug. In several methods he tried the effect of the odor of perspiration on the insect. However, he obtained no positive reaction. The olfactory response to thirty-seven chemicals, including acids, fatty acids and other substances, were tested, all of which called forth no positive reactions. As a result of these experiments, that writer stated as follows: "Eine wanzenanlockende Wirkung liess sich bei keiner der untersuchten Substanzen feststellen. Die Bettwanze besitzt ein Wahrnehmungsvermogen fur die Dämpfe einiger flüssiger Präparate, während sie sich denen anderer gegenüber vollkommen indifferent verhält."

Observations and Experiments.

While trying to feed a starved female, the writer observed that she refused to feed upon his finger. She approached it but soon retreated without having touched it with the tip of the proboscis. The same female was next placed upon the arm, above the wrist, whereupon she began to feed. Several reactions similar to this were observed with many other individuals, both larvae and adult. On one occasion, the finger was placed near groups of bugs, whereupon some individual moved away and hid under a piece of paper. When the finger was again placed near them, they again moved away. On another occasion, one starved female was allowed to crawl on the table. The finger was placed about 25 cm. ahead of her. Upon reaching

a point of about 15 mm. in front of the finger, she changed her direction. This was repeated a few times with the same result. When some other object, instead of the finger, was placed in her path, this female did not hesitate to crawl under or upon the object. Generally speaking, although the bugs were often fed upon the finger, it was always easier to feed upon the arm above the wrist rather than upon the hand because they hesitated more often to feed upon the latter.

Those reactions, as well as the fact mentioned in the introduction, that some people are subject to attacks of bed bugs while others are immune, led the writer to assume that there is present in the human body, in addition to a stimulus which attracts the bugs, also another which repels them. Furthermore, the concentration of these stimuli or their balance differs in various organs of the body and with different individuals.

Assuming, like most writers, that the odor of the body is the main attracting stimulus, guiding the insect to its prey, some experiments in chemotaxis were carried out to discover, first, which particular odor calls forth these positive reactions and second, which odor repels it. As a positive reaction in this case, the writer designates one in which the insect manifests reflex action associated with feeding - e.g. extending the antennae and proboscis in the direction of the stimulus, walking toward it, and attempting to pierce with

the proboscis the object from which the odor emanates. When the insect evaded the source of odor, the reaction was considered negative. In the term "neutrality" the writer designates indifference to the stimulus. In the tables below, these reactions are labeled with the signs, (+), (-), and (0), respectively. In the course of experimenting, some bugs manifested some hesitation before assuming a definite position toward the stimulus. To indicate this hesitation a "?" was placed in front of the sign. Oftentimes an insect showed a positive reaction, but upon coming closer to the stimulus, it retreated. In such cases, the respective signs of both reactions were given in their order of appearance, the latter designating the final reaction - e.g. (+/-).

In order to ascertain whether the bug possessed an olfactory sense, the odor of xylol was tested. After several trials, it was found that bugs do perceive the odor of this substance from a short distance. Only when a drop of xylol on a cover glass was placed in the immediate vicinity of the bugs did they retreat; otherwise they remained indifferent. That the retreat was due to negative olfactory reactions was established by the fact that the same bugs remained indifferent when clean cover glasses were placed near them. Therefore, in the following experiments, in order to ensure that the insects perceived the odor of the substance in question, it was placed in close proximity of the insect instead of at a distance.

Experiment on the Odor of Blood:

When an attempt is made to study the olfactory reaction of an insect, naturally the effect of the odor of its food is tried. While the writer was dubious as to whether the odor of the blood permeated the skin, mingling thus with the general odor of the body, he attempted, nevertheless, to discover its effects upon the bug.

A drop of fresh, human blood, put on a cover glass, was placed near various groups of bugs, as well as near isolated individuals. When the blood was fresh and moist, the reactions were distinctively negative. It seems the moistness of the blood repelled the bugs. When it dried, the creatures remained rather indifferent. This experiment was repeated on several occasions; also, the blood of rabbit and chicken were tried but definite positive reactions were not observed. Table I, below, contains the tabulation made of one of these experiments when human blood was used.

Table I - Olfactory Reactions of Bed Bugs to Human Blood.

Description of the Bugs	Description of Reactions	
8 adults--5 females; 3 males; over 5 weeks old; not fed for 10 days.		7(-) 1(+/-)
7 adults--4 females; 3 males; molted 5 days ago; not fed.	4(0)	3(-)
6 nymphs--V instar; molted 2 days ago; not fed.	4(0)	2(-)
7 larvae--IV instar; molted 1 day ago; not fed.	5(0)	2(-)
15 larvae--III instar; molted 3-4 days ago; not fed.	7(0)	8(-)
Total - 43 bugs	20(0)	23(-)

The single temporary positive reaction indicated in the second column of the table was probably due to the heat of the blood. However, as shown, this particular individual was repelled immediately upon coming nearer to the blood.

Experiment on Odor of Animal Tissue:

It might be suggested that the tissue of the animal host possesses an odor which attracts the bed bugs. Or perhaps the subcutaneous tissue, beneath the derma, possesses some substances acting as the attractant. The following experiments were conducted in an endeavor to find out whether such was the case.

The effects of fresh hypodermal and muscle tissue of

a lizzard, mouse and rabbit were tried. Oftentimes the olfactory responses toward these tissues were negative, but more often they remained indifferent. In one case, however, a definite positive reaction was observed toward the muscle tissue of a rabbit. A female approached it with extended proboscis and pierced it until the entire proboscis was in the tissue. However, this was the only individual in which positive olfactory responses to the muscle tissue were observed.

Different reactions, of extreme interest, were observed in several individuals toward liver tissue of cattle. The bugs that were tried, as indicated in Table II, were starved. Most of them advanced toward the liver tissue with extended probosces, but retreated immediately upon coming to, or in closer contact with it. Assuming that the moistness of the tissue, as discussed in a later chapter, repelled the insects, the surface of the tissue was allowed to dry, and then again placed near the bugs. Precautions were also taken to avoid thermotaxis. In this case, too, the bugs exhibited the same tendencies as before - approaching the tissue with extended probosces but retreating upon coming closer to it. Some of the insects encircled the piece of tissue, coming nearer every now and then, and occasionally even touching the tissue but always retreating. It seemed obvious that the liver contained some substances which called forth positive

olfactory reactions, but it possessed, also, other substances which strongly repelled them. On several occasions the bugs appeared hesitant about approaching the tissue. They exhibited at such times quivering-like, reflex actions in the legs. The writer has made no attempt to discover which of the substances in the liver acted as the attractant. Several of the experiments described below may offer some suggestions in this respect. The olfactory effect of the bile taken from the gall bladder of the same liver was tried on the same bugs and proved to be a very marked repellent.

Table II - Reactions of Bed Bugs to Odor of Liver and Bile.

Description of the Bugs	The Reactions to the Odor of	
	Liver	Bile
6 adults--3 females; 3 males; molted 10 days ago; not fed.	6(+/-)	6(-)
4 nymphs--V instar; molted 4 days ago; not fed.	4(0)	4(-)
4 larvae--III instar; molted 6 days ago; not fed.	4(+/-)	4(-)
Total - 14 bugs	10(+/-) 4(0)	14(-)

Experiment on Skin Odor:

On several occasions, the writer observed that bed bugs attempted to feed upon dried skin of animals. Thus a leg

of a mouse and the ear of a rabbit attracted the insects four or five days subsequent to the removal of the organs from the bodies. In the last-mentioned instance, in order to be convinced that heat was not the attractant, the organs were cooled to a temperature lower than that of the room and then placed near the bugs. The stimulus was still present, calling forth positive reactions. It appeared obvious, therefore, that the general odor of the skin attracted the insects. It is understood that the skin odor in general is a compound odor composed of those from the corneous layer, the perspiration, and sebaceous secretion. In addition, the products of decomposition of these secretions influence the general odor to a great extent. To determine which of these odors acts as the attractant, a series of elimination experiments were carried out.

First, the odor of the corneous membrane was tried. The pieces of skin from the mouse and rabbit were washed in ether and this latter substance poured off. This procedure was repeated, and the skin dried. Other pieces of skin were washed in hot, soapy water and then the soap thoroughly washed off in clean, hot water and the skin allowed to dry. When these treated pieces of skin were tested, no positive reactions were observed. See Table III.

Table III - Reaction to the Odor of Rabbit Skin.

Description of the Bugs	Reactions to the Odor of	
	Untreated Skin	Treated Skin
7 adults--4 males; 3 females; 10 days since molted; fed 8 days ago.	3(+) 3(0) 1(-)	7(0)
8 nymphs--V instar. molted 2 days ago; not fed.	4(+) 4(0)	8(0)
Total - 15 bugs	7(+) 7(0) 1(-)	15(0)

The reactions of bugs to pieces of skin removed from the palms of human beings were variable, as shown in Table IV. A piece of this skin was then treated in soapy water as mentioned above. To such treated skin the bugs remained indifferent. Pieces of clean finger nails were also tried but called forth no reactions.

Table IV - Reactions to the Odor of Human Skin.

Description of the Bugs	Reactions to the Odor of	
	Untreated Skin	Treated Skin
7 adults--4 males; 3 females; 10 days since molted; fed 8 days ago.	4(+) 2(0) 1(-)	7(0)
8 nymphs--V instar. molted 2 days ago; not fed.	3(+) 4(0) 1(-)	8(0)
7 larvae--IV instar. molted 2 days ago; not fed.	4(+) 3(0)	7(0)
8 larvae--I instar. Hatched 2-4 days ago; not fed.	2(+) 6(0)	8(0)
Total - 30 bugs	13() 15(0) 2(-)	30(0)

It is obvious, therefore, that when the odor of the secretions is removed, the odor of the skin does not attract the bugs.

Experiment on Odor of Perspiration and its Constituents:

The chief contribution to the general body odor is that of perspiration and the products of its decomposition. This excretion was the subject of controversy among many writers in connection with olfactory responses of various blood-sucking insects. As mentioned above, Kemper (1929) tried the effect of the odor of sweat upon bed bugs and found

that these insects did not react to it. The following experiments were conducted before the writer had had the opportunity to read Kemper's paper. The study presented here was made from a different viewpoint; other procedures were employed and different results were obtained. The time and distance factors were temporarily ignored, the purpose being to learn whether there would be any response, even from a short distance, such as 1 cm.

Perspiration from the body was scraped off on a cover-glass and then placed in a dish in which there were several bugs. The bugs showed no positive reaction. Some retreated when they came near it; others remained indifferent, even when the glass was brought quite close to them and was left there for some time. Cotton was employed to wipe sweat from the body and was afterwards placed in a dish in which bugs were kept. As a control, clean cotton was used. As a rule the insects were indifferent to this stimulus. At times, however, their reactions were negative, while in a few of the several trials, positive reactions were observed. After several similar attempts, which resulted only in slight positive reactions, the writer was inclined to believe, like Kemper, that sweat exerts no olfactory influence upon the bed bugs.

However, one factor was not taken into consideration in the reactions discussed above - namely, moisture. Bed bugs, as will be discussed in the chapter on Hygrotropism, avoid

humidity. In the two procedures described above, the moisture was not removed; in the following procedure it was. A needle holder was contaminated with the odor of sweat merely by rubbing it with the hand, cooled, dried and then placed near the bugs. In this instance the bugs showed more distinct positive reactions. The number of bugs and their reactions in a few of these experiments is given in Table V.

Table V - Olfactory Reactions to Perspiration.

Description of the Bugs	Reaction to Odor of Perspiration from				
	Palm of Hand			Arm Pit	
7 adults--2 males; 5 females; over 5 weeks old; not fed for over 10 days.	5(+)	1(0)	1(-)		
The same the following day.	1(+) (1 died)	2(0)	3(-)	3(0)	3(-)
7 adults--3 males; 4 females; 4-5 days old; not fed.	3(?+)	1(0)	3(-)		
The same the following day.	2(+)	5(0)			7(-)
6 nymphs--V instar. molted 2 days ago.	1(+)		5(-)		
20 nymphs--V instar. molted 3 days ago; not fed.	1(?+)	17(0)	2(-)		
7 nymphs--V instar. molted 3 days ago; not fed.			7(-)		
7 nymphs--V instar. molted 1 day ago; not fed.			7(-)		
7 larvae--IV instar. molted 1 day ago; not fed.		2(0)	5(-)		
15 larvae--III instar. molted 2-3 days ago; not fed.	4(+)		11(-)		
Same the following day.	9(+)	6(0)		5(0)	10(-)
16 larvae--I instar. molted 2 days ago; not fed.	7(+)	9(0)			
20 adults--6 males; 14 females; molted 3-4 days ago; not fed.	8(+)	9(0)	3(-)		
Total - 140 bugs	41(+)	52(0)	47(-)	8(0)	20(-)
Percentage	29.3	37.1	33.6	28.6	71.4

It is true that quite a large percentage of the individual trials showed negative reactions or indifference, but the positive reactions, although they were not intense, cannot be overlooked. It should be noted that the perspiration of the palm of the hand was used where no contamination of the odor of sebaceous secretion could take place. Furthermore, the hands of the person whose perspiration was tried washed his hands thoroughly before the experiment to avoid the odor of the products of decomposition. It must be noted, also, that the perspiration of the various individuals had diverse effects upon the insects.

What is there in the secretion of the sweat glands that may cause this positive reaction? According to Howell (1930) the following substances are found in the sweat: water, chloride salts, urea, uric acid, aromatic oxyacids, ethereal sulphates of phenol and skatol, serine, a trace of albumen and cholesterol. In experimenting with sodium chloride, urea and uric acid, no positive reaction was yielded toward these substances; the experiments with cholesterol are discussed below.

The perspiration from the body proved to be more repellent than that from the palm of the hand. These reactions vary greatly depending upon the nutrition factors in the individual insect. One may suggest that on the body where

hair is abundant, the odor of sebum may contaminate the odor of sweat and cause this negative reaction. However, this is not the case as shown below. The reason probably lies in the fact that on the body the sweat is allowed to undergo decomposition and it is the odor of substances of decomposition which cause the repellent effect. One of these substances is butyric acid. A trace of this substance was smeared on a cover-glass and placed in a petri dish containing bugs. Its odor proved to be very repellent to the insects. Within a short time most of them were found at the most remote distances from the cover-glass.

Summarizing, we may say there are some elements in perspiration which call forth slight positive reactions in the bed bug. Others, however, especially where the secretion is allowed to undergo decomposition, have a very repellent effect upon this insect.

Experiment on the Odor of Sebum:

Another important contribution to the general body odor is that of the secretion of the sebaceous glands. These glands, with a few exceptions, are located around the hair roots and the characteristic hair odor of man, as well as other mammals, is due to the oil secreted by these glands. To test the effect of this secretion, the odor of hair was tried and proved to be quite attractive. Some of the bugs experimented with perceived the odor of a lock of hair at a distance of 3 cm. and the percentage of bugs attracted to the human hair was quite great.

Several strands of hair of the same person were soaked in cold alcohol and washed with cold water several times. After drying the hair, it was tested again. A few bugs still exhibited marked positive reactions, but the number attracted to it was reduced. It seemed, therefore, that the attractant was still present. A part of the hair to which the bugs were attracted was then washed - first in hot, soapy water, and then with clean, hot water, and dried. When this treated hair was placed in the dish where the bugs were located, no positive reactions were manifested. It appeared obvious that the oil on the hair, which had been washed off, was the cause of the positive reaction. It was found that any object, which is contaminated with the odor, caused by stroking the hair a few times, called forth positive reactions. The tabulations below were made from individual trials with a needle holder contaminated with odor of hair. As shown in Table VI, a great percentage of the bugs that were tested exhibited distinct positive reactions. Care was taken in each instance to avoid thermotropism.

An attempt was made by the writer to separate this oil from the hair in order to test the effect of its odor upon the bed bug. This was accomplished by washing the hair with ether and allowing the same to evaporate, leaving a fatty residue. The odor of this oil was tested; most of the bugs remained indifferent while very few showed faint positive reactions. A greater percentage of the same bugs reacted positively to the odor of fresh hair. It seems that the oil lost some of

its properties in the process of evaporation. Similar results were obtained with oil separated from rabbit's hair and commercial lanolin. The latter occasionally produced a distinct positive reaction, but as a rule indifference to the fat was manifested.

The secretion of the external auditory meatus - the cerumen - contains a substance closely related, if not identical, with the sebum. The effect of this odor upon the bugs was tried by holding close to the individual bug tested a piece of paper or needle holder contaminated with this odor. The results are given in Table VI, which presents a high percentage of positive reactions to this odor. The sebaceous secretion, according to Howell (1930) contains a large percentage of cholesterine. This material, in its pure form, was obtained in order to test the effects of its odor upon the insect. The responses were variable. At times distinct positive reactions were manifested, while at other times a repellent effect was noticed. Usually they remained indifferent when the substance was placed near them. More distinct positive reactions were noticed when the powder was moistened slightly with water. Sodium glycocholate and taurocholate, also, were tried. The latter, especially when used in a paste form, attracted a small percentage of bugs.

Table VI - Olfactory Reactions to Sebaceous Secretion.

Description of the Bugs	Reaction to the Odor of					
	Hair			Cerumen		
7 adults--2 males; 5 females; about 5 weeks old; fed over 10 days ago.	7(+)			6(+)	1(0)	
7 adults--3 males; 4 females; molted 4-5 days ago; not fed.	4(+)	2(0)	1(-)	4(+)	1(0)	2(-)
6 nymphs--V instar. molted 2 days ago; not fed.	6(+)			3(+)	1(0)	2(-)
20 nymphs--V instar. molted 3-4 days ago; not fed.	11(+)	7(0)	2(-)	8(+)	7(0)	5(-)
7 larvae--IV instar. molted 3 days ago; not fed.	2(+)	5(0)		4(+)	3(0)	
15 larvae--III instar. molted 2-3 days ago; not fed.	10(+)	3(0)	2(-)	8(+)	6(0)	1(-)
8 larvae--II instar. molted 2 days ago; not fed.	6(+)	2(0)		6(+)	1(0)	1(-)
Total - 70 bugs	46(+)	19(0)	5(-)	39()	20(0)	11(-)
Percentage	65.7	27.1	7.1	55.7	28.6	15.7

Summarizing the foregoing, of all the substances tested, the sebaceous secretion connected with the hair roots exerted the greatest positive olfactory influence upon the bed bugs.

The Influence of Distance and Time on Olfactory Reactions:

As mentioned above, the sense of smell in the bed bug is very weak and it cannot be compared with that of some insects

which can detect food or their mates from a great distance by the guidance of odor. The object of the two experiments below was to measure the intensity of the sense of smell of the bug in terms of minutes and centimeters.

A drop of bile, which was repellent to the bugs, was put in a petri dish wherein there were several hungry adult individuals. These were forced, by the use of a strong light, to crawl freely in the dish. The object was to see how near a bug must approach the substance before it detects the odor. The paths of the bugs verging about the drop of bile were traced while they were crawling and are reproduced in Fig. 7. As shown, the bugs were unable to detect the odor from a distance greater than 1 cm.

A few hungry adult bugs were permitted to remain on a piece of paper in a petri dish undisturbed for about a half hour. A lock of hair was then placed $3\frac{1}{2}$ centimeters from the bugs. A strip of paper, serving as a bridge between the bugs and hair, offered freedom of movement. The object was to see how much time would elapse before the bugs perceived the odor and would begin to advance toward the hair. Six minutes passed before the first perception of the odor was indicated. The reaction was manifested by slightly raising the head, extending the antennae and stroking the proboscis with the fore tarsi. One individual displayed, also, quivering reflex actions in one hind leg. Four minutes later some of the bugs turned toward the hair and began to crawl toward it. A few advanced a short distance and then returned; others ventured nearer to the hair. The paths of

these individuals were traced immediately and are reproduced in Fig. 8 . The oblong areas along the path of an individual indicate a pause of a few seconds. As noted, the paths were not straight. Even at a distance of one or two centimeters some individuals changed their course of direction as if searching for the source of odor.

Experiment on Sense of Taste in the Bed Bug:

Kemper (1929) states that he could not find any taste organs in the mouth cavity of the bed bug similar to those found in the mouth cavities of other Hemiptera. He adds, also, that he does not see any need for such organs in this bug since it obtains blood from a host which it has already located. McIndoo (1916) advanced the theory that insects cannot taste, while Minnich (1924) suggests that the so-called olfactory organs on the feet of some insects are organs of taste.

The following experiments in artificial feeding of the bed bug may perhaps offer some suggestions regarding the problem. By the artificial method described in another paper, the writer offered the bed bugs liquids other than blood. These were: pure water, sugar solution, chicken broth, and blood serum from which the hemoglobin was removed.

Of these liquids, blood serum was always more acceptable and the bugs of all stages gorged themselves with this

fluid. After they had succeeded in puncturing the membrane, all of them fed without hesitation.

Chicken broth was taken by many specimens but in most cases only small quantities were ingested. Some individuals withdrew their probosces immediately after they started pumping.

The sugar solution, which had been stained with guinea green B as an indicator, was ingested by some individuals in a scarcely sufficient quantity to even still their hunger; few obtained sufficient quantities to render the alimentary canal green. More often the bugs refused to continue feeding after they had tasted the fluid. This tasting could be indicated by a green tinge in the alimentary tract which was easily seen in larvae of the earlier instars.

Pure water was never ingested, although the writer cannot say definitely whether it was tasted or not.

General Discussion:

It has been stated above that the bed bug can smell and that it is attracted to some odors emanated from the human body, while it is repelled by others. The odor of perspiration, which is the most conspicuous of the body odors, attracts the bugs very slightly; on the contrary, when this secretion has gone through decomposition, it repels them. The odor of the sebaceous secretion, especially when it is fresh, acts as a great positive olfactory stimulus to this insect.

However, the sense of smell in the bed bug is very slightly developed and it cannot detect the odor from afar. Hence, it does not appear feasible that the odor serves as a guide to the insect during its search for food.

One may suggest that with this insect, since it is guided also by heat, the odor serves as a means of discriminating between a source of food and a dangerous object. However, it is to be noted that the insect is often repelled by an animal odor and, on the other hand, may show an extreme effort to pierce objects of glass or metal which have no odor, as long as they radiate heat.

It might be suggested that the olfactory stimulation in the insect is of the nature of taste, as suggested by Minnich in connection with Butterflies. According to Minnich, the contact or proximity of a sugar solution with the tarsi brought a reflex action in the proboscis. In the bed bug, too, a perception of a positive odor causes an extension of the proboscis with an attempt to pierce the object from which the odor emanates. However, it seems that the insect possesses the ability to discriminate between various foods only after it has taken them into the mouth cavity. It should be remembered, also, that the food of the insect exerts no olfactory influence upon it and that the odors that do cause the reflex action in the bug come from an entirely different source. Furthermore, the insect was quite often fed artificially where

the effect of the odor was of least importance, as long as it was not repellent. The chicken skin, which was employed in the artificial feeding, called forth no reaction until warm liquid was poured into the tube.

The following attempt to explain the role of odor in the bed bug may be considered a phylogenetic hypothesis. It is quite probable that the bed bugs originally were guided to their hosts by means of odor only. The ancestors of the bed bugs - before the age of man - which were capable of flying, probably nourished themselves on mammals and birds and detected them by means of the odor. This assumption explains, also, the positive effect of the odor of sebaceous secretion, which is more characteristic of hairy and feathery animals. Then, too, they developed the ability to detect the host by its heat, since the approach to a host always meant approaching a warm object. In more recent ages, the establishment of the insect in the dwellings of its hosts - perhaps nests of rodents, bats, birds, and homes of man - caused the gradual loss of ability to locate the host from a distance by means of odor. Together with this, it lost, also, the ability to fly. The sense of smell, which the bugs now possess, is merely a rudimentary vestigial sense, just as its hemelytra are vestigial organs of flight.

HYDROTAXIS AND HYGROTAXIS.

Definition and Literature.

In most previous literature no distinction is made between the term hydro- and hygrotaxis. In the following paragraphs, however, the term "hydrotaxis" is used to designate a reaction to water, while the term "hygrotaxis" is employed for a reaction to air humidity. In both kinds of reactions, the stimulus is water. In the one case, however, it is in the liquid state, whereas in the second case it is in the form of vapor. The stimulations of water and vapor may be of entirely different classes. They may perhaps stimulate different sense organs, just as the fumes of some chemical substances stimulate the olfactory organs, while direct contact with them stimulates other organs - i.e. those of taste. Furthermore, we find some insects - Odonata, Culicidae, etc. - which are attracted to an atmosphere of 100% relative humidity while water repels them.

Very little investigation has been done in this field with hemipterous and blood-sucking insects and most

of our knowledge regarding these reactions rests upon casual observations rather than upon experiments. In aquatic Hemiptera apparently negative and positive hydrotropisms alternate with the change of light intensity and temperature. Positive hydrotropism has been observed in female mosquitoes at the time of oviposition.

From Hase (1917) and others, we learn that Cimex lectularius L. is very strongly negatively hydro-tactic. This is quite common among terrestrial animals and this matter would not have been discussed were it not for the following: (1) When the bed bug cannot escape moisture, it always assumes a definite characteristic position. (2) The food of the bug is liquid and whereas one might expect the insect to be positively hydrotactic, the opposite is the case. (3) Hygrotaxis has an important bearing upon the food habits of the bed bug.

Observations and Experiments.

Throughout the period of rearing and experimenting with C. lectularius, the writer observed that this bug is negatively hydro- and hygrotactic. Bed bugs avoided touching exposed blood which is their food. Rats were quite readily attacked by these creatures when dry, yet

when the mammals were moist, they were not touched. Bugs eagerly attempted to pierce dried skin, but refused to touch it when moist. To ascertain these observations, the following experiments were carried out.

A piece of moist paper, about 3 mm. square was placed inside, against the wall of a test tube. This spot was then slightly heated from the outside by placing a finger on it. Soon, some of the bugs, which were in the tube, attracted by the heat, advanced toward this spot. However, upon coming to a point about one centimeter from the paper, they turned and retreated. Upon other occasions, when the moist paper was not present, the bugs advanced further and stroked the glass with the probosces as described in previous experiments.

A test tube, containing warm water of 40° C., was placed two centimeters away from a group of hungry adult bugs. Soon some of the insects approached it and stroked the surface with the tips of their probosces. The tube was then removed and wrapped with a warm, moist piece of cheese-cloth of a temperature of about 35° C. Again, the bugs showed positive thermotaxis. However, upon coming near the moist cheese-cloth, they retreated before touching it.

A little water was poured in a watch glass and two adult bugs were placed in it. They began to walk and

wade in the water attempting to find a dry place. When the surface of the water touched the ventral side of the abdomen, they straightened out their legs and appeared as if walking on stilts. A short while later, since they could not keep their bodies dry, they stood still, their legs straightened out, abdomen obliquely raised and their posterior ends bent upward. Similar reactions were observed in other adults and in larvae.

Discussion:

The observations and experiments show clearly that the bed bugs are negatively hydrotactic and hygro-tactic. These reactions, the writer believes, partly explain why some people are not annoyed by these creatures, while others are attacked by them. Since the amount of perspiration differs in individuals, the repellent effect upon the bugs may differ also.

The writer attempted to learn what relative humidity may be regarded as the optimum conditions for the bed bug. This, he tried to discover from probable indications of lack of "comfort" in the bugs when placed under various conditions of humidity. Such indications would be derived from restlessness of the bugs and the attempt to locate different environments. He failed, however, to obtain any such indications as the insects proved to be very inactive. Furthermore, as shown in a later chapter, the

bed bugs can thrive well in extremely variable conditions of humidity.

STEREOTAXIS VS. PHOTOTAXIS.

Literature.

The term stereotaxis - reactions to solid objects - has been discarded in recent literature, and the term thigmotaxis - orientation according to touch - has taken its place. The writer, however, for the reason given elsewhere (The Tropisms Effecting Copulation in the Bed Bug) intends to restore the former term which is more suitable. Several Hemiptera exhibit, under certain conditions, the tendency to be in contact with solid objects. Riley (1921) reviewed the literature treating the reactions of aquatic Hemiptera to contact and light. From his own conclusions, and that of other observers, it is to be noted that stereotropism underlies the gregarious instinct, as well as the habits of hibernation and selection of retreating places in Notonectidae, Nepidae, Belostomidae, Gerridae and other aquatic Heteroptera. These stereotactic tendencies may be counterbalanced by positive phototropism in which case the insects fly towards the light. Thus Torre-Bueno (1914)

lists several species of Heteroptera observed around street lights. According to Clark (1925) Plea striola Fab. and Notonecta undulata Say, are both phototropic and stereotropic. In the former, the reactions to contact are stronger, whereas in the latter, the reactions to light are more powerful. As the temperature increases, phototropism becomes stronger in both.

Regarding the bed bug, many authors report that it is a true nocturnal insect and that during the day it hides in dark corners, cracks, crevices and other similar places. De Geer (1773), for instance, says "elles sont de vrais insectes nocturnes, elles se cachent le jour et ne se mettent en mouvement que la nuit." Often groups composed of several individuals of different ages are found in one group. Hase (1917) reports an instance of more than one hundred specimens in one place. This author believes that the gregarious tendency is due to their negative reactions to light. The first bug, he states, may settle near some object which throws a slight shade. Its own shade serves as the hiding place for another bug, and the shade of this latter attracts others and so on. His conclusion, to quote him word for word, is: "Wir können sagen aus ihre Vorliebe für die Dunkelheit kommt es zu dieser Heerdenbildung der Wanzen."

Bohn (1905) is the only one who carried out experiments and who made a study of the reactions of the bed bug to light. The results he obtained, however, are doubtful. To

quote an example, this author states that Cimex always preferred to walk in a shaded area, and that upon reaching a lighted area it turned 180° . A change in the intensity of light, according to him, brought forth a reflex action manifested by this rotation. This change in direction always occurred even though it brought the creature back to a lighted area. He believed, therefore, that "l'animal est en quelque sort victime d'une habitude acquise." His experiments were repeated by the present writer but none of the bugs experimented with showed such reactions or "acquired habit." Another statement of the same author is as follows: "Une diminution d'éclairement produit sur elle le même effet qu'une augmentation d'éclairement. Quand la variation est brusque, c'est une inhibition de mouvements, quand elle est progressive, c'est une impulsion rotative dans un sens déterminé." Regarding this last statement, in a second paper Behn (1906) again states that every individual seems to have an inherent tendency of rotating in a definite direction, clockwise or counter-clockwise, and no matter from whence the light comes, the same individual will always rotate in the same direction. None of the bugs experimented with by the present writer showed such tendencies.

Experiments and Observations.

From observations in infested cages of rats and other rodents, it seemed evident that cracks, crevices and the

corners between the wire nets were preferred by bed bugs to a much greater extent than any other part of the cage. Such places, however, were quite often exposed to light and yet the creatures stayed there undisturbed. In a very dark corner of a cellar of an apartment house, several specimens of bugs were found crowded in between folds and corners of an old mattress. In this instance the place was in total darkness and light could not disturb them, yet they crowded together in the folds. Similarly, bugs which were reared in the vials, chose as retreating places, notches or holes in the cork. If such were not available, the space between the vial or the cork served the purpose, or a fold in the paper, or even a slight concavity. These were not always concealed in darkness. Generally speaking, although the bugs preferred darkness, it seemed as if the light, when not too intense, did not disturb them very much. The creatures seemed to prefer to retreat to a place where they could be in contact with some object in spite of the fact that such places were often exposed to light.

Hase and others maintain that because of their love for the darkness, bugs aggregate, one selecting the shade of the other as a place of retreat. If this is true, we should presume that when a group of bugs are placed in total darkness, where there is no shade of individuals, that no groups will be formed. The experiment below indicates that such was not the case.

Twelve bugs of the first instar were put in a

petri dish in the center of which a piece of glass was located. The dish was placed in a box and was covered so that no light penetrated through it. About an hour later, the cover of the box was removed. The bugs were found crowded together near the glass in the formation shown in figure 6. The dish was then placed in the sunlight, whereupon the larvae became restless and dispersed within a minute. This procedure was repeated again. When examined a few hours later, the bugs were again found in about the same formation as indicated in figure 6.

It seems it is the tendency to be in contact with some object, rather than the preference for darkness, that is the underlying cause for the formation of groups. That this positive stereotaxis is also an important factor in selecting places of retreat is shown by the following experiment.

In a petri dish filled with water, a glass plate was placed upon some objects so that the water touched the lower surface of the plate but did not cover the upper surface. Upon this surface, a smooth piece of paper was tightly pasted avoiding all concavities or irregularities in the surface. Although the experiment was conducted during the day, major light factors were removed by throwing a uniform shade upon the dish. Ten larvae of the second instar, which had molted two days previously, were allowed to crawl freely upon the plate. They crawled for some time indicating no intention of settling down to a particular spot. A piece of wood was then placed in the center of the plate (position a, Fig. 5). A short while later

the bugs began to aggregate along the sides of this piece of wood. When they all collected, they were brushed away and the wood removed to "b". After a short period of wandering, the bugs again aggregated near the wood in a new position. Once more the insects were brushed away and placed in position "e" and later at "d", but they always collected near the piece of wood (Fig. 5).

Should we adhere to Hase's theory, we would say that in this case the bugs came to the shade thrown by the wood. However, that this is not the case can be seen from the following experiment.

A quadrangular sheet of paper ABCD (Fig. 9), 5 x 15 cm., was pasted tightly upon the flat surface of a glass plate. In order to keep the bug from trespassing this field, a boundary of water was drawn around the field ABCD. A cardboard was erected at EF, which threw a shade EFGH. The light came from a desk lamp of 40 W, at a distance of 30 cm., at an angle of 30° . Ten larvae of the first instar were placed in this field, together with their mother. All the bugs began to wander about in this vicinity in every direction. They paced back and forth from one margin to the other. By no means did any of them show a preference for the shaded area rather than for the lighted one. Fifteen minutes after the beginning of the experiment, a pin was placed in the position PQ (Fig. 9), in order to see whether the bugs would prefer to stay near it regardless of its exposure to light. Every now and then one or two of the larvae would stop for a few seconds near the pin and then

resume wandering. Only one larva stayed by it for about eight minutes and then walked away. Forty-five minutes from the beginning of the experiment, as the bugs still continued wandering, a square piece of blotting paper 1 x 1 cm. and about 1 mm. thick was placed in position XYZV. About five minutes later, two bugs were along the side XY. Other larvae collected and crowded themselves against the sides of the paper trying to crawl under it. One hour from the start of the experiment, two larvae had crawled under the square paper; seven were along its sides and one larva and the adult female were settled near corner D, along the margin of the paper as presented in figure 9.

This experiment indicates that not the negative reaction to light, but rather the positive reaction to contact, caused the selection of the place of retreat. There surely was more shade in the area EFGH than along the blotting paper. The reason the bugs did not choose to aggregate along the pin is, as noted on other occasions, because of its smooth surface. They usually prefer to be in contact with a rugged or rough surface.

Discussion:

Summarizing the foregoing, we can say that the bed bug is negatively phototactic to strong light and is positively stereotactic. These two reactions dominate its habit in selection of places of retreat. When light is not too disturbing, stereotropism is the major factor in choosing a place for

retreat. When light is too strong, they will move away in search of another spot wherein they can exhibit the tendency to solid objects. At any rate, it is not their love for shade that causes group formation or underlies the habit in selecting places of retreat.

THE INTERRELATIONSHIP OF TROPISMS.

Tropisms govern behavior to a very great extent. Holmes (1912) states that they are the foundations of behavior; their study, therefore, is essential for one who desires to understand the behavior of an organism.

The reactions toward an external stimulus depends, naturally, upon the intensity of the stimulus, its duration and frequency. However, the same reactions depend, to a greater extent upon the internal physiologic conditions of the creature. These, in turn, may be influenced by the external stimuli. Furthermore, one tropism may stimulate one reaction or may hinder another. All these reactions are interlocked, interdependent, influencing and influenced by each other so that they are manifested as a whole in the behavior of the organism. In the previous chapters some tropisms were discussed as separate units. In the following paragraphs a summary will be given wherein the interrelationship of the

tropisms of the bed bug will be pointed out, and their effect upon the behavior of the organism during its feeding.

Kemper (1929) came to the conclusion that "the human body or any other warm-blooded animal has no enticing stimulation (Anlockungsreiz) upon a bed bug which is at a distance. This insect is capable of coming into the neighborhood of its victim by means of memory of the locality (Ortgedächtnis) in cases where the latter is found in a place which has been previously occupied by a host; otherwise, as it wanders at random, it may find the victim by chance. From a short distance, the heat radiating from the body may perhaps exert some influence upon it." The present writer agrees with the first part of this conclusion, namely, that from a distance the human body exerts no influence upon the bed bug. However, he cannot accept this entire hypothesis. It is rather far-fetched to say that the obtaining of food by a bug is pure chance. It is quite safe to assume that the bugs wander in search of food because of an internal urge rather than because of external stimuli. Thus, individuals may be seen crawling on the walls and furniture of infested rooms although there is no host in evidence. This internal urge, however, may be stimulated by a heat wave. As brought forth in the chapter under thermotropism, a wave of a temperature two degrees centigrade higher than the surrounding temperature will cause the bugs to start crawling. This does not necessarily mean that the heat wave will cause them to crawl directly to the source of heat. As pointed out

in the chapter on thermotropism, direct guidance by heat takes place within a circumscribed area. When bugs are located in a bed or mattress, a slight wandering may bring them into a vicinity where the heat radiation guides them directly to the host. In the case where the insects are found on the walls, it is quite probable that in many instances the wandering never brings them in the proximity of a host.

In literature, a story is quoted time and again of a bed bug, which, unable to reach a sleeping person, crawled on the ceiling over the bed and dropped upon the prey. This was probably an accident. The aimless wandering no doubt brought it to the ceiling. There, the radiation of heat from the sleeping person was more stimulating and the insect made efforts to reach the source. In such an instance, the bug usually extends the head and antennae and forelegs and, under these circumstances, it is quite easy to see how it might lose its foothold.

Strong light may inhibit the tendency of wandering but dim light does not interfere with their activities. Bed bugs are thus found crawling in daylight on walls and furniture.

Once in the proximity of a host, positive thermotropism may be counterbalanced by other external stimuli. Humidity checks the insect from further advance; if the host is wet, the bug will not attack it. Odor, if not pleasant to the bug, will equally check the insect from approaching a host. As mentioned heretofore, these two factors may explain the

fact that some people are attacked by bugs while others in the same bed are not annoyed. On the other hand, when the odor is attractive, it may add to the strength of the thermotropism in overcoming the repellent effect of humidity.

Upon reaching the warm object, the creature shows positive stereotactic reactions manifested at the tip of the proboscis. From observations and feeding experiments, the writer learned that a bed bug would make no attempt to pierce with its proboscis a surface which is too smooth. Usually, when an object radiates heat or an attractive odor emanates from it, the bug will first stroke it with the tip of the proboscis. Should the surface of the object be slightly roughened like that of an animal tissue, it will attempt to pierce it. On the other hand, if the surface is too smooth, like that of a finger nail, chitin, horn, reptile-scale, iron, glass, rubber, egg shell, etc., the positive tropisms gradually diminish until they no longer exist. The bug retreats. Naturally, as is the case with other reactions which diminish under a continuous stimulation, a recovery of the original reaction may take place after awhile, upon a renewed and stronger stimulation. A slight roughness or crack in a smooth surface stimulates it to attempt to pierce it. The tendency then is to insert the proboscis deeper and deeper into the tissue.

To summarize the foregoing, during the procedure of obtaining food, four phases may be distinguished, as follows:

- A. The advance to the host: The reactions during this period are thermotropic and chemotropic. The antennae are directed usually anteriorly and obliquely upward, and together from an acute angle from 65 to 90 degrees.
- B. The search for a suitable place to pierce: The reactions during this period are stereotactic. The proboscis is extended and its tip is in contact with the surface of the host.
- C. The drilling: The reactions during this period are stereotactic. The labium of the proboscis is geniculate. Antennae are directed laterad, forming approximately a straight line.
- D. The ingestion of food: The reactions during this period are gustatorial. The pumping apparatus is functioning. The antennae are directed slightly posteriorly, making an angle of over 180 degrees.

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EXPLANATION OF PLATES.

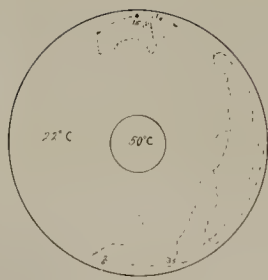
Plate I.

- Figure 1: Routes of bed bugs under the stimulation of a temperature of 50° C.
- Figure 2: Routes of bed bugs under the influence of a temperature of 43° - 45° C, first approaching it and then retreating.
- Figure 3: Routes of bed bugs attracted to a temperature of 40° - 42° C, hardly touching it and retreating immediately.
- Figure 4: Routes of bed bugs approaching a finger.
- Figure 5: Formation of bed bugs in selecting a place of retreat.
- Figure 6: Formation of a group of bed bugs under condition of total darkness. The diameter of the petri dish in every case being 12 cm.

Plate II.

- Figure 7: Route of bed bugs in the proximity of a drop of bile, the odor of which is repellent.
- Figure 8: Routes of bed bugs approaching a lock of hair, the odor of which is attractive.
- Figure 9: The retreat of bed bugs showing their preference for contact with a piece of paper exposed to light, rather than for shade in which no contact stimulation is available.

PLATE I



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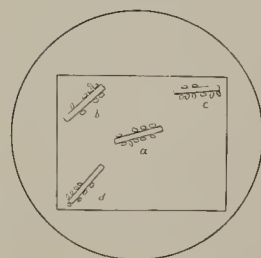
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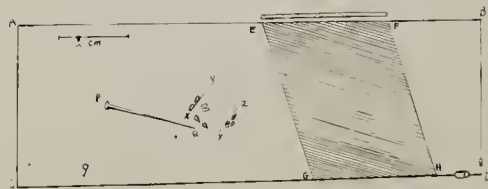
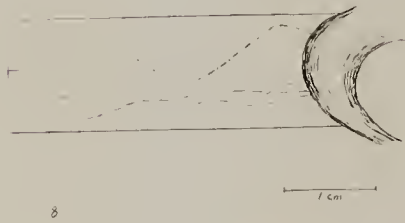


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PLATE II



HOST SELECTION AND CANNIBALISM IN THE BED BUG
CIMEX LECTULARIUS L.

In the paper on the tropisms of the bed bug, the writer stated that the heat is the major stimulus which attracts the bug to its host - man. Furthermore, he found that every warm object calls forth such reactions, and that these reactions depend upon the difference between the temperature of the object and that of the immediate environment of the bed bug. If this is true, one would expect that any warm-blooded animal would equally attract this creature, and that it would readily feed upon any host without discrimination. The discussions in the literature dealing with this subject tend to support this view for we find long lists of animals and birds upon which the bed bugs have been found feeding. According to Martini (1923) the following hosts have been recorded: Mammalia: Bat, cat, calf, dog, guinea-pig, hare, mouse, rat, monkey and rabbit. Aves: Duck, goose, hen, pigeon, sparrow, starling and swallow. Several authors believe, however, that these animals or birds are attacked only in emergency - when human blood is not obtainable, and should a human being be available, the bugs would attack man rather than animal. If this assumption is

correct, the theory advanced in the beginning regarding thermotropism is false - for then one would expect that some other stimulus present in man and lacking in other animals is the alluring agent. In an attempt to throw light upon this subject, the writer made a study, the results of which are given herewith:

The specimens used in this study belonged to the progeny of females obtained from an old mattress, and from the cages of rodents reared in the Pharmacological Laboratory of the Food, Drug and Insecticide Administration at Washington. Adult bugs were kept separately in small vials 1.5 cm. in diameter and 15 cm. long or in small test-tubes 1 cm. in diameter and 10 cm. long. A piece of blotting paper was placed inside of these to provide a foothold for the bugs and to reduce the humidity. The individual bugs were labeled with Arabic numerals - e.g.: Female 3; male 9; etc. The progeny of a female, the eggs of which were laid in a period between one feeding and another, were labeled with the same numerals but an additional Roman letter was added to identify the individuals - e.g.: 20A, 20B, etc. By this labeling method, it was not difficult to keep records of parentage and offspring during the course of the study. Individual records of feeding, molting, mating, egg-laying, etc. were kept in most cases.

Feeding Experiments of Bugs Upon Warm Blooded Animals.

Several feeding experiments were carried on wherein bugs, collected in cages of rodents, were fed upon man and those collected in infested mattresses were fed upon rodents. Similar experiments were carried on also upon the progeny of these insects and extended over a period of about four months, including the offsprings to the fourth generation. The hosts upon which they were fed were rat, guinea-pig, cat, rabbit, pigeon and canary. During all this time, the writer never observed any marked tendency showing a preference for one host over another. Seldom did any of the bugs hesitate to attack any of the animals or birds. Even those that had been fed the day before approached them quite freely. Often a meal was given to one individual from two different kinds of hosts. Thus, to quote my notes, "On June 19, nymphs 9A and 9B fed part of their meal on a cat, and completed it on a rat; both molted June 25. On June 25, larva 1B fed part of her meal on a pigeon and part on a rat; she molted June 30." In several cases, while handling these animals, the hand of the writer was as near to the bugs as the skin of the experiment animal, yet they seldom showed any preference toward the hand. This was the case with all insects whether they were bugs reared on human blood or of those reared on animal blood.

Summarizing the results of all the experiments

throughout this period, we may say that the bed bugs show no preference in selecting the host. This is due to the fact that heat is its major guiding agent to its prey.

The Feeding Experiment on Cold-Blooded Vertebrates.

The question might arise: If the heat radiating from the animal is the major guiding agent of the bug to its host, how was it possible for Chatton and Blanc (1918) to feed Cimex lectularius L. upon cold-blooded reptiles, such as the gecko, chameleon, Gongylus ocellatus, and even upon the amphibian Rana temporaria? Before explaining this, let us review first the experiment of those authors. Chatton and Blanc (1918) placed a gecko in a narrow test-tube so that it could not move, and also ten bugs of various ages together with it. They prepared twelve such tubes, five of which were placed in darkness at ordinary room temperatures (lot A); two were left in daylight at ordinary room temperatures (lot B); and the remaining five were placed in an incubator at 37° C. (lot C). Half an hour later, they were taken out and examined and the results were as follows:

	Lot A.	Lot B.	Lot C.
Temperature	19° C.	19° C.	37° C.
Light condition ..	Dark	Light	Dark
No. of bugs in Exp.	50	20	50
No. of bugs fed ..	24	12	37
Percentage of bugs fed	48%	60%	74%

These results indicate that light conditions did not affect the feeding desire of the bugs or at least did not hinder their feeding. We see, also, that a greater percentage of bugs fed at a high temperature rather than at a lower one. However, these results apparently do not agree with the thermotactic theory given at the beginning of this paper. In the first place, in the case of Lot A and Lot B, why did the bugs feed on the gecko at a temperature of 19° C? Was there a difference in the temperature of the gecko and that of the immediate environment of the bug? Then in the case of Lot C, when the temperature of the gecko was raised to 37° C., the temperature, also, of the immediate environment of the bugs was raised to that degree and thus there was apparently no heat current to stimulate the thermotactic reactions. In order to check the above results, the writer carried out the following feeding experiments:

Adult bugs, quite hungry, were placed upon the snakes, Natrix sipedon and Diadophis punctatus, but they made no attempt to attack these reptiles, although they were left with them for some time. One of the snakes was in a glass container and quite moist and this may have caused the negative attitude of the bugs, but the other snake was in a dry box and yet no positive reactions were observed. The same procedure was carried on with the lizard, Eumeces fasciatus, but they did not attack it. It was evident, therefore, that reptiles at ordinary room temperature and under natural conditions do not attract the bed bugs.

I then held the lizard, Eumeces fasciatus, in my hand,

and stretched out one of its legs against a few bed bugs. They attacked it. The same thing occurred when I placed a slightly heated forceps near one of the legs of the lizard. In these two cases the bugs did not succeed in piercing the skin of the lizard. It is clear, however, that when a reptile's temperature is raised somehow above the room temperature, the bed bugs do not hesitate to feed upon it.

The same lizard, Eumeces fasciatus, was used to carry on an experiment similar to that described by Chatton and Blanc. I placed it in a small vial with 5 larvae of the third instar. Immediately upon my placing them there, they began to attack the lizard and within ten minutes four of them were feeding on the tender skin between the toes of the hind foot. After twenty minutes all four were engaged with the blood of the lizard. The fifth one made several attempts to pierce the skin of the lizard but without success. This feeding experiment was repeated successfully several times.

The following heat measurements explain the results obtained above:

With the aid of a thermocouple and potentiometer, I recorded the temperature in the immediate vicinity of the reptile, about 5 mm. over its back in comparison with the ordinary room temperature. Two series of measurements were made: (a) when the reptile was not enclosed in the narrow vial; and (b) when the reptile was enclosed in a narrow vial.

In the first case the difference between the room temperature and that of the immediate environment of the lizard was very slight. In the latter case the difference was quite marked. When the reptile was free, a difference of 0.04 millivolts or about 1° C. was recorded. When the reptile was enclosed, its heat was preserved in the immediate environment so that a difference of 0.13 millivolts or about 3° C. were shown above the room temperature. In his paper on the tropisms of the bed bug, the writer has shown that the difference between the temperature of an object and that of the immediate environments of the bug must be at least 2° C. before any reactions may take place. Bearing this in mind, we can understand why the bugs failed to attack the reptiles when they were free and did not hesitate to attack them when they were enclosed in a vial. Furthermore, the experiments show that with reptiles heat is the only agent stimulating the bugs to feed.

Summarizing these experiments and including a few thigmotactic and hygrotactic reactions which I observed in bed bugs in their attempts to feed upon reptiles, I would say that C. lectularius L. under natural conditions does not attack cold-blooded vertebrates for the following reasons:

(1) The temperature of cold-blooded vertebrates varies with that of the environment and is very slightly above it. The difference between the two, however, is not sufficient to attract the attention of the bugs.

(2) The surface of reptiles is covered with scales and in addition to the physical difficulty in piercing those scales, the bugs will not attempt to do so because of the smoothness of their surface.

(3) The surface of many amphibians is moist and the bed bugs will not attack these because of their negative hygrotaxis.

When these difficulties are removed, namely, when the heat which the reptiles give off is preserved, or their temperatures are artificially raised far beyond that of the environment; when a scaleless surface is offered to them, such as between the toes or joints; and when the moisture is removed, the bugs freely feed upon these animals as the experiments of Chatton and Blanc and of the present writer have shown.

Cannibalism.

A great deal has been written regarding cannibalism in Cimex, and while early authors believed that bed bugs did attack each other in case of emergency, when no other food is available, later authors deny this phase in the feeding habit of the bug and consider this as impossible. Quoting De Geer (1773) we read as follows: "ce n'est sans doute pas leur unique nourriture, n'ayant pas toujours occasion de se rassasier de sang humain. Elle s'entre-tuent quelquefois et se sucent les unes les autres, les plus faibles ou les jeunes devenant la proie des plus fortes, comme j'en ai eu l'expérience

sur celle que j'avais rassemblées dans un poudrier." Recent authors consider this as an inaccurate observation because they never observed it taking place.

If the heat is the sole stimulant awaking the feeding appetite in the bugs, why should they not attack one of their own when the stimulus comes from that source? The present writer succeeded in making one of the bugs feed upon another as follows:

A larva in the second instar was fed upon the arm of the writer. It was then held carefully in a dish between the tips of a fine forceps which were slightly heated against a lamp to about 30° C. This temperature was maintained by the heat of the hand. In the dish there were two larvae of the third instar recently molted and ready to feed. Attracted by the heat, the two approached the forceps and began to stroke the metal tips with the probosces. Soon they began to stroke in the same manner the body of the captive larva. The chitin of the latter was too smooth and therefore they did not attempt to pierce it. This stroking continued for several minutes because the heat conducted from the hand to the tips of the forceps exerted a continuous influence upon the two hungry insects. Finally one of the bugs happened to strike upon the membrane connecting the metasternum and the coxa of the left hind leg of the captive insect, and with a few darts pierced this membrane as well as the wall of the digestive tract. Very soon, without warning, I saw the blood being pumped from the captive bug into

the tract of the attacking one. This did not continue for a long time because a movement of the captive bug forced the attacker away.

The writer made several similar attempts before and also afterwards but never again did any of the bugs succeed in piercing the chitin or membrane of the captives, although in every case they continuously stroked the surface of the same.

Under natural conditions "cannibalism" may take place immediately after feeding of a bug. Then the blood which has been ingested is still warm and, no doubt, radiates heat through the body walls of the insect. Other bugs that may be in the environment of a recently fed bug may thus be stimulated to attack it. A few times the writer observed how hungry larvae follow one of their own, right after it had been fed. A normal and active bug would naturally show resistance upon such attempts on the part of members of its kind. Often, however, it happens that a bug is somehow crippled after its meal. At times the digestive tract of a bug bursts during its meal or immediately after it. Upon this the ingested blood fills the coelomic cavity and hinders the activities of the creature until it finally dies. Bugs in such a state may be attacked by others. A larva in this condition happened to be placed in a petri dish together with other bugs. On the following day, the posterior half of the abdomen was dried and shrunken, whereas the rest of it was normally soft and filled with darkened blood. The creature had been probably attacked by another bug.

In view of these observations the writer is inclined to

support the statement made by De Geer (1773) regarding cannibalism in bed bugs.

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TECHNIQUE IN ARTIFICIAL FEEDING OF THE BED BUG,
CIMEX LECTULARIUS L.

Several students, who made a study of *Cimex* species as probable carriers of disease, attempted to feed the bugs artificially, but with little success. André (1912) attempted to feed the bed bugs cultures of pathogenic organisms mixed in bouillon, blood serum and blood; none of them were accepted. He also enclosed the above mentioned mixtures in spherules made of chicken skin, and tried to feed them to the bugs. However, he did not succeed. His own statement reads as follows: "Nous avons essayé d'enfermer du sang frais souillé de microbes dans des petites spherules faites d'epiderme de poulet, mais les *Cimex* ont refusé de piquer autre chose que des animaux vivants." He concluded, in other words, that the bug would feed on nothing but living animals.

Cornwall and La Frenais (1916), in their many futile attempts to feed the bug artificially, found that *Cimex rotundatus* refused to feed through parchment or even skin which had been kept in a refrigerator for twenty-four hours. Concluding that the bug would not feed through anything but live skin, they tried the following method:

The end of a glass cylinder, open at both ends, was placed inside the wound formed in a rabbit, close against the

cleanly shaven skin. The bugs were placed near the skin from the outside, while the culture of pathogenic organisms with citrated blood was poured through the other opening of the tube. It was believed that the bugs would not feed except on blood. By this technique, the authors claimed they succeeded in feeding the bugs pathogenic cultures. Shroff and Swaminath (1924) followed this technique with satisfactory results. In the foregoing method, however, a host was used, and the technique, it seems to me, was quite complicated.

The present writer, in studying the tropisms of the bed bug, C. lectularius, succeeded, he believes, in determining some factors governing the feeding habits of this insect. He found, for instance, that the odor of an animal is of secondary importance in attracting the bug, but that heat is the major attracting stimulus. The writer's experiments have shown that the bed bug will search for a suitable place to pierce any object radiating heat even though such an object be of metal or glass. It was this latter finding that stimulated the writer to develop, if possible, a technique of artificial feeding.

There are four main factors to be considered in attempting to feed the bug artificially. These are as follows:

- (1) Heat is an important agent which attracts the bug and stimulates its feeding desire.

- (2) The bed bug will not attack any object which emanates a repellent odor, even though that object radiates

(3) The bug will make no attempt to pierce any moist object, nor feed on any exposed liquid.

(4) Cimex lectularius will not attempt to pierce too smooth a surface.

EXPERIMENTS

Exp. A. A small piece of rabbit intestine, which had been previously washed and dried, was tied at one end and inflated to form a tube (Text Fig. A,t). This tube was filled with filtrated egg albumen and its closed end was slipped into the opening of a small test-tube in which there were two adult female bugs. The test-tube was held near its mouth by the thumb and first finger. Due to the heat of the finger and the thumb, the bugs approached the opening of the tube and stroked the glass with their probosces. By allowing the intestine to rest against one side of the tube, and shifting the finger to that point of contact, the bugs were induced to take notice of the intestine. They made no attempt to pierce or even stroke with their probosces the portion of the intestine above the string (m) which was filled with the egg albumen; they did, however, pierce the free end (d) of the intestine below the string. The albumen penetrated the intestinal wall, causing the external surface of the "tube" to be moist; the wet surface repelled the bug. The free end of the intestine below the string was dry and of the proper texture and was, therefore,

attacked. Water was substituted for egg albumen in another piece of intestine, and the procedure repeated. The results were the same.

Exp. B. A portion of shell was removed from a fresh egg so as to expose a small area of thin membrane. The egg was slightly heated by dipping it partially into hot water. Care was taken that the exposed thin membrane was not immersed. The shell was thoroughly dried and the egg was placed close to a group of bugs. They approached the egg with extended heads and antennae and upon reaching it, they stroked the shell with the tips of their probosces. The egg was then turned slightly to expose the uncovered membrane. This, the insects treated in the same manner as they had the shell - stroking continuously with the probosces but never actually attempting to pierce. Apparently the membrane was too smooth.

Exp. C. Membrane from a fish intestine was spread in a drum fashion over the opening of a glass tube (Text Fig. B). Through the other opening some warm chicken broth was poured into the tube and filled the drum. This was held in a petri dish wherein there were two adult female bed bugs. The latter were attracted by the heat and advanced toward the tube. However, upon reaching a point about 5 mm. away from the membrane, they retreated. Apparently the odor of the latter repelled the insects.

Exp. D. The procedure in this experiment is like that in Experiment C, except that the fish membrane was replaced by chicken skin which had been in a refrigerator for several hours, and the adult bugs were replaced by three larvae of the third instar. Attracted by the heat of the chicken broth, they approached the skin, extended their probosces and began to drill into the skin. They worked in this manner continuously for three to four minutes changing their positions now and then, as well as their piercing places. Being unable to obtain food, they finally retreated. When the broth, which had been cooled in the tube, was replaced by warmer broth, the above futile attempts were repeated again. Apparently the membrane was too thick and tough for them to pierce through it.

Exp. E. A tender piece of chicken skin, which had been in the refrigerator for several days, was stretched, and its adipose tissue carefully scraped off. This was then spread over the opening of a glass tube as in the preceding experiments, tied with a string, and dried with blotting paper. Warm chicken broth was poured through the other opening into the tube. This was then placed in a petri dish (Fig. C), wherein there were three bugs of the third instar. Attracted by the heat of the broth, they approached the tube and began drilling into the skin. In two or three minutes, I noticed the flat abdomen of one of the three bugs becoming inflated. A short while later,

after many attempts, the other two bugs also succeeded in getting food, although much less than the first.

Exp. F. Procedures are as in the experiment described above, with the exception that a diluted sugar solution stained with Guinea Green B replaced the chicken broth. The three larvae described in Experiment E (one of them having in the meantime molted), approached the warm solution and fed from it sufficiently to render green the intestinal tract which had been visible through the transparent body walls of the insects. The three larvae were kept under observation for a week and were finally preserved in glycerine, when traces of green were still visible in the intestinal tracts. The feces of these larvae were greenish brown. The same solution was also fed to two adult females. These, too, were kept under observation and their feces were as described above.

Exp. G. Procedures are as in Experiment E, with the following exceptions: (1) Blood serum obtained from fresh chicken blood replaced the chicken broth. This solution was heated slightly so as to prevent coagulation and hardening. (2) One adult female and her progeny, eleven recently hatched larvae, replaced the three larvae in the petri dish. The adult female fed to her full capacity, so that her abdomen was exceedingly distended. Nine of the larvae also succeeded in piercing the skin and fed to their full capacity, thereby becoming a pale pinkish-yellow.

After these successful experiments, several similar feedings were conducted in connection with other problems. These will be discussed in a later paper.

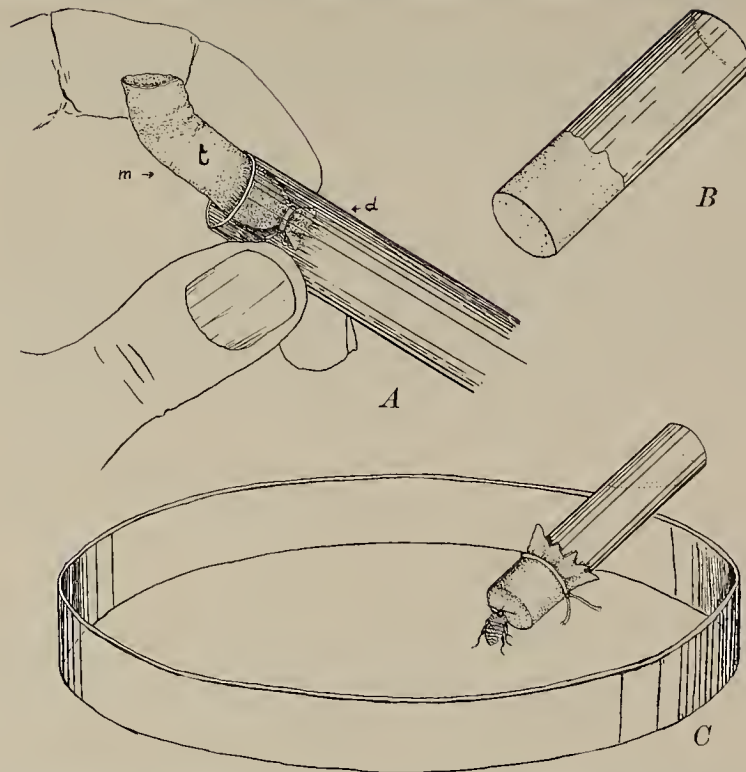
Summary

By taking advantage of the positive thermotropic reactions of the bed bug, this insect was fed on liquids other than blood.

The following factors helped in accomplishing this: The chicken skin employed was very thin and its surface of proper texture; moisture over the skin was blotted out; and all possible sources of repellent odors were removed.

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Artificial Feeding of the Bed Bug
Explanations in Text.

THE TROPISMS EFFECTING COPULATION IN THE BED BUG.

The fact that the female of the bed bug has a special asymmetrical opening for the reception of the male copulatory organs, rather than the ordinary vagina, makes this study extremely interesting. It is astonishing that this fact escaped the attention of early investigators and that the copulatory organs of so well-known an insect were unknown until comparatively recent years. A complete and detailed description of copulation in bed bugs was published by Hase (1918), and the most complete study of the sexual organs and their functions was made by Cragg (1914, 1920 and 1925). Copulation of bed bugs was observed by the present writer during the course of rearing them in connection with other studies. The peculiarity in this act is that the male mounts the female obliquely in such a manner that his head falls over the left side of the pronotum of the female; his left legs grasp the posterior part of her abdominal margin; and his posterior abdominal segment is bent deeply so that the tip reaches the right side of the ventral segments of the female. They remain in this position anywhere from one to several minutes.

No attempt was made by previous observers to establish the facts as to how the male locates the female, and what

tropic reactions govern the act of copulation, which is so unique in this insect. In the following paragraphs, the results of a study are given wherein the writer attempts to discover some of the facts regarding this problem.

In some insects, chemotropic reactions are of extreme importance in bringing together the two sexes of the same species for mating purposes. Mayers (1900) demonstrated what attracting force the odor from the female of the C. promethea moth has upon the male. In the case of the Japanese beetle, the female apparently diffuses some odor which is attractile to the males. On several occasions, the writer observed in the field, early in the season, over twenty males clustered around one female. Several of these males were attempting to mate with each other, a phase which will be discussed later. The ball-formed cluster, with the female in the center, would lead one to believe that some odor emanating from her attracted all these males. However, observations and experiments described below indicate that this "smell mind" idea cannot be applied in the case of Cimex lectularius.

A female approached a male from the rear and remained in his vicinity for a long time, yet the male did not perceive her. Only when the female passed in front of the male did the latter take cognizance of her and soon made attempts to mate with her. Such observations occurred upon other occasions. If odor signals the presence of a female, its effects should be manifested regardless of the position of the female, as long as

she is in the proximity of the male. This did not seem to be the case in the above-mentioned observations. In order to verify these casual observations, the following experiments were conducted.

Five females were placed in a vial, two cm. in diameter and a piece of cheese-cloth was spread and fastened over its opening. This was then turned upside down so that the cloth served as the foothold for the five bugs; it was then placed in a petri dish, allowing space for free circulation of air and odor. A similar vial, not containing bugs, was placed in the dish as a control. Five vigorous males were put in the dish and left there for 30 minutes. Although the males were in close proximity of the females, they did not pay any attention to them but contrarily made attempts to mate with each other. This experiment was repeated several times with similar results. If there is a secretion, the odor of which serves to entice the male, one would expect this odor to be characteristic of the female only. As a result, one would presuppose that a few males, if brought near females, would cluster around them or around their container in the attempt to mate with them. This was not the case in the experiments.

Again, three males were placed in a petri dish. Not long afterwards, one female was placed together with them. All remained inactive because the room temperature was rather low. Upon increasing the temperature slightly, the bugs became more active. One male soon mated with the female, while the other

male attempted to copulate with the third one. Contrary to expectation, the three males did not crowd around the single female as would have been the case had the female radiated some attractive odor.

From the observations mentioned previously, the writer was inclined to believe that it is more likely that the sight of the moving image guides the male to the female rather than the odor. The following experiments were carried out to discover whether such was the case.

A dead female was placed at the rear of a male and was left there for two or three minutes. The male did not observe her. The dead female was then placed about 15 mm. in front of the male and left there for three or four minutes. Here, also, the male did not notice her. The female was then moved slowly with the aid of a fine camel's hair brush, imitating the crawling of a live bug. The male, which had remained inert all this time "woke up", extended his antennae in the direction of the dead female, and suddenly jumped upon her and made every effort to mate with her. Similar procedures were carried out several times and also at other occasions with different males, and very often similar results were obtained. On one occasion, the two were tipped over so that the writer could observe, under the microscope, the protruded genitalia, attempting to open the copulatory slit situated between the fourth and fifth abdominal sternites of the dead female.

The question will arise as to whether the dead female

bed bug had some odor emanating from her which stimulated the male. It might, also, be suggested that the odor of the glandular secretion, if there is such, may be preserved in the female a long time after she is dead. Attempting to clarify this matter, one female was chosen which had been preserved in 70% alcohol for sixteen weeks. After she had been blotted and dried, she was placed in front of the male and was then moved slowly with the brush, imitating the crawling of the live bug. The male reacted to this dead female in the same manner as described heretofore. However, a still better proof that the sight of the crawling female, rather than the odor emanating from her, brings the male to her, may be derived from the following experiment.

A piece of cork was carved out into the size and approximate shape of a bed bug. After it was painted with ink and dried, it was placed in front of a male and moved slowly with the brush, again imitating the crawling of a bug. The male suddenly jumped upon it in the same manner as if it were a live female bed bug, but soon dismounted. A few other males reacted in like manner.

It is clear, therefore, that not the odor, but the sight of a moving female, awakens in the male, when he is under proper physiologic conditions, the desire to come in direct contact with her. It is also a noteworthy fact that the males lack the faculty of distinguishing between the two sexes, or even a lifeless object of the same size and shape. Recognition

of the female occurs through the sense of touch when the male is in direct contact with her. It is then that the male orients himself in a definite manner with reference to the surface of the body of the female.

Such reactions were observed by the writer in some beetles. In the potato beetle, L. 10-lineata, the male is of the same hemispherical shape as the female; consequently males attempt, often, to copulate with others of their own sex. They even fail to differentiate between mature larvae and adults which are of approximate size and shape. The identical shape of the two sexes in the Japanese beetle, P. japonica, was also the reason for similar behavior in the case described above. The odor may have guided the males to the female; however, upon coming in close contact with each other, they failed to discriminate between the two sexes. The male of the lady beetle, C. 9-punctata, previous to the act of mating, places the forelegs over the middle of the hemispherical body of the female and pivots over her, touching with his posterior legs and the tips of his ventrum the margins of the female. One observer relates how a male of the Scarabaeid species, Dynastes tityus L., having been permitted to crawl over his fingers, upon reaching the thumb, oriented himself upon the nail and attempted to insert his genitalia in the space between the nail and skin. One who is familiar with the size

and shape of this beetle, and the similarity of the same to a thumb nail, will understand the cause of such a reaction.

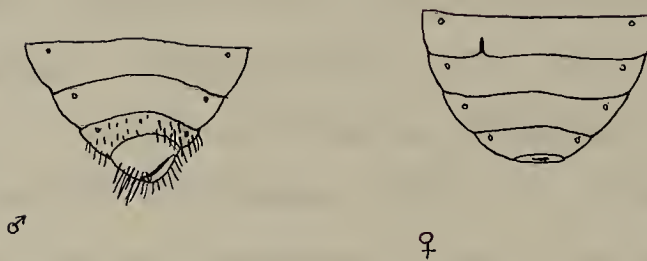
Reactions of such a nature were designated by early observers as "stereotropic" - indicating reactions to solid objects. This term, the writer believes, is not specific and he suggests the term "morphotaxis" for the particular kind of reaction discussed previously. This term is more suitable because it is the particular shape of the surface of the female or her specific form which calls forth the definite orientation. Morphotaxis may be considered as a more specific division of stereotaxis. The general term "thigmotaxis", substituting "stereotaxis", the writer believes, is entirely inappropriate for this reason: Most, and perhaps all of the technical names of the various tropisms are based on the Greek name of the stimulus which causes the reaction and not on the name of the sense by which the stimulus is perceived. Thus the terms are "phototaxis" or "chemotaxis" and not "optiotaxis" or "olfactotaxis". Hence, why should "thigmotaxis" - orientation according to touch - substitute "stereotaxis" - reaction to solid objects?

In the case with the above-mentioned Coleoptera, although the males manifested definite orientations with respect to the characteristic shape of their own species,

they lacked the faculty to "recognize" the female even after they came in direct contact with the other individual. The bed bug in this respect is more sensitive. It is true, by the sense of sight it does not distinguish a dead object from a live individual, but, upon coming in contact with it, it immediately recognizes the female. As mentioned above, the piece of cork was mounted and dismounted very quickly. The crude carving could not produce the natural shape of the bed bug and the male recognized the imitation very readily. When a male mounts another male, the lower one usually bends the tip of his abdomen upward; he thereby causes a change in his normal shape and form which, in turn, causes the upper male to dismount. Otherwise, the latter orients himself in the characteristic fashion as if he were a female. The shape of the latter stimulates the male to adjust himself obliquely as described in the foregoing, rather than laterally. The sense organs (Fig. /) of touch, along the ventral sides of the last abdominal segments of the males, are unequally distributed. It seems that the shape of the female in this position is so stimulating that even a dead individual calls forth the final copulatory reactions.

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Ventral View of Last Abdominal Segments of Male and Female Bed Bugs, Showing in the Male the Asymmetrical Distribution of Sense Hairs, and in the Female the Asymmetrical Copulatory Slit.

RATE OF GROWTH OF THE BED BUG AND SOME FACTORS
AFFECTING IT.

Literature.

The fact that the temperature affects the rate of development of plants and some animals has long been recognized, and several early writers attempted to establish the relationship of these. Peairs (1927) reviewed the literature and enumerated all these attempts showing the various steps leading to our present day conception of this relationship. Blunck (1923), in his study of the development of the larvae of *Dytiscus*, attempted to put his data in the form of the formula $T(t - c) = \text{Constant}$. In this formula, T is the development time of the individual; t is the temperature at which development takes place, and c is the critical point, or the threshold of development of other writers - that is, the temperature at which development ceases. With reference to the bed bug, in earlier literature, its rate of development was given without reference to the temperature. It is only recently that the factor of temperature with reference to the rate of metabolism has

been given any attention. The latest and most complete data are given by Jones (1930) who reared the bug under constant conditions of temperature and humidity. These data do not coincide very well with the data of earlier workers. To illustrate this discrepancy, his data, together with those of Martini, are given together in the following table:

Rate of Development of the Individual Instars of the
Bed Bug as Given in the Literature.

Jones (1930)			Martini (1923)	
Temp. 27° C.			Temp. 30° C.	
I. Instar	5.0 days		6	days
II. "	4.5 "		5	"
III. "	4.2 "		5	"
IV. "	4.6 "		5	"
V. "	6.0 "		6	"

If we take into consideration the two respective temperatures given, these, as discussed later, are contradictory. Bodenheimer (1924), collecting the data of Martini and other workers, attempted to apply Blunck's formula to the development of the bed bug. However, he did not have sufficient data for that purpose; furthermore, in verbal communication, he expressed to the present writer the difficulties in applying the formula to this bug.

The influence of humidity on the rate of development on some animals has been studied by Bachmetjew who, according to Headlee (1914) came to the conclusion that there is an optimum condition of humidity characteristic of each species, under which its metabolism is best carried out. Pierce (1916), as a result of the studies on the Cotton Boll Weevil, further expounded this theory in advocating that in humidity, like in temperature, the rate of development decreases when the insect is brought under conditions above or below its specific optimum. The data obtained by Headlee (1914) with reference to some Hemiptera are of extreme interest. This writer maintains that the rate of development of those insects was not at all influenced by the different conditions of humidities and he came to the conclusion that "the rate of metabolism in certain actively feeding insects, with an abundant supply of succulent food is not affected by large differences in atmospheric moisture."

To the knowledge of the present writer, no one made a study of the effects of humidity on the conditions of the bed bug. Jones, as stated above, studied the development rate of this insect under a constant relative humidity of 75% and the effect of humidities on the rate of starvation, but he did not test the effect of various humidities on its rate of normal metabolism. In brief, the following were the problems designed to be determined in this study: (1) The application of the temperature-development formula to the

bed bug and the derivation of the constant threshold of development from this formula, if possible. (2) Whether different conditions of relative humidity affect the rate of metabolism of the bed bug and if so to what extent. (3) What other factors may influence the rate of development of this insect.

Methods.

Ecologic Conditions:

The rearing of the individuals was carried on under three different temperatures, namely, 22° C, 27° C and 32° C. Six different humidities were applied for each temperature so that there were altogether 18 combinations of temperature and relative humidity. The various humidities were obtained by means of saturated salt solutions and concentrated sulphuric acid, as follows:

Water	or					
Potassium sulphate						yielding a relative humidity above 90%.
Potassium bichromate	or					
"	bromide	"	"	"	"	between 80% and 90%.
Sodium chloride		"	"	"	"	of about 75%.
"	bromide	"	"	"	"	between 50-60%.
Calcium chloride		"	"	"	"	from 28-32%.
and Con. Sulphuric acid		"	"	"	"	below 10%.

Information regarding the respective humidities yielded by these salts were obtained from Spencer (1926) and Shelford (1927). In addition, a few of these salts were tested with the aid of a dew-point apparatus (Marvin 1915). Before using this apparatus, its accuracy was tested by measuring with it the air humidity and comparing it with the readings of a sling psychrometer. The specific humidities obtained by the writer varied sometimes from those given by Spencer from about 2-4%. Therefore, the approximate humidity is given. With the exception of NaBr, all the above substances were tested as to their yield of humidity.

The bugs were put in small vials which, in turn, were put in a tightly closed jar containing the particular salt solution.

Obtaining Data:

The data of every instar were obtained separately. The date and exact time of the feeding and the average time of molting were taken in every case. It was found that immediately after their hatching or molting, bugs are not ready to feed. Their mouthparts are still soft and are not suitable for drilling purposes. The writer also observed, and his observations have been substantiated by the experiment described later on, that during this period the rate of metabolism is retarded to the extreme. Development begins

practically with the ingestion of a meal -- no matter how light it may be. The period of an instar is therefore divisible into two periods (1) Before the feeding -- during this period practically no development takes place and its termination depends upon the chance and ability of obtaining food. (2) A post feeding period -- during which time development takes place, its rate being influenced mostly by ecologic factors. Due to the fact that during the first period practically no development takes place, this period was disregarded for the purpose of measuring the rate of growth. Care was taken throughout the rearing that this pre-feeding period was not prolonged over a period of a day or two. In the following discussion, therefore, the length of an instar is not the period from molt to molt but from food to molt. Although this does not present the actual length of the instar, for our purpose it is preferable because more uniformity could be obtained in establishing the beginning of an instar. The day, as a unit of time, was found to be too great. The difference of the rate of metabolism of various groups was often so small that the hour, as a unit of time, proved to be more satisfactory. For this reason, also, it was of importance to collect the data as often as possible. Recording of data was done every two hours or so and when the case required, even oftener. However, the data were greatly interrupted by the night periods or when other duties demanded attention.

It was also noticed that there are individual varia-

tions in the rate of development. Each group, upon which records were based, consisted of from 5 to 10 individuals. In establishing the average of the molting time, some discrepancies may have slipped into the data because the exact hour of each individual molt could not be obtained. In spite of every effort, errors could not be avoided. To avoid possible influence of variable quantities of food upon the rate of metabolism, all individuals were fed once during each instar to the full capacity of the bug.

Experiments.

The effect of relative humidity upon the rate of metabolism will be discussed first. Before doing so, the writer wishes to point out a discrepancy between his data and that of other workers. As indicated previously, Jones (1930), as well as Martini (1923) and others find the first instar longer than the second, third and fourth instars, and these three are about the same length, while the fifth instar is the longest. The data obtained by the present writer indicates that the first instar is the shortest, while the others increase by a few hours in length. The second instar is slightly longer than the first; the third slightly longer than the second, etc., while the fifth is very much longer than the rest of them. This progression is especially noticeable in some groups as shown in Table I and Plate I.

In attempting to explain this discrepancy, the first

cause for error that the writer can think of is the fact that the previous writers probably included in their data the period before feeding. This period, as one would expect, is longer in the first instar than in the other, since the bug is very delicate and soft when it hatches and a longer time is required before it can obtain food. As far as rate of growth is concerned, after it has ingested the food, there is no reason to believe that it should differ from the other instars. In fact from all indications, it does not. During the last instar, essential changes of structure take place which explain its longer period of development.

Effect of Humidity:

The length of the development of individual instars under the respective conditions of humidity and temperature as obtained by the writer are given in the following table:

Table I - Development Time of Individual Instars of Bed Bugs
At Respective Ecologic Conditions.

Ecologic Conditions			Instars							
Temp. C°	Hum. Per Cent	No. of Bugs	I	II	III	IV	V	Total Hours	Total Days	
32	Below 10	10	53	53	53*	61*	87*	307		
32	28-32	6	56	59	67	64	92	338		
32	50-60	10	62	62	56	62	91	333		
32	70-80	8	56*	56*	66	58	86	322		
32	80-90	7	54	63	58	62	91	328		
32	Above 90	18	52	62*	61*	65*	88*	326		
			55.5	59	60	61.5	89	326	13.5	
27	Below 10	10	57	68	70	84	128	407		
27	28-32	6	74	77	80	80	128	439		
27	50-60	10	62	68	72	80	118	400		
27	70-80	8	72	80	77	80	116	425		
27	80-90	5	67	67	72	82	120	408		
27	Above 90	16	68*	72*	76*	79*	116*	411		
			66.5	72	74.5	81	121	414	17.2	
22	Below 10	10	159	152	156	180	215	862		
22	28-32	8	165	168	152	155	249	889		
22	50-60	7	152	158	167	150	237	863		
22	70-80	5	134	179	145	154	230	842		
22	80-90	5	150	144	167	150	239	850		
22	Above 90	12	142*	135*	171*	145*	229*	822		
			150	156	160	156	233	855	35.6	

In the table, the unit of time as stated is one hour. It is to be noticed that in only a very few cases is the difference in the development of the individual group of any instar at one constant temperature for more than one day. Some of these discrepancies are due to unavoidable errors. However, there seem to have been others as a result of the special humidity condition at which development took place. The graphic presentation of this table (Fig. 1) indicates that the shortest development period, at a temperature of 27° C and 32° C, was under the lowest percentage of relative humidity. The longest period of development at these temperatures was under 28-30% relative humidity. It is quite probable, however, that this retardation may have been due to some other factors. As Tomlinson (1927) suggested, CaCl and MgCl entrains heavily in the air. At a temperature of 22° there seemed to be no marked influence of humidity upon the rate of development. Generally speaking, the influence of the humidity is so slight that one would be inclined to believe like Headlee (1914) that with insects whose food consists of substances which are composed greatly of water, the external condition of humidity does not affect the rate of metabolism of the insect. The affect of the moisture of the outside atmosphere, therefore, depends upon the supply of moisture from the inside. In other words, it depends upon the amount of nutrition.

The influence of humidity upon the starvation period

is entirely different. Jones (1930) studied this influence on the first instar and found that the drier the air and the higher the temperature, the quicker they died. His data are presented graphically in figure 2.

Influence of Quantity of Nutrition:

The writer did not make an extensive study to establish the exact data as to the relationship of the amount of nutrition and the rate of development. From his observations throughout the period of rearing these insects, he was inclined to believe that quantity of food has some definite influence upon the rate of metabolism. He planned to carry out some feeding experiments with the view of establishing this relationship. In the preliminary experiment, however, he encountered great difficulties, the most important being the impossibility to feed the bug certain limited quantities of food. It was observed that the consumption of one meal by an adult bug is about 10 minutes, and by a larva of the first instar, from 4.5 to 5 minutes. Assuming that the rate of ingestion of blood is uniform throughout this period, the amount of food ingested can be regulated by the time the bugs are allowed to feed. He, therefore, carried out the following preliminary experiment:

A group of 10 bugs of the first instar were allowed to feed on the wrist of the writer, each one individually. The insects in this stage are transparent and blood can be

seen as it is being ingested. Every bug was permitted to feed just one minute from the moment the ingestion of blood was noticed. Ten individuals of a second group were permitted to feed 2.5 minutes; 10 individuals of the third group were allowed to feed 4 minutes; while 10 individuals of a fourth group were kept in separate vials under the same conditions of humidity and temperature. Toward the end of the period, when their molting was due, the bugs were examined as frequently as every hour to see which of these would molt first. From this experiment and from a similar experiment with individuals of another instar, it was found that on the average those individuals which were fed the medium quantities molted first, whereas those that fed the minimum, as well as those that fed the maximum quantities, were retarded. The records of these experiments, which are given in Table II, as explained below, are incomplete. Nevertheless, they give a fair idea and indicate that at a temperature of 27° C, in full fed individuals development may be retarded five hours or more. This retardation may be due to congestion in the coelomic cavity due to the expansion of the digestive tract which thus hinders free circulation of blood and exchange of substances. The reason the records cannot be regarded as complete is because the rate of ingestion of blood differs with the individuals. Also, often, as pointed out by Hase (1930) a blood corpuscle may partly close the lumen of the proboscis and result in irregularities. Thus, in a few instances, bugs

which were allowed to feed 2.5 minutes apparently received much more food than those which were allowed to feed four minutes, while others probably obtained less food than those which were allowed to feed one minute only. Furthermore, continuation of the observation was not carried out between 9:00 P.M. and 8:00 A.M. the following morning when the rest of the individuals had in the meantime molted.

Table II - Molting Time of Individuals Fed Different Quantities of Food.

Hour of Molting	Length of Time in Minutes Permitted to Feed:			
	1	2.5	4	Full Capacity
4:15 P. M.	1	3	1	1
5:15 "	1	0	0	0
6:45 "	0	0	1	1
7:45 "	1	2	0	1
8:45 "	0	1	0	0
Total	3	6	2	3

The Pre-Feeding Period:

It was stated previously that metabolism, leading to the molting, takes place only after food has been ingested. It has been observed time and again that no matter how long a period a larva was starved, its development, after it had

obtained food, was not influenced at all and it molted at the same time as those that were fed normally. Naturally, when a larva has obtained the food the day before its last molt, conditions are different. Two experiments were carried out at two different temperatures, both of which substantiated the above statement and are described herewith.

In each instance, two groups of bugs of the first instar were fed at the same time and reared under absolutely the same conditions of humidity and temperature. The only difference between the two groups was their age. The individuals of one group hatched from 6-10 days before the individuals of the second group. Regardless of this fact, there was no difference in their time of molting. The length of the instar from feeding to molting was the same in both groups, as follows:

Temperature	Date of Feeding	Date of Molting
32° C.	Jan. 28, 11:00 A.M.	Jan. 30, 7:00 P.M.
27° C.	" " " "	Jan. 31, 10:00 P.M.

Effect of Temperature on Rate of Metabolism:

The greatest ecologic factor in the normal rate of growth seems to be the temperature. The influence of detrimental temperatures - that is, the temperatures far above or below the optimum, at which no development takes place - was not studied.

The data presented in Table I are used for the purpose

of establishing the relationship of temperature and rate development. Converting the hour data of the first instar into day units, and adding to these an additional record of the development time of this instar at a temperature of 17° C, we have the following table:

Table III - Relationship of Temperature and Development of the First Instar in the Bed Bug.

Temperature in C.	Development in Days	Average Per Cent of Daily Development
32	2.3	43
27	2.75	36
22	6.25	16
17	19	5.2

These values are presented in the form of a graph (Fig. 3) which shows the threshold of development to be in the neighborhood of 15° C.

The curve in Figure 4 is traced from the total average of time of development of the groups for the three temperatures. These are 13.5, 17.2 and 35.6 days for the temperatures 32° C, 27° C and 22° C, respectively.

Blunck (1923) claims he is able to obtain the developmental zero or the threshold of development by his formula, $T(t - c) = \text{Constant}$, determined from studies with *Dytiscus*. When two temperatures t and t' are given and two development times T and T' are obtained, we may have the following equation:

$T(t - c) = T'(t' - c)$. From this equation, it is possible to obtain the value c , which is the threshold of development, as follows:

$$T(t - c) = T'(t' - c)$$

$$Tt - T't' = Tc - T'c$$

$$c = \frac{Tt - T't'}{T - T'}$$

Applying the values in the above tables to these symbols, we have:

$$T'' = 35.6 \quad t'' = 22^{\circ}$$

$$T' = 17.2 \quad t' = 27^{\circ}$$

$$T = 13.5 \quad t = 32^{\circ}$$

With the data obtained under temperatures of 22° C and 27° C, the value of c will therefore be:

$$c = \frac{17.2 \times 27 - 35.6 \times 22}{17.2 - 35.6} = 17.3$$

When using the data obtained at the temperature of 22° and 32° , the value of c will be:

$$c = \frac{13.5 \times 32 - 35.6 \times 22}{13.5 - 35.6} = 15.8$$

However, the value of c does not correspond with the foregoing when the data of the temperatures 27° and 32° are used, as is indicated in the following equation:

$$c = \frac{13.5 \times 32 - 17.2 \times 27}{13.5 - 17.2} = 8.76$$

The fact that no death occurred at a temperature of 32° C indicates that that temperature is not detrimental to the insect. It has been suggested (Bodenheimer in personal communication) that this temperature may be beyond that at which the shortest development takes place. The straight line drawn in figures 3 and 4 indicates that at the point of 32° the straight line curves slightly. However, additional data are necessary to make a decided statement regarding this point.

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Explanation of Plates

PLATE I

Relative Lengths of the Development of Individual Instars
Under Six Different Conditions of Humidity at Temperatures
of 27° and 32° Centigrade.

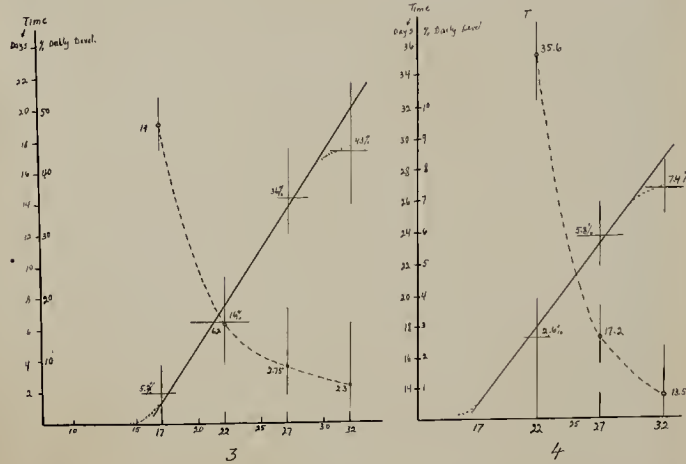
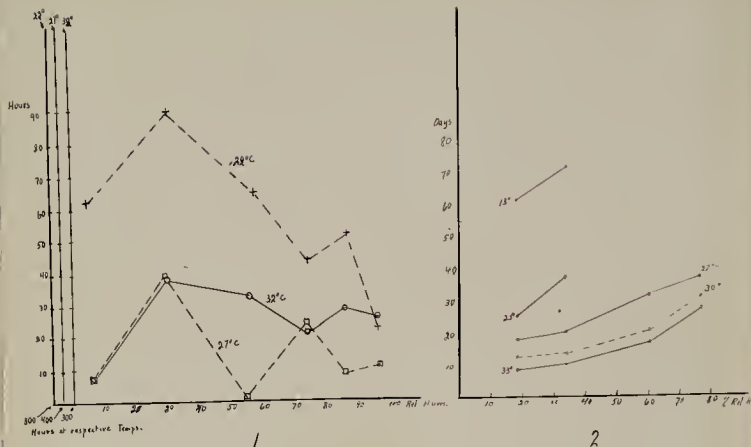
PLATE II

- Fig. 1 - Curve Showing Effect of Humidity upon the Development
of Bed Bugs at Three Different Temperatures.
- Fig. 2 - Curves Showing Effect of Humidity upon the Starvation
Period at Different Temperatures.
- Fig. 3 - Temperature-Development Curve and Reciprocal of the
First Instar of the Bed Bug.
- Fig. 4 - Temperature-Development Curve and Reciprocal of
Adult Bed Bug.

PLATE I



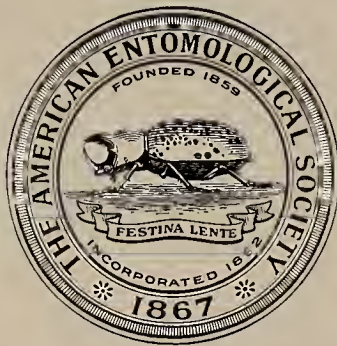
PLATE II



MEMOIRS
OF THE
AMERICAN ENTOMOLOGICAL SOCIETY
NUMBER 6

REVISION OF THE
RHIPIPHORIDAE
OF
NORTH AND CENTRAL AMERICA
(COLEOPTERA)

BY
EZEKIEL RIVNAY



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CONTENTS

	PAGE
I. Introduction.....	I
II. History of the Family.....	4
III. Morphology.....	6
IV. Classification and general Description.....	12
V. Taxonomy	
Key to the genera.....	14
A. Pelecotoma.....	14
B. Trigonodera.....	16
C. Toposcopus.....	20
D. Rhipidius.....	22
E. Macrosiagon.....	23
F. Rhipiphorus.....	41
VI. Bibliography	
A. Catalogues.....	64
B. Taxonomic literature.....	64
C. Morphologic literature.....	65
VII. Plates.....	66

INTRODUCTION

The Rhipiphoridae are comparatively rare insects, and many species belonging to this family were originally described from one specimen. Several species are still represented by a single specimen, the monotype. Because of the rarity of this group of

¹ Submitted as part of the requirements for the degree of Master of Science at the Massachusetts Agricultural College, Amherst.

insects, few students treated and studied it, and, as a result, the taxonomy of this family has been unsatisfactory, especially in the United States. Of all the Rhipiphoridae listed in Leng's Catalogue, about 12% were described after the days of Leconte and Horn, while in many other groups the percentage of recently described insects is considerably greater. The literature of this family also reveals the lack of definite conclusions as to the validity of certain species and varieties. This is due, naturally, to the fact that several species were described from single specimens. There has existed also a diversity of opinion as to the proper names of certain genera, and their correct position in the family.

The present paper is the result of an attempt to bring this family into better taxonomic order. The author does not claim to have settled all the difficulties that are involved in the taxonomic study of this group; on the contrary, he frankly admits that considerable work is still to be done. But in preparing this paper he has attempted to do the following: (1) To study the different species already described and wherever it seemed necessary, redescribe such species or make additional references to characters which have been omitted in the original descriptions, with the hope that the student may more easily determine his material; (2) to find definite means of correlating the two sexes and describe the other sex in cases where it has not heretofore been known; (3) to describe new forms, based on undetermined material or upon wrongly identified specimens found in the various collections; (4) to divide the family properly, and base the division upon morphological features and biologic characteristics as far as possible; and (5) to collect scattered important data in regard to the biology of the group.

To accomplish the above the writer has studied the types or paratypes of such species as could be obtained in the eastern states. For that purpose he has visited Boston, Washington and Philadelphia. In addition, several collections were kindly placed at his disposal in the American Museum of Natural History, where a taxonomic study as well as a morphologic comparison of the group has been pursued.

The material studied was obtained from the following sources: American Museum of Natural History, through Dr. F. E. Lutz

and Mr. A. J. Mutchler:—American Museum Collection, containing the Henry Edwards, Charles Palm and other collections. Mr. Charles W. Leng, Director, Public Museum, Staten Island, N. Y.:—Mr. Leng's private collection. Mr. William T. Davis, Staten Island, N. Y.:—Mr. Davis' private collection. Mr. Howard Notman, Brooklyn, N. Y.:—Mr. Notman's private collection. Museum of Comparative Zoology, Cambridge, Mass., through Mr. Nathan Banks:—The Leconte, Bowditch and other collections. Mr. Charles Schaeffer, Brooklyn Museum, Brooklyn, N. Y.:—Mr. Schaeffer's private collection. Mr. C. H. Frost, Framingham, Mass.:—Mr. Frost's private collection. U. S. National Museum, through Dr. J. M. Aldrich, Dr. E. A. Chapin and Mr. H. S. Barber:—specimens from Pierce, Schwarz, Hubbard Green, Casey and other collections. Academy of Natural Sciences of Philadelphia, through Mr. E. T. Cresson, Jr.:—the Horn, Mason and other collections.

To all of the above institutions and private collectors, I wish to extend my sincere thanks. I also wish to express my appreciation to those members of the staffs in the above-mentioned institutions who have so willingly assisted me in my work.

As stated above, this paper was prepared at the American Museum of Natural History and it is to this institution that I am deeply grateful for the privilege of using the Entomological Laboratory and its facilities. I cannot fully express my sincere thanks to Dr. F. E. Lutz, Curator of Entomology, to Mr. H. F. Schwartz and Miss Jeanette Alexander of that department, for the kind manner in which they have assisted me, nor to Mr. A. J. Mutchler who has followed this work and assisted me in getting together literature and checking up references relating to the several species. At this moment I cannot but repeat the words of Mr. C. W. Leng in his introduction to the bibliography of his famous Catalogue, which are as follows: "I am under heavy obligations to Mr. Andrew J. Mutchler, of the American Museum of Natural History, for continual assistance in preparing this bibliography. His knowledge of the great collection of books in that Museum is remarkable. I am glad to gratefully acknowledge his help." I am also under obligation to Drs. H. T. Fernald, C. P. Alexander and G. C. Crampton, who have read the manuscript and offered many helpful suggestions.

HISTORY OF THE FAMILY

Linné described in 1761 the European *Metoecus paradoxus* and placed it in the genus *Mordella*. In later editions of his *Systema Naturae*, and in the *Systema Entomologiae* of Fabricius (1775) a few species of *Macrosiagon* (Rhipiphoridae) were also included in the genus *Mordella*. Bosc first described *Rhipiphorus subdipterus* in 1792. The derivation of the generic name is from the Greek, ῥίπις a fan and φορος bearing, and the name was suggested to him by the fan-shaped antennae of the male. In addition to the detailed description, there are also figures that indicate clearly the species he described. In his discussion, Bosc states that the *R. subdipterus* has some characteristics in common with *Apalus 2-maculatus* (Meloidae) and with *Necydalis humeralis* (Cerambycidae). The similarity with the latter is, as we may understand, superficial. Bosc expresses his opinion as to the position of *Rhipiphorus*, and states that it should be placed near *Mordella*, with which it has many characteristics in common. In later works of Fabricius, his *Entomologia Systematica* (1792) and his *Systema Eleutheratorum* (1801), we find the early-described Rhipiphorids separated from the Mordellids, and together with *subdipterus*, included in the genus *Rhipiphorus* Bosc. Of the species listed there, we find four from North America, namely, *limbatus*, *dimidiatus*, *pectinatus* and *6-maculatus*.

The genus *Rhipidius* was described by Thunberg in 1806, while *Pelecotoma* was described by Fischer von Waldheim in 1809. In 1830, Hentz separated the genus *Macrosiagon* from *Rhipiphorus*, and designated *R. dimidiatus* as the genotype. A new genus was added to the group when Guérin described *Evaniocera* in 1835. In his Catalogue, Dejean, in 1834, listed among other Rhipiphoridae a group of insects in the genus *Trigonodera*, and Castelnau, in 1840, described a new genus *Pelecotoides*. All the authors mentioned treated the group as belonging to the family Mordellidae. In 1855, Gerstäcker wrote his excellent monograph on the Rhipiphoridae and separated them from the Mordellids. This separation was based on the following characteristics: The Rhipiphorids are parasitic; their sexes antigenous; antennae flabellate or pectinate, with their insertion near or above the eyes and not below them; last segment of maxillary palpi not hatchet-

like, and pronotum without distinct lateral carina and suture. He divided the family into four tribes representing twelve genera as follows:

- I. Ptilaphorini—(1) *Trigonodera*, (2) *Geoscopus*, (3) *Pelecotoma*, (4) *Clinops*, (5) *Ancholaemus*, (6) *Euctenia*, (7) *Ptilaphorus*, (8) *Ctenidia*.
- II. Rhipidiini—(9) *Rhipidius*.
- III. Myoditini—(10) *Myodites* (*Rhipiphorus*).
- IV. Rhipiphorini—(11) *Metoecus*, (12) *Rhipiphorus* (*Macrosiagon*).

The family was treated afterwards by Lacordaire in 1859, and by other authors in connection with description of local faunas.² New genera have since been added to the family, so that we have today the group as represented in the *Catalogus Coleopterorum*, W. Junk, Pars 54, 1913. E. Csiki, who arranged the group for this *Catalogus* divided the family into three tribes as follows:

- I. Pelecotomini—seventeen genera.
- II. Rhipiphorini—three genera, namely, *Macrosiagon*, *Metoecus* and *Rhipiphorus*.
- III. Rhipidiini—seven genera.

In America, we find in the *Catalogue of Insects of Pennsylvania*, by Fred. Val Melsheimer, 1806, page 56, nine species in the genus *Kipiphorus*. No doubt the "K" is due to a typographical error and should be replaced by *R*. Some of those names we find published later in 1846 by his son, F. E. Melsheimer, but most of them are now either synonyms or varieties of *pectinatus* Fabricius. Thomas Say, in 1823, described the first American species of the genus *Rhipiphorus*, namely, *Dorthesia fasciata*, and Leconte, in 1868, described the genus *Toposcopus*. Other authors who contributed to the literature of American Rhipiphoridae by adding new species from North and Central America were Germar (1824), Newman (1838), Guérin (1844), Gerstäcker (1855), Horn (1875 and 1892), Champion (1899), Pierce (1902–1920), and Fall (1907). Horn, in 1875, monographed the genus *Macrosiagon*

² For reference to these see Rhipiphoridae, E. Csiki—*Catalogus Coleopterorum*—W. Junk, Pars 54, 1913.

(as *Rhipiphorus*), and Champion treated the species of the entire family found in Central America; while Pierce, in addition to taxonomic notes on the genus *Rhipiphorus* recorded some valuable ecological notes and observations, and added important facts to our knowledge of the life history of the family.

MORPHOLOGY

To the student of comparative morphology, the Rhipiphoridae present a very interesting study, because this group includes ordinary Mordelloid beetles on the one hand, and highly specialized Strepsipteroid beetles on the other. In this family, therefore, one may find intermediate stages between the Coleoptera and Strepsiptera.

Early taxonomists believed that some groups which are included in the Rhipiphoridae have little relationship to each other; they thought that the grouping of this family was based on superficial characteristics; Sharp and Muir for instance, grouped the genus *Pelecotomoides* (*Trigonodera*, Rhipiphoridae) in the Mordellidae. Those authors may have been right to a certain extent, as will be shown later, but there are certain tendencies occurring in the entire family, that make it into a unit. In addition there existed also a diversity of opinion as to the proper division of this family. It is therefore the aim of the following paragraphs to discuss the similarity and differences of the various genera from a morphological view point, and conclude as to their possible phylogeny and proper classification. Because of lack of material, only the genera occurring in the United States have been studied, although other exotic genera are mentioned to make the discussion more complete. In the following discussion the minute details, and minor differences of parts are omitted; only the general form and structure of certain organs are discussed.

Antigeny.—(Pl. I, fig. 1-6 C; Pl. III, fig. 4.) In every genus included in the Rhipiphoridae the antennae in the two sexes are of a different form, and therefore represent the most important secondary sexual characteristic. Nothing in addition to this is found in the genera *Pelecotoma*, *Trigonodera* and *Toposcopus*. In *Macrosiagon*, however, the males of some species may differ in color from the females; and in *Rhipiphorus*, the males, in addition

to the difference in color, have their tarsal claws more finely and closely pectinate than those in the females. In the genus *Rhipidius* (fig. 4) the female is without elytra and wings, and seems to be of an entirely different form than that of the male. The Stylopoid females have lost, in addition to the wings, also the legs and other important organs. In antigeny, therefore, *Rhipidius* approaches very much the Strepsiptera.

Head Capsule.—(Pl. I, fig. 1-6 A, B.) In the less specialized genera, *Pelecotoma* and *Trigonodera*, the head is broadly round, and the vertex is on the same level with the anterior margin of the pronotum. In *Toposcopus* and *Rhipidius* the vertex is but slightly elevated above the margin of the pronotum, while in *Macrosiagon* and *Rhipiphorus* it is much more elevated. The relative size of the sclerites of the head differs in the genera. In making this comparative study, one should bear in mind the demarcations used in Comparative Morphology of insects in general. The epicranial suture, and its arms which separates the vertex from the frons are of great importance. This suture is not noticeable in some species, while it is distinct in others.

Upon comparing the respective figures, one may readily see that the frons in *Pelecotoma* (fig. 1 B) is much enlarged and is not distinctly separate from the vertex, while in *Trigonodera* (fig. 2 B) and *Toposcopus* (fig. 3 B) it is much smaller. In some species belonging to the genera *Macrosiagon* and *Rhipiphorus*, the epicranial suture is visible; when it is present in *Macrosiagon*, as it is in the case of *M. octomaculatum* and *M. sayi*, it may be seen when looking upon the head from the rear (see Pl. III, fig. 16). The arms of the suture are along the carina; in other words, the entire frontal surface of the head is the clypeo-frons, and in some species a small part of it is the vertex. When present in *Rhipiphorus* as it is in the case of *Rh. scaber* and *Rh. simplex*, the suture is seen on the conical process between the antennae and its arms in front of the tubercle. In other words, this process is the true vertex, and the entire broad surface between the large eyes is the clypeo-frons. In the last two mentioned genera, therefore, the anterior sclerites of the head have enlarged very much, while the posterior sclerites, the occiput and vertex, have become much smaller. This change in the head capsule causes the apparent change of position of the eyes and antennae as will be seen in the next paragraphs.

Eyes.—(Pl. I, figs. 1-6 A, B.) The size and form of the eyes varies not only in the genera, but also in the species of one genus. One could readily point out, however, the outstanding eye characteristics of the groups. While the eyes in *Pelecotoma* (fig. 1, A, B) are small and widely separate, they are much larger, much closer to each other, and more coarsely granulate in *Trigonodera*. The eyes in *Toposcopus* are finely granulate, almost entirely divided, and the line connecting the two divisions is obsolete of facets. In all the three genera mentioned the eyes are emarginate to some degree. In the genera *Macrosiagon* and *Rhipiphorus* (figs. 5 and 6, A, B) the eyes are very finely granulate, regularly oval, not emarginate, situated on the sides of the head, and leaving a wide clypeo-frons. Upon comparison, one may readily see that the eyes of *Macrosiagon* are proportionately much smaller than the eyes of *Rhipiphorus*. The male of *Rhipidius* (Pl. I, fig. 4 A, B) has the eyes larger, subcontiguous, with the facets large and distinct. In the supposedly female *Rhipidius* (Pl. III, fig. 4 A) the eyes are very small, situated on the side of the head, the facets few and distinct, as is the case in the eyes of the male Strepsiptera which are berry-like.

Antennae.—(Pl. I, fig. 1-6 C.) As a rule the antennae are eleven-segmented, but in some cases the last segment is obsolete. In the males of *Pelecotoma* and *Trigonodera* the antennae are pectinate. The segments are elongate, and the short rami, therefore, are widely separated from each other. The female antennae are much like those of the male, except that the processes of the segments are much shorter than those of the male antennae. The first segment in this type of antenna is much thicker and larger than the rest, while the second is the smallest. The number of the processes varies in the species, some having eight while others seven or six, that is, in addition to the first and second; some other segments are without any processes. In *Toposcopus*, the male antennae are of an entirely different type. The first segment is the largest, and the second smallest; but the third segment is also large and bears a process at its proximal end, while the remaining eight segments are very closely compact and their rami are very long and close together (see fig. 3 C). The female antennae of *Toposcopus* are like those of *Trigonodera*,

except that the third segment indicates traces of a process. The same type of antenna is found in *Evaniocera*, and as far as I could make out from the drawing, also in *Ancholaemus*. In the male of *Rhipidius* the antennae are of the same type as in *Evaniocera*, except that the rami are broader, lamellate-like, and the third segment is smaller and without a process. In the supposedly female *Rhipidius*, the antennae are filiform. In the males of the genera *Macrosiagon* and *Rhipiphorus* we find the third type of antenna, namely those of the male are bilabellate, every segment bearing two rami, and pectinate in the female. In the male of *Macrosiagon* the first segment is large and the second is distinct, while in *Rhipiphorus* the first segment is broad and short, and the second is very short and sometimes quite indistinct. The length of the rami varies in the species of one genus, but as a rule they are longer in *Rhipiphorus* than in *Macrosiagon*. In both genera, they are straight or curled. The female antennae in both genera vary from deeply serrate to pectinate. In some cases the processes are equal while in others they increase in length toward the apex or toward the base. In the female *Rhipiphorus* the last segments show a tendency to fuse, and in most cases the eleventh segment has disappeared.

Pronotum.—(Pl. I, fig. 1-6 A). In the genus *Pelecotoma* (fig. 1 A) the prothorax has a distinct suture separating the pronotum and pseudopleuron; this suture is present also in other members of this family, but is obsolete in all other genera represented in the United States. In *Trigonodera* and in *Toposcopus* the pronotum shows a distinct lateral carina near the base only, but the sides are more or less rounded at the anterior part of the pronotum. In the genus *Rhipidius* the pronotum has become much smaller in comparison with the head, and has a distinct lateral carina; in the two other genera, *Macrosiagon* and *Rhipiphorus*, the pronotum is very broad while the pseudopleuron is quite small, and is represented only by a narrow projection. In the last two named genera, the mesoscutellum is usually under the posterior lobe of the pronotum.

Metanotum.—Because of the enlarged wing muscles, the metathorax is enlarged in most Coleoptera, but is developed more than the average in the genera *Macrosiagon* and *Rhipiphorus*, and

exceedingly so in the genus *Rhipidius*. The metanotum, being uncovered, is much more chitinized than is the case in other genera where the elytra cover the entire body. The median groove on the metascutum is obsolete in these genera, since the elytra are short or dehiscent. In the male *Rhipidius* (Pl. III, fig. 4 V) the metathorax is very large, while the prothorax (fig. 4 A) is very small; this is noteworthy, because in the Strepsiptera the prothorax is very narrow, collar-like, and the metanotum forms the greater part of the body.

Elytra.—The elytra in the genera *Pelecotoma*, *Trigonodera* and *Toposcopus* are of ordinary form, as in other Coleoptera. In the genus *Macrosiagon* the elytra are little reduced, but are dehiscent and attenuated posteriorly, while in *Rhipiphorus* they are much more reduced, becoming convex, scale-like appendages. The elytra of *Rhipidius* are narrower, more hairy, and of softer texture than those of the other two genera mentioned, seeming to approach the form of the club-shaped elytra of the Strepsiptera.

Wing Venation.—(Pl. III, fig. 2-7 W.) As in all other Coleoptera the costa, subcosta, radius and their branches, are crowded together and occupy a small area along the anterior margin of the wing. The median, cubitus and the anal veins occupy the greater part of the wing surface. In the genus *Trigonodera* (fig. 2 W) the wing venation is like other Mordelloid beetles. The vein CuM₄ is quite distinct, with the recurrent vein M present. Also some radial branches are present and the anal branches are evident. In the genus *Evaniocera* (fig. 7 W), which is closely allied to *Toposcopus*, the cubitus is a little curved before it unites with the median (M), but both are distinct, while the anal veins are reduced in number. In *Rhipidius* all the veins have disappeared except at the base and the cubitus (Cu) is the only distinct one. In the two genera, *Macrosiagon* and *Rhipiphorus*, a reduction of the number of veins is also noticeable; but they are replaced by secondary thickenings of the wings through depositions of chitin as is shown in figures 5 and 6 W.

Abdomen.—(Pl. III, figs. 4, 5 and 6 V.) As in other Coleoptera, modifications in the structure of the first abdominal segments have taken place. The first segment is membraneous, and is visible only when the abdomen is detached from the metathorax.

In the females of *Macrosiagon* and *Rhipiphorus* the eighth segment is in the form of a tube which surrounds and protects the ovipositor (Pl. II, 5 F, and 6 F). The seventh tergites in *Macrosiagon* is considerably enlarged, shield-like, and is termed the pygidium. In the male of this genus the eighth tergites is the pygidium. In both genera the sternites are quite large and cover the pleurites at their margin. The abdominal segments in *Macrosiagon* are arranged telescope-like and are compressed, while they are depressed in *Rhipiphorus*. The male abdomen in *Rhipidius* (fig. 4 V) is very small, as is the case in many Strepsiptera, and that of the supposed female has eight distinct segments.

Male Genitalia.—(Pl. II, figs. 1–6 M.) In the male genitalia of Coleoptera we distinguish the tegmen, composed of a basal piece and two lateral lobes which, as a rule, are variably modified. The median lobe, according to Sharp and Muir, is the central portion of the aedeagus in which the median orifice is situated. In the family Rhipiphoridae we find two types of structure in the genitalia. The one is the type which we find in the genera *Pelecotoma*, *Trigonodera*, and with slight modifications in *Macrosiagon* and *Rhipiphorus*. In general the median lobe is long, curved, and the tegmen consists of a large basal sclerite on the dorsal aspect of the median lobe and with a pair of highly modified lateral lobes. The lateral lobes are richly chitinated; they are elongate and slightly curved in *Pelecotoma* (fig. 1 M) and crescent-shaped in *Trigonodera* (fig. 2 M). In *Macrosiagon* (fig. 5 M) the left lobe is as a rule modified into a hook-like projection, while in *Rhipiphorus* they are flat and of the shape presented in fig. 6 M. The common feature in the genitalia of these genera is that the median lobe is quite differentiated from the tegmen, which envelops it.

The other type of genitalia is the one which we find in the genus *Evaniocera* and *Toposcopus*. This type, according to Sharp and Muir, is characteristic also of the genus *Anaspis*. In this latter, quoting Sharp and Muir, "The median lobe is slender, tubular and semi-chitinous, and with median orifice at tip. Tegmen consisting of pair of pointed lateral lobes consolidated at their base, and a narrow, long basal piece." From figure 3 M and 7 M we can see that the male genitalia of *Evaniocera* and *Toposcopus* are

of this type and therefore quite different from the genitalia in the other genera. In *Evaniocera* the tegmen is broader, the median lobe points ventrally with the median orifice at its dorsal side; in *Toposcopus* as the figures show, the tegmen, median lobe and lateral lobe are very slender and semi-chitinized.

Female Genitalia.—(Pl. II, figs. 2, 5, 6 and 7 F.) The female genitalia of *Trigonodera* and *Evaniocera* do not differ very much from each other as do the male genitalia in these genera. In both, the style, coxites, etc. are distinct. In the genera *Macrosiagon* and *Rhipiphorus* the genitalia have become much more chitinized and the delicate styli have disappeared. This may be explained by the fact that the females oviposit in the ground, and need, therefore, smoother and harder ovipositors. That difference in structure of the ovipositors suggests also that in the genera *Trigonodera* and *Evaniocera*, the females do not oviposit in the ground.

CLASSIFICATION AND GENERAL DESCRIPTION OF THE FAMILY

The family Rhipiphoridae according to the classification of Leconte and Horn belongs to the series Heteromera, which is differentiated from other Coleoptera by the fact that the hind tarsi have only four segments. In this series, it belongs to the group of families which are known to have the front coxal cavity open behind. Of these the families Melandryidae, Pythidae and Oedemeridae, have the head not strongly constricted behind the eyes, while the Mordellidae, Anthicidae, Pyrochroidae, Meloidae, and Rhipiphoridae, have it strongly constricted behind the eyes. The Mordellidae and Rhipiphoridae have the pronotum as wide at base as the elytra, while the remaining three families have the base of the pronotum narrower than the elytra. To differentiate them from the Mordellidae, the Rhipiphoridae have the sides of thorax rounded, at least at the anterior part, the antennae flabellate, pectinate, or deeply serrate (with exception of the females of *Rhipidius*), and the last segment of maxillary palpi not hatchet-like. The Rhipiphoridae seem to be more closely related to the Meloidae than to the Mordellidae, since they both are hypermetamorphic in their development, and members of both groups are parasitic in their immature stages upon other insects.

Adding a few features to the above we may summarize the char-

acteristics of the Rhipiphoridae as follows: Head as a rule vertical, constricted at base, neck inserted in prothorax; antennae, with some exceptions, inserted between the eyes or above them, and usually flabellate, pectinate or deeply serrate. Pronotum at base as wide as elytra, and without a sharp lateral carina; no distinct suture, with some exceptions, separating the pronotum from the pseudo-pleuron; anterior coxa prominent and conical, coxal cavities open behind. Elytra in some cases cover the entire abdomen, while in the more specialized forms they are reduced. Claws pectinate or bifid, seldom simple. Development hypermetamorphic.

From all the facts concerning the general morphology of the various genera of this family, we may divide it as follows:

PELECOTOMINAE

Vertex not elevated above anterior margin of pronotum. Male antennae pectinate, rami separate from each other and shorter than head, at least first three segments without any process. Median lobe quite elongate, lateral lobe modified. This subfamily will include *Pelecotoma*, *Trigonodera*, and others with such characteristics.

EVANIOCERINAE

Vertex little elevated above anterior margin of pronotum. Male antennae monoflabellate, rami longer than head, compact, third segment with a process, which may be reduced. Female antennae deeply serrate, third segment with reduced process. Male genitalia of slender form, in which the median lobe is closely surrounded by tegmen and lateral lobes reduced to small pointed projections. This subfamily includes *Toposcopus*, *Evaniocera*, and probably also *Clinops*, *Ancholaemus* and other genera with the same characters.

RHIPIPHORINAE

Vertex distinctly elevated above anterior margin of pronotum. Male antennae bi-flabellate; female antennae monopectinate. Elytra reduced in size. Median lobe elongate. Ovipositor heavily chitinized, pointed and smooth. This subfamily includes *Rhipiphorus*, *Metoecus* and *Macrosiagon*.

RHIPIDIINAE

Male antennae monoflabellate, rami long and close together. Female wingless. This subfamily would include *Rhipidius*, *Rhysostylops* and other genera which have the same characteristics.

Key to the Genera of Rhipiphoridae of North and Central America

1. Elytra long, covering the entire abdomen and the folded wings. Antennae inserted below middle of eyes.....2
 Elytra short, dehiscent; wings partly or entirely exposed. Antennae inserted near middle of eyes or above them.....4
2. Eyes divided, the two divisions of each eye connected by a strip of non-faceted corneous membrane.....**Toposcopus**
 Eyes entire or emarginate.....3
3. Small insects, not over 6 mm.; eyes small; claws not pectinate but provided with two minute denticles.....**Pelecotoma**
 Large insects, over 6 mm.; eyes large; claws pectinate.....**Trigonodera**
4. Elytra reduced to scale-like convex plates, not extending beyond second abdominal segment; claws pectinate.....**Rhipiphorus**
 Elytra longer, dehiscent; posterior lobe of pronotum covering scutellum; tarsal claws bifid.....**Macrosiagon**

PELECOTOMA Fischer von Waldheim

1809. *Pelecotoma* Fischer von Waldheim, Mem. Soc. Nat. Mosc., p. 293.
 1823. *Pelecotoma* Fischer von Waldheim, Entomogr. Russ., II p. 170.
 1855. *Pelecotoma* Gerstäcker, Rhipiph. Col. Fam., p. 8.
 1859. *Pelecotoma* Lacordaire, Hist. Ins. Col., v p. 619 and 622.

Small insects, not over 5.5 mm. Elongate and subparallel, punctured and covered with silky hair. Head bent down, vertex broadly rounded, not elevated above anterior margin of pronotum. Eyes comparatively small, emarginate; antennae 11-segmented, situated below eyes, pectinate in the male, deeply serrate in the female. First three segments in both sexes without any processes. Pronotum strongly tapering toward the front, slightly emarginate on both sides to produce a rounded broad lobe, but short and not sufficient to cover scutellum. Hind angles not very prominent, lateral carina distinct at base, lateral suture present, separating the pseudopleuron from disc. Elytra long and narrow, and cover entire abdomen. Abdomen depressed, legs short, claws very small, not pectinate, but armed with two minute denticles.

GENOTYPE: *Pelecotoma fennica* (Paykull). Paykull described *fennica* as *Rhipiphorus* in 1799. In 1809 Fischer von Waldheim described the genus *Pelecotoma* with the species *mosquensis* belonging to it, but the latter has been placed in the synonymy of *fennica*.

Two species have been recorded belonging to this genus, *P. fennica* (Paykull) in Europe, and *P. flavipes* Melsheimer in North America.

***Pelecotoma flavipes* Melsheimer**

1846. *Pelecotoma flavipes* Melsheimer, Proc. Acad. Nat. Sci. Phila., II, p. 318.

1855. *Pelecotoma flavipes* Gerstäcker, Rhipiph. Col. Fam., p. 9.

This species may be distinguished from *Pelecotoma fennica* as follows: The legs of *P. fennica* are of the same color as the elytra, and the pronotum is of a darker shade while the legs of *P. flavipes*, as mentioned, are yellow and the pronotum is of the same shade as the elytra. The specimen of *fennica* in Mr. Leng's collection is larger than any of the *flavipes* examined.

Black or brown, mouthparts and legs yellowish; elongate, sides subparallel. Head broadly rounded, sparsely punctate and pubescent. Eyes emarginate near middle, frons broad, clypeus truncate. Antennae 11-segmented, the first three segments without process and pale, the others bear processes and are fuscous, fourth segment bears a process usually shorter than the following; processes of female antennae short, compact and acute at tip, those of male long and rounded.

Pronotum strongly tapering toward front, conical, pubescent, base indented on each side to produce a broad posterior lobe. Elytra long, narrow, covered with silky pubescence, abdomen depressed.

Length, 4 to 5 mm.

Distribution.—Melsheimer described the species from specimens taken in Carolina; the specimens examined seem to be distributed along the Atlantic Coast and more in the northern states than in the southern.

MAINE: Monmouth, July, [Frost Collection].

NEW HAMPSHIRE: Contoocook, July, [Schaeffer Collection; (E. and G. Wheller), Frost Collection].

MASSACHUSETTS: Tyngsboro, (Blanchard), [M. C. Z.; Schaeffer Collection].
Petersham, July, [Frost Collection]. "Mass.", [Leng Collection; A. M. N. H.].

NEW YORK: [Casey Collection; U. S. N. M.].

NEW JERSEY: [Schaeffer Collection].

NORTH CAROLINA: Black Mountains [Leng Collection; A. M. N. H.].

OHIO: Cincinnati, (H. Soltau), [U. S. N. M.].

MICHIGAN: Marquette, [Hubbard and Schwartz Collection].

MEM. AM. ENT. SOC., 6.

Biology.—We know nothing of the biology of *P. flavipes*. As for the ecological surroundings, we know that it is taken by sweeping in July. Since it is so similar to the European *fennica*, which is also taken in July and is also found under similar climatic conditions, we may infer that its life history and biology may also be similar to *fennica*.

In regard to the biology of the latter, Schuman (1899) records that he collected the *P. fennica* during the end of June and the beginning of July in holes of *Ptilinus pectinicornis* L. and of *Trypoxylon clavicornus* Lep., and it is probably parasitic on the latter. The genus *Trypoxylon* is found in America, and probably our species may be parasitic on the same.

TRIGONODERA Dejean

- 1834. *Trigonodera* Dejean, Cat. Col., Ed. 1833, p. 217.
- 1840. *Pelecotoides* Castelnau, Hist. Nat. Ins., Col., II, p. 263.
- 1855. *Trigonodera* Gerstäcker, Rhipiph. Col. Fam., p. 2.
- 1859. *Trigonodera* Lacordaire, Hist. Ins. Col., V, p. 619.
- 1891. *Pelecotomoides* Champion, Biol. Cent.-Amer., Col., IV, pt. 2, p. 350.
- 1901. *Caspyria* Fairmaire, Rev. Ent., p. 194 and 248.
- 1904. *Pelecotomoides* Schaeffer, Jour. N. Y. Ent. Soc., XII, p. 231.

Larger species; elongate; head comparatively small, vertex not elevated above anterior margin of pronotum. Eyes large and in some species subcontiguous; antennae with eleven segments, usually situated below middle of eyes, pectinate in the male, and deeply serrate in the female. Mandibles are not large, lacinia of maxillae broad and short. Pronotum very broad at base, and strongly tapering anteriorly, lateral margins curved, lateral carina distinct at base only, lateral suture obsolete; hind angles acute but not prominent. Elytra elongate, covering the entire abdomen. Tarsal claws serrate.

GENOTYPE: *Trigonodera leachii* (Latreille).

A diversity of opinion has existed as to the proper generic name of this group of insects. In 1833-1834, Dejean published the catalogue of his insect collection, in which he placed *Pelecotoma leachii* Latreille, together with a group of undescribed species from Brazil, in the genus *Trigonodera*. Castelnau in 1840 described the same genus as *Pelecotoides* with the species *maculata*, *gigantea*, *strigata*, etc. Gerstäcker, however, used the generic name *Trigo-*

nodera and was followed by Lacordaire, while Gemminger and Harold replaced it by *Pelecotomoides* the amended name of Castelnau. This name has been somewhat generally used by later authors but Leng changed it to the original spelling. Because of its priority, and because of the validity of one of the species included in the genus *Trigonodera* Dejean, that name should stand, and is therefore used in this paper.

Csiki lists about forty species, most of them taken South of the Equator, both in the Eastern and Western Hemispheres; a few species have been taken in Central America but only one north of Mexico. The following is a key to the species of North and Central America.³

Key to the North and Central American Species of Trigonodera

1. Eyes very large, coarsely granulated, subcontiguous, antennae with four basal joints simple.....2
Eyes smaller, more finely granulate, and distant from each other in front...3
2. Frons with a glabrous area between base of antennae; rami in the male shorter than the first four segments; in the female shorter than the third and fourth segments taken together.....**schaefferi**
Frons thickly pubescent, rami of male antennae as long, or longer than the first four segments taken together; in the female as long or longer than the third and fourth segment taken together.....**nubila**
3. Antennae with the three basal joints simple.....**lineata**
Antennae with the five basal joints simple.....**bivittata**
Antennae with the four basal joints simple, the fifth acutely produced within.....**nebulosa**

***Trigonodera nubila* Gerstäcker**

1855. *Trigonodera nubila* Gerstäcker, Rhip. Col. Fam., p. 4.

1891. *Pelecotomoides nubilus* Champion, Biol. Cent.-Am., Col., IV, pt. 2, p. 351.

Elongate, brown covered with silky pubescence varying from golden-yellow to brown, sometimes variegated.

Head inserted in thorax to the eyes, vertex round, finely punctate and pubescent. Eyes coarsely granulated, very large, subcontiguous, especially in the males, being separated by a very narrow strip of chitin. Frons punctate and pubescent. Clypeus and labrum quadrangular, their anterior margins sometimes yellow and smooth. Mandibles curved, black and smooth at tip, pubescent on the sides near base. Antennae pectinate with the first four segments simple; the first segment longest and thickest, third segment longer than the second or fourth, which are subequal. In the male the processes are broad at tip and longer than the first

³ This is slightly modified from Champion's key.

four segments taken together; in the females the processes are acute and slightly longer than the third and fourth segment taken together.

Pronotum at base wide, lateral sides curved, anterior margin very narrow. Posterior lobe broad truncate, and two slight depressions on each side at base. Hind angles slightly produced. Elytra long and narrowly rounded at tip.

Length, 6.5 to 12 mm.

Distribution.—Gerstäcker described the species from Peru, and Champion records it from Mexico, Nicaragua and Panama.

The specimens studied were the following:

MEXICO: Venodio Sin, (Kuche). [U. S. N. M., 12 ♂], Jicaltepec, Vera Cruz, March, [F. C. Bowditch Collection, 2 ♀].

Trigonodera schaefferi new name

1904. *Pelecotomoides nubilus* Schaeffer, Jour. N. Y. Ent. Soc., XII, p. 231. (non Gerstäcker 1855).

Mr. Schaeffer did not compare his specimens with the true *T. nubila* Gerstäcker. Upon comparison with some males supposedly of the latter in the National Museum and two females in the Museum of Comparative Zoology, I find this species to be quite different. The two may be separated by the following: *T. schaefferi* has a smooth glabrous area in front between the antennae while *T. nubila* Gerstäcker has the entire clypeo-frons thickly pubescent. In the male of *T. schaefferi* the ramus of the fifth segment is shorter than the first four segments combined, while the *T. nubila* has it equal or longer than the four segments. In the female of *T. schaefferi* the process of the fifth segment is shorter than the third and fourth segments combined, while *T. nubila* has it equal or longer. In one female the eyes are not so close to each other as with other females. This characteristic varies apparently in the individuals. *T. schaefferi* is the only species of this genus in the United States, since no other specimens of *T. nubila* were found north of Mexico.

Elongate, subparallel, brown, covered with golden yellowish pubescence. Head, small, eyes very large, subcontiguous, occupying entire head, leaving a small rounded vertex and a very small front. Clypeus truncate at apex, punctured and hairy, with a small, elongate, smooth area between the antennal sockets; labrum truncate and hairy; mandibles very curved. First four segments of antennae without process, first and third segments longer than second and fourth. Male antennae pectinate, first ramus shorter than the first four segments taken together, also shorter than other rami; female antennae deeply serrate, first process shorter than third and fourth segments taken together. Pronotum conical,

broad at base as long, sides much curved, and anterior margin narrow, posterior lobe broadly rounded, and very slightly truncate. Scutellum longer than broad, quadrangular. Elytra long, slightly tapering toward apex, rounded at tip. Second segment of hind tarsus slightly longer than third.

Length, 5.5 to 9.5 mm.

Holotype.—Male; Esperanza Ranch, Brownsville, Texas, (C. Schaeffer). [Schaeffer Collection.]

Allotype.—Female; Same data as holotype, [Schaeffer Collection].

Distribution.—This species has been collected in Esperanza Ranch, Brownsville, Texas, June–July by Mr. Charles Schaeffer and May–June by Mr. H. S. Barber. Paratypes with the same locality label are also in the U. S. National Museum (No. 41864), Leng, and Frost Collections. Mr. Schaeffer, (1904), taking it as *nubilus*, writes the following:

“A small number of this interesting Rhipiphorid were beaten from different trees at Esperanza Ranch, most of them in July. Specimens are recorded from Panama as having ill-defined transverse or oblong patches of a fuscous color but all my specimens belong to the unicolorous form. This insect is of a grayish fuscous color, eyes large, divided in front by a very narrow line, antennae with the first four joints simple, the remaining flabellate in the male, strongly serrate in the female. My specimens are from 5.5 to 9.5 mm.”

Trigonodera nebulosa (Champion)

1891. *Pelecotomoides nebulosa* Champion, Biol. Cent.-Am., Col., IV, pt. 2, pp. 351, 352.

“Length, $7\frac{1}{2}$ to 11 mm.”

Type.—Champion records the species from Taboga, Panama, and Columbia. [British Museum.]

Trigonodera lineata (Champion)

1891. *Pelecotomoides lineata* Champion, Biol. Cent.-Am., Col. IV, pt. 2, p. 351.

According to Champion, *P. lineata* differs from all other species described by Gerstäcker in having the three basal joints only, simple.

“Length, $7\frac{3}{4}$ to 10 mm.”

Type.—Jalapa, Mexico. [British Museum.]

MEM. AM. ENT. SOC., 6.

Trigonodera bivittata (Champion)

1891. *Pelecôtomoides bivittata* Champion, Biol. Cent.-Am., Col., IV, pt. 2, p. 351, 352; (Chevr. in litt.).

Champion comparing this species with *T. lineata*, makes the following comment:

"Closely resembling the same sex of *P. lineata*, but differing from it by the small non-serrate fourth and fifth joints of the antennae. This specimen has the seventh antennal joint on one side abnormally formed, it being diserrate. Length, $8\frac{1}{2}$ mm."

Type.—Cordova, Mexico. [British Museum.]

TOPOSCOPUS Leconte

1868. *Toposcopus* Leconte, Trans. Am. Ent. Soc., II, p. 54.

Head round, sparsely pubescent, vertex rounded, very little elevated above anterior margin of pronotum. Eyes completely divided, the two divisions connected by corneous membrane destitute of facets. Antennae eleven-segmented, inserted near side of lower division of eye. Third segment about half the length of first, bearing a process shorter than those of the following segments; those of the male flabellate, with long rami of female pectinate with process rounded at tip. Pronotum strongly tapering anteriorly so that its anterior width is about one-third the posterior. Hind angles acute and prolonged, lateral carina prominent near hind angles only. Posterior lobe truncate, scutellum exposed, rectangular. Elytra slightly tapering posteriorly. Claws bifid at tip and with three additional small denticles along the edge, basally.

GENOTYPE: *Toposcopus wrighti* Leconte.

Leconte has pointed out both the differences and similarities between this genus and *Evaniocera*. We need no better comments than his, and it will be best to quote them: ". . . the eyes are divided into two portions connected by a slender line of smooth corneous material, which is destitute of lenses, while in *Evaniocera* they are only deeply emarginate. The third joint of the antennae of the male is longer, with a basal process about four-fifths as long as the processes of the following joints, while in *Evaniocera* the third joint is short, prolonged externally into a process one-fifth as long as those of the following joints. The side margin

of the prothorax is more developed, extending from the hind angles nearly to the apex. The claws are not finely pectinate as in *Evaniocera* but bifid at the tip, and armed with three slight teeth, somewhat as in *Ancholaemus* Gerst"

The genus *Evaniocera* is widely distributed in the Eastern Hemisphere, and its representatives have been taken in Europe and Northern Africa as well as in Siberia and Australia, while the one species of *Toposcopus* has been found so far only in the Southern part of the United States.

***Toposcopus wrighti* Leconte**

1868. *Toposcopus wrighti* Leconte, Trans. Am. Ent. Soc., II, p. 54.

1904. *Toposcopus wrighti* Schaeffer, Jour. N. Y. Ent. Soc., XII, p. 232.

Elongate, brownish-black and black; elytra ferrugineous or brown, covered with grey-golden pubescence. Head opaque, frons with slight impression near antennae, clypeus closely punctured, broadly truncate; mandibles much curved. Antennae of male flabellate, first segment large, black with tips red, second segment small, third larger, subcylindrical bearing the process at its proximal end, four-fifths the length of the following rami, other segments compact with rami close together. Female antennae pectinate and processes round at tip. Pronotum punctured and pubescent in the male, sparsely so in the female. Scutellum quadrangular, of the same color as pronotum, elytra long, punctured, covering entire abdomen; thorax beneath densely pubescent, claws bifid with three denticles.

Length, 6 to 10 mm.

Type.—Male; Tecalote Creek, south of Las Vegas, New Mexico. [Leconte Collection.]

Alloplesiotype.—Female; Texas. [Leconte Collection.]

Distribution.—Leconte described this species from 10 males collected during the survey under General W. W. Wright in New Mexico. Four of the ten males are in the Leconte collection; other males bearing the label "N. M." are in the following collections: Schaeffer,⁴ Horn, Hubbard and Schwarz (L. C. V. Riley) and Casey.

In addition to these I examined one male from Arizona in the Palm Collection, one male from Texas in the Casey Collection, and one female from Texas in the Leconte Collection. The female of this species was not known to Leconte at the time he

⁴ Mr. Schaeffer informs me that the specimen in his collection was given to him by Henshaw, and is no doubt one of the 10 mentioned by Leconte. Probably the other specimens bearing the same label in other collections are of the same origin.

described it. The one female was added to his collection later on, and is now with the type. This is the only female I have seen of this species, and agrees with the type in all respects except that the thorax is less punctured and pubescent and elytra are darker in color. This female, which was collected in Texas, should be considered as the allotype.

Variation.—The type specimen and some other males have the posterior part of the prothorax beneath, red, while others have it dark. One male in the Casey Collection is of darker shade and considerably larger than the others.

RHIPIDIUS Thunberg

1806. *Rhipidius* Thunberg, Vet. A K. Nya Hand, xxvii, p. 5.
1831. *Symbius* Sundevall, Isis, p. 1230.
1855. *Rhipidius* Gerstäcker, Rhipiph. Col. Fam., p. 14.
1859. *Rhipidius* Lacordaire, Hist. Ins. Col., v, p. 619.

As far as the writer knows, no species of *Rhipidius* have been found on the continent of North America. In the collection of the U. S. National Museum there is one female collected on a steamer in the Panama Canal. This female was identified by Dr. Schwarz as a *Rhipidius*, and on the basis of this record Leng listed it in his catalogue among the Coleoptera of North America. The writer has not made a study of this genus because of lack of material, and does not wish to state with certainty what species this is. However, a short description of this female and some drawings made from it will be of great value in this place, since it is the only record of this genus in this part of the world, regardless of the fact that it may have been brought by its host, perhaps a roach, from another locality. The general characteristics of a male *Rhipidius* are as follows:

"Labial palpi two-segmented, first very small, second large oblong-oval; head globose, flat on vertex, front lineate. Eyes granulate, occupy the entire anterior part of head, narrowly separated on front. Antennae inserted between them. Eleven segments, first cuniform, two to three short, others lamella very long and slender. Prothorax very transverse, or longer than wide, attenuate, slightly biseminated at base, no suture. Scutellum large, transverse. Elytra dehiscent. Legs simple. Claws simple, abdomen oblong, obtuse at end."

The female just mentioned is a small creature about 3 mm. long, brownish-black, and opaque. Head short and broad, frons concave with distinct elevations near the insertion of antennae. Eyes small, granulate, facets distinct, four facets more outstanding than the others. Antennae filiform, 11-segmented. Thoracic segments distinct and subequal, the third one being a little smaller; every one bears a pair of legs not very strong. Elytra and wings obsolete, abdomen 8-segmented with an ovipositor. (Pl. III, 4, 4 A' and 4 B').

MACROSIAGON Hentz

- 1792. *Rhipiphorus* Fabricius, Ent. Syst. II, p. 109.
- 1830. *Macrosiagon* Hentz, Trans. Am. Phil. Soc., Sec. 2, III, p. 462.
- 1840. *Emenadia* Castelnau, Hist. Nat. Ins., Col., II, p. 261.
- 1855. *Rhipiphorus* Gerstäcker, Rhipiph. Col. Fam., p. 19.
- 1859. *Emenadia* Lacordaire, Hist. Ins. Col., v, p. 627.
- 1875. *Rhipiphorus* Horn, Trans. Am. Ent. Soc., v, p. 121.
- 1891. *Emenadia* Champion, Biol. Cent.-Am., Col., IV, pt. 2, p. 353.

Form slightly compressed, broadest across metathorax. Vertex much elevated above anterior margin of pronotum; clypeus usually more sculptured than vertex. Eyes small, oval, prominent. Antennae, which are situated near the middle of the inner margin of eyes, pectinate or deeply serrate in the females, and biflabellate in the males, every segment bearing two rami. In both sexes the first and second segment without any process. Mandibles curved, acute, glabrous, base sometimes pubescent. Maxillae with lacinia filiform and hairy; labrum elongate, round at tip. Pronotum tapering toward front, longer than, or as long as wide at base; base with distinct lobe, which covers the scutellum. No distinct suture or lateral carina between disc and pseudo-pleuron; the latter narrow and small. Coxae separated in some species by a prosternal spine; in other species this spine is small so that the coxae are contiguous. Elytra dehiscent, tapering toward apex, as long as abdomen or longer. Tip of wings uncovered. Abdomen compressed, sternites much larger than the hard tergites, and curved so that their upper margin extends over pleurites. Front femora indented at apex; hind femora very much compressed, with inner surface glabrous and smooth. Claws bifid.

GENOTYPE: *Macrosiagon dimidiatum* (Fabricius).

Until 1830 the species of this genus were included in *Rhipiphorus*. Hentz separated them on the basis of the lacinia of maxilla which is elongate, their short abdomen, and habits. He designated *M. dimidiatum* as the genotype.

The length of the last tarsal segment varies with the species and serves as a specific characteristic. Some species have a distinct process on pronotum, others have excavations on the disc while others are smooth. The sexes are easily separated by the structure of the antennae. Some species have other distinct secondary sexual characteristics such as colors and markings. The genus may be separated into two groups, the group of *dimidiatum*, with sides of thorax strongly convex and bulging beyond sides of pronotum, and with front coxa contiguous, and the group of *limbatum* with sides of thorax flat and not bulging beyond lateral sides of pronotum, and prosternal spine separating front coxae. In the latter group, the species are usually more shining and less sculptured and the elytra are less dehiscent.

This genus is widely distributed. Species of *Macrosiagon* are found almost in every continent, but as a rule are limited to warm or temperate zones. Of the one hundred and twelve species listed by F. A. Schilder, sixty are from America. In other words, more than half of all the species recorded in this genus are American.

Key to the Species of Macrosiagon of North and Central America

1. Mesepisternum convex, bulging beyond lateral margin of pronotum, anterior coxa contiguous (in some cases only at tip).....2
 Mesepisternum more or less flat, not bulging beyond lateral margin of pronotum; anterior coxae separated by a prosternal spine.....11
2. Posterior lobe of pronotum with distinct process, vertex much elevated, with its front surface concave; second segment of hind tarsus not flat above and subequal to third.....3
 Posterior lobe of pronotum little convex, or with small cup-like concavity at tip, but never with distinct process; vertex without distinct concavity...4
3. Head and thorax brown, tibial spines truncate; wings yellowish-hyaline; antennal processes of female bifurcate (Pl. III, fig. 14)**fernaldum**
 Head and thorax black, tibial spines acute, wings brown; antennal processes of female acute or truncate. (Pl. III, fig. 15).....**flavipenne**

4. Pronotum with distinct excavations on the disc on both sides.....5
Pronotum may be slightly depressed near base, but without distinct excavations on the disc.....7
5. Excavations on sides of pronotum very deep, abrupt and triangular.
bifoveatum
Excavations on sides of pronotum longitudinal, less abrupt and shallow..6
6. Species somewhat robust, elytra shorter, sparsely punctured, strongly dehiscent.....**carinipennis**
Delicate species, elytra long, moderately dehiscent and sharply pointed.
excavata
7. Second segment of hind tarsus longer than third.....**cruentum**
Second segment of hind tarsus equal to or shorter than third.....8
8. Second segment of hind tarsus subequal to third, slightly thicker, and flat above; vertex much elevated; front surface convex, body entirely black, elytra yellow with tips black or brown.....**dimidiatum**
Second segment of hind tarsus shorter and thicker than third.....9
9. Vertex rounded, front surface convex, occiput without distinct suture (Pl. III, fig. 17).....**pectinatum**
Vertex truncate, front surface flat or slightly concave, occiput with distinct suture.....10
10. Distal end of first and second segments of hind tarsus produced (Pl. III, fig. 18); pronotum red, elytra yellow.....**sayi**
Distal end of segments of hind tarsus not produced, pronotum and elytra of the same color (Pl. III, fig. 16).....**octomaculatum**
11. Elytra short, not extending beyond end of abdomen.....**discicollis**
Elytra long; extending much beyond end of abdomen.....12
12. Second segment of hind tarsus longer than half the length of the third, not flat above; male antennae longer than the pronotum.....**lineare**
Second segment of hind tarsus about half the length of the third, flat and shining above; male antennae shorter than the pronotum.....**limbatum**

Macrosiagon flavipenne (Leconte)

1866. *Rhipiphorus flavipennis* Leconte, New Sp. North Am. Col., Smiths. Misc. Col., 6, p. 153.
1866. *Rhipiphorus abdominale* Leconte, Smiths. Misc. Coll., 6, p. 154.
1875. *Rhipiphorus flavipennis* Horn, Trans. Am. Ent. Soc., v, p. 121.
1891. *Emenadia flavipenne* Champion, Biol. Cent.-Am. Col., iv, pt. 2, p. 354.
1907. *Emenadia flavipenne* Cockerell, Trans. Am. Ent. Soc., xxxi, p. 211.
1915. *Macrosiagon flavipenne* Barber, Proc. Ent. Soc. Wash., xvii, p. 187.

Robust species, opaque black. Antennae yellowish brown in male, brown in female; the first two segments pale. Abdomen black in male, red in female with the last abdominal segments and posterior margin of the other tergites black or brown. Elytra entirely yellow in the male; yellow in the female, with a narrow strip at base and apical half black; the line of demarcation between the yellow and black surfaces usually semicircular. Wings yellowish brown.

Head elongate, vertex much elevated, the upper carina rounded, sometimes truncate or slightly emarginate; front surface concave and coarsely punctured, clypeus narrow and acutely rounded; mandibles long and very little curved, labrum elongate and pubescent. Antennae flabellate in the male, pectinate or deeply serrate in the female. Pronotum coarsely punctured, with two slight impressions on disc near front, posterior lobe with distinct broad process projecting posteriorly; apex of process truncate or feebly emarginate. Elytra punctured, slightly impressed, strongly dehiscent and acute. Second segment of hind tarsus not flat above as long as third.

Length, 7 to 11 mm.

Holotype.—Male, New York.⁵ [Leconte Collection.]

Allotype.—Female. [Leconte Collection.]

Distribution.—Leconte described the species from three males taken in Missouri and New York. In the Leconte Collection there are some females which he apparently acquired later, and one of these, the one placed nearest to the holotype, may be considered as the allotype. Horn records the species from Pennsylvania, Illinois, Georgia and California; Fall and Cockerell record it from New Mexico, while Champion records it from Villa Lerdo in Durango, Mexico. The specimens examined were from the following localities:

Massachusetts, New York, New Jersey, Virginia, Michigan, Florida, North Carolina, Georgia, Louisiana, Alabama, Texas, California and Kansas.

This species is widely distributed and accordingly varies much in form, size, etc. This fact led Leconte to describe *M. abdominale* which, according to the original description (I have not seen any specimen in the Leconte Collection bearing the label *abdominale*) is conspecific with *flavipenne*.

Biology.—Two hosts are recorded for this species, as follows: *Prosopis glandulosa*, Rincon, New Mexico (Cockerell), recorded by Fall and Cockerell, 1907, p. 211. *Bembex spinolae*, Brookland, District of Columbia, June 26, 1914 (J. B. Parker), recorded by H. S. Barber, 1915, p. 187.

Macrosiagon fernaldum new species

The specimens in Mr. Frost's collection bear the label "*flavipenne* Lec." Those in Mr. Notman's collection are also confused with those of *flavipenne*. Dr. Horn, in his monograph on the

⁵ In the Leconte Collection the specimen at the extreme left, which is considered the type, has no locality label. This specimen is no doubt from New York, since the other males bear the label "Mo."

genus, mentions a variety of *flavipenne* from California in which the abdomen of the male is red. Dr. Horn referred, no doubt, to the male of this species. *M. fernaldum* is very closely allied to *M. flavipenne*, and the male especially is very similar to the male of *M. flavipenne*. The difference between them, however, is quite distinct, and the following are the most outstanding features by which the two may be separated.

The female of *M. fernaldum* has the processes of the antennae bifurcate, the elytra yellow with a brownish tinge at apex, the wings hyaline, while in *flavipenne* the antennal processes are acute or truncate, elytra yellow with posterior half black and the wings are brown. The male of *M. fernaldum* has the abdomen red or brown red, wings hyaline, while *M. flavipenne* has a black abdomen and wings smoky at least near costal margin.

Robust. Head dark brownish or black; lacinia yellow; antennae of male orange yellow, of female brown; pronotum brown or dark brown with margins often red. Elytra yellow with narrow strip near base brown; the tips of elytra in the female with brownish tinge. Wings yellow-hyaline; abdomen in both sexes red; in the males sometimes dark red or brown.

Head elongate, vertex elevated into a rounded carina, with the front surface concave and roughly punctured. Clypeus narrowly rounded, punctate with its margins often red. Labrum elongate, tapering anteriorly, pubescent. Lacinia of maxillae filiform; mandibles but little curved, smooth with pubescent areas on sides near base. Antennae of male with rami comparatively short, process of female antennae bifurcate.

Pronotum tapering anteriorly; disc sparsely, sides more closely punctate, two slight depressions on disc near anterior margin. Posterior lobe acute, with a distinct elevated process, and two depressions on each side. Elytra dehiscent, acute at tip, finely punctured; a narrow strip near base brown, tips of female elytra with brownish tinge. Tibial spines truncate, smooth at tip. Second segment of hind tarsus equal to third and not flat and smooth above.

Length, 7 to 11 mm.

Type.—Male: Lindsay, California, Aug. 4, 1911, (J. C. Faure). [U. S. National Museum, No. 41867.]

Allotype.—Female; Lindsay, California, July 29, 1909 (W. A. Davidson). [U. S. National Museum.]

Distribution.—The above description was made from four males and nine females from Lindsay, California, in the U. S. National Museum; from one female and two males collected in Palm Spring, California in the Frost Collection; from three females

bearing the label "Cal.", in Notman Collection, and from one male in the Horn Collection. The above specimens are labeled paratypes. Together with additional records the distribution is thus:

CALIFORNIA: Lindsay, July (W. A. Davidson) (J. E. M. Gautt); Aug. (J. C. Faure), [U. S. N. M.]. Palm Spring, (Dr. Fenyess), [Mason Coll.; Frost Coll.]. Jewetta, Sept., (Rehn and Hebard), [Mason Coll.]. "Cal.", [Horn Coll.; Notman Coll.].

Specimens of this species have been taken on *Asclepias*.

I call this species *fernaldum* in honor of Dr. H. T. Fernald, my first teacher in Entomology and much respected friend and guide.

Macrosiagon bifoveatum (Horn)

1875. *Rhipiphorus bifoveatus* Horn, Trans. Am. Ent. Soc., v, pp. 121, and 123.

1891. *Emenadia bifoveata* Champion, Biol. Cent.-Am. Col., IV, Pt. 2. p. 354, t. 16.

The species is quite distinguishable by its excavation of pronotum; it differs from *M. excavatum* and *M. carinipenne* in having the same more abrupt.

Robust. Color black or dark brown. Antennae of male orange yellow with the tips of rami slightly fuscous, antennae of female dark brown; elytra of male brownish, gradually becoming darker at base, often a small arcuate space at base of elytra yellowish; posterior margins of hind coxae and metaepimeron pale. Wings of male yellowish, those of female brown.

Head broad, vertex rounded sparsely but distinctly punctate, frons and clypeus more densely punctate, the margin of the latter broadly rounded. Mandibles reddish at base, smooth, with a pubescent area on side of mandibles near base. Labrum pubescent. Rami of antennae moderately long; in the female the processes increase in length toward the apex. Pronotum heavily punctured, disc elevated with two triangular excavations on each side near base, posterior lobe triangular its posterior angles not prominent. Elytra acute, strongly dehiscent, punctured, with smooth curved groove along sutural margin. Under side of body sparsely punctured, second segment of hind tarsus slightly shorter than third, flat and glabrous above.

Length, 8 to 14 mm.

Type.—Male; Illinois.⁶ [Horn Collection, A. N. S. P., No. 8122.]

Alloplesiotype.—Female; Guatemala, (Sallé). [Horn Collection.]

⁶ This species is more common in Central America and Mexico. The locality of the type is the only record north of Texas, and it is rather strange to note that no specimens have been taken in any place between Illinois and Texas.

Distribution.—Horn describes the species from a male taken in Illinois. Champion records the species from Mexico and Nicaragua. Specimens examined were from:

ILLINOIS: Type, [Horn Colln.].

GUATEMALA: (Salle), [Horn Colln.] [Bowditch Colln.; labeled Homotype.] [Edwards Colln.] (P. Sprague), [U. S. N. M.]

MEXICO: Oaxaco, (Hoegel), [M. C. Z.]

TEXAS: (G. D. Smith), [M. C. Z.]

Variation.—The Holotype and one male from Guatemala have the thorax black, while the other males of Guatemala have it brown or dark brown. One of the males has a transverse impression on the disc of pronotum in front of the two excavations.

Macrosiagon excavatum (Champion)

1891. *Emenadia excavata* Champion, Biol. Cent.-Am., Col., iv. pt. 2, p. 354.

Champion makes the following remark on this species and its difference from *M. bifoveatum* Horn:

"Though very variable as regards the colour of the head, thorax, under surface, and legs, *E. excavata* is unusually constant in the colour and markings of the elytra, these latter only varying in the predominance of the yellow or of the black, the markings being always distinct. *E. excavata* is nearest allied to *E. bifoveata* (Horn), from which it differs, apart from the colour and markings of the elytra, by the shallower, longer, and much less abrupt depression on either side of the disc of the thorax behind; also by its narrower general shape, and less dehiscent and less acuminate elytra."

Color ferruginous or black. Head red or black, antennae of male testaceous or reddish with the rami blackish; in the female black with the two basal joints reddish testaceous. Pronotum ferruginous. Elytra yellowish, with base, margins and longitudinal line extending from apex to a short distance behind base, dark fuscus or deep red. Thorax beneath and abdomen black or ferruginous. Posterior margin of metepimeron and hind coxa yellowish.

Vertex rounded convex, very finely and sparsely punctate; clypeus narrowly truncate or slightly notched at apex. The process in the female antennae increases in size toward apex. Pronotum gradually narrowing toward front, finely punctured, disc slightly raised and with two longitudinal excavations on each side near base. Posterior lobe acute, not much elevated, hind angles acute but not projecting backward. Elytra long, sharply pointed, becoming gradually dehiscent a little behind the base; with a longitudinal channel from base to apex and a more or less

elevated ridge near the channel. The channel is more excavated about a fifth the distance from apex. Thorax beneath sparsely punctate and shining. Second segment of hind tarsus shorter than third and broad and flat above.

Length, 4.5 to 9 mm.

Type.—Male; Oxaca, (Hoegel). Mexico. [British Museum.]

Allotype.—Female; Oxaca, (Hoegel), Mexico. [British Museum.]

Distribution.—Champion described this species from forty-one specimens, all taken in Mexico.

Four of the specimens I have examined were sent from the British Museum to various institutions in this country. They all bear the label, Oxaca Mexico (Hoegel)⁷ and are distributed as follows: Two females in Museum of Comparative Zoology, one female in the American Museum of Natural History, one female in the U. S. National Museum. Two other females in the Bowditch Collection bear the label "Mex."

Macrosiagon carinipenne (Champion)

1891. *Emenadia carinipennis* Champion, Biol. Cent.-Am., Col., IV, Pt. 2, p. 355.

According to Champion the species differs from *M. excavatum* as follows:

"Broader and less elongate; the elytra much more sparsely punctured, more dehiscent posteriorly, less sharply pointed at the tip, and with a well-defined sub-lateral carina, the base only black; the longitudinal groove on either side of the disc of the thorax behind shallower, the intermediate space much less convex; the vertex a little flattened in front; the antennae, the extreme tips of the rami excepted, brownish-yellow; the legs reddish-testaceous, with the femora piceous."

"Length $8\frac{1}{2}$ mm."

Monotype.—Male; Yantipéc in Morelos, (Hoegel). [British Museum.]

Macrosiagon dimidiatum (Fabricius)

1781. *Mordella dimidiata* Fabricius, Spec. Ins., I, p. 332.

1792. *Rhipiphorus dimidiatus* Fabricius, Entom. System., p. 112.

1795. *Rhipiphorus dimidiatus* Olivier, Ent. Col., III, 65, p. 8.

1801. *Rhipiphorus dimidiatus* Fabricius, Syst. Eleuth., II, p. 120.

1855. *Rhipiphorus dimidiatus* Gerstäcker, Rhipiph., Col. Fam., p. 21.

1866. *Rhipiphorus marginale* Leconte, New Spec. N. Am. Col., p. 154.

1875. *Rhipiphorus dimidiatus* Horn, Trans. Am. Ent. Soc., V, pp. 121, 122.

This species is in many collections confused with those of *M. flavipenne*, *M. pectinatum*, and in one case a small specimen was

⁷ The specimen from the Museum of Comparative Zoology bears the label "Cotype."

found with those of *M. cruentum*.⁸ It may be separated from *pectinatum* and *cruentum* by the hind tarsal segments. In *cruentum* the second tarsal segment is longer than the third, in *dimidiatum* they are subequal, while in *pectinatum* the second is shorter than the third. Although Dr. Horn, in his description of this species, states that the second segment is shorter than the third, the term "subequal" will better describe it. I have measured the segments and found the difference is hardly noticeable. The third segment, being more slender, appears longer than the second. In its general appearance *M. flavipenne* is very much like *M. dimidiatum*; on closer examination, however, the following differences are clearly noticeable: the abdomen of the female of *flavipenne* is red, while it is black in *dimidiatum*; the elytra of the male *flavipenne* are entirely yellow, while their tip is black in *dimidiatum*. The vertex of *flavipenne* is concave in front and the pronotum has a distinct process, while the frons of *dimidiatum* is flat or convex, and there is no distinct process on the pronotum.

Black, elytra yellow with a narrow strip along the base; and the tips, black or brown. Head elongate, vertex elevated, rounded above, its front surface convex or flat, sparsely punctate; clypeus broad, obtusely angulate, rounded at apex and sometimes slightly emarginate on sides of angle. Labrum elongate, with its apex rounded, hairy; lacinia of maxillae longer than palpi, and filiform. Mandibles slightly curved, acute, smooth with punctured area on sides near base. Male antennae yellow luteous. Female antennae pectinate, processes acute, first and second segments reddish, otherwise brownish-black. Pronotum punctured, posterior lobe slightly convex with a cup-shaped depression near apex or with the same truncate. Elytra flat, punctured, rapidly narrowing toward the apex, tips very acute; in the male a small area at tip is black, while in the female, about the entire posterior half is black, and the line of division between the black and the yellow is oblique. Second segment of hind tarsus subequal to third, and both are flat above. Abdomen and thorax opaque and finely punctured in both sexes.

Length, 5 to 11 mm.

Distribution.—The species was described by Fabricius from North America (Mus. D. Yeats). Horn records the species from

⁸ This confusion with *M. cruentum* in Mr. Leng's collection caused an error in the List of Insects of New York, edited by Dr. Leonard. *M. cruentum* is a Southern species and of all the specimens examined, I found none from New York, and although Blatchley records it from Indiana, I doubt whether it would be found in New York. The specimen with the record of Peekskill in Mr. Leng's collection, upon examination, was found to be a *M. dimidiatum*.

New York, Florida and Missouri. The specimens which have been examined were from the following localities:

New Hampshire, New York, New Jersey, North Carolina, Virginia, Florida, Missouri, Texas, Arizona, Arkansas, Kansas, and California.

Macrosiagon acutipenne (Pierce)

1904. *Rhipiphorus acutipenne* Pierce, Stud. Univ. Nebr., iv, p. 163.

The holotype and paratypes (U. S. N. M. No. 8255) were examined, but I could not find any characters by which it may be distinctly separated from *M. dimidiatum*, Fab.

Macrosiagon octomaculatum octomaculatum (Gerstäcker)

1855. *Rhipiphorus octomaculatus* Gerstäcker, Rhipiph. Col. Fam., p. 22.

1858. *Rhipiphorus puncticeps* Leconte, Jour. Acad. Nat. Sci. Phila. (2), iv, p. 20.

1875. *Rhipiphorus octomaculatus* Horn, Trans. Am. Ent. Soc., v, pp. 122, 123.

1891. *Emenadia octomaculata* Champion, Biol. Cent.-Am., Col., iv, pt. 2, p. 356.

Robust. Head entirely black or red, or partly red and black. Antennae blackish, pronotum red with two black oblong spots which are often obsolete; elytra with three spots, humeral, middle and apical. Thorax beneath, varying from red to black; legs varying from reddish to black. Wings pale brown. Abdomen always red.

Head short and coarsely sculptured. Vertex very broadly truncate, occiput densely pubescent, with distinct occipital suture which extends to the tip of vertex. Distinct humeri present above each eye; frons punctate with a smooth median line, punctation very close near the eyes and sides of clypeus, the latter broadly truncate, slightly emarginate or bilobed. Labrum short, emarginate or bilobed, setiferous. Mandibles curved, smooth; punctured only on sides near base. Antennae situated under small tubercles near middle of eyes; in both sexes shorter than head. Processes of female antennae bifurcate; in the male the rami are comparatively short. Pronotum coarsely punctured, pubescent, short, broad and very much bent; posterior lobe short, and sometimes truncate; elytra short, gradually tapering, coarsely punctured. Thorax beneath very finely and closely punctate, covered with dense golden pubescence. Second segment of hind tarsus slightly shorter than third and rather broad and flat above.

Length, 5 to 12 mm.

Distribution.—Gerstäcker described the species from Illinois and Brazil. ["Zool. Mus. Berlin u. Greifswald"], Horn records the species from Florida, Georgia, Kansas and Texas. Specimens examined were from the following localities:

NORTH CAROLINA: Wilmington, August, (G. P. Engelhardt), [Schaeffer Colln.].

FLORIDA: Jacksonville, [Leng Colln.].

GEORGIA: Jekyll Island, September, (Bromley) [A. M. N. H.].

ALABAMA: Mobile (Loding).

TEXAS: [Leng Colln.].

ARIZONA: Huachuca Mountains, August, [Notman Colln.; Schaeffer Colln.; A. M. N. H.; Charles Palm Colln.; Leng Colln.] Phoenix, [Leng Colln.].

Variation.—*M. puncticeps* Leconte, which has been considered by Horn as a variety of *octomaculatum*, is practically identical with this. The type in the Leconte Collection has no distinct black spots on the thorax, but this characteristic is not of value since there are many intermediate stages between the two extreme forms. As to other characteristics, Leconte's type is practically identical with the specimens compared. Most of the specimens before me have reddish legs but some have them dark red, while still others have black legs; the color of the legs therefore is not of great varietal value.

***Macrosiagon octomaculatum maritimum* new variety**

Very robust. Head and thorax like in the preceding. Elytra shorter, with distinct humeral spot, and the two others confluent with each other. In some specimens the humeral spot is also confluent with the median, while in still other specimens the apical is connected with the middle only by a narrow strip along the suture. Legs reddish or black. The male is similar to that in the preceding variety except that the middle spot on elytra is more conspicuous.

Length, 6 to 14 mm.

Type.—Female; Springhill, Alabama, November. [American Museum of Natural History.]

Paratypes.—All females; Gulfport, Florida, (Reynold), [Leng Colln.]. Springhill, Alabama, [Schaeffer Colln.]. Florida, [U. S. N. M., 1, no. 41868].

Distribution.—In addition to the above, material has also been examined from Mobile, Alabama, June, (Loding), [Frost Colln.], and Jacksonville, Florida, [M. C. Z.].

Variation.—The variation in size in the different specimens of this variety is extreme. One specimen from Mobile is 6 mm. while others are 14 mm. long and very robust. As in the preceding variety, the pronotum may be without distinct spots.

This variety is mostly confined to the gulf states and apparently thrives best along the coast.

Macrosiagon sayi (Leconte)

1823. *Rhipiphorus bicolor* Say, Jour. Acad. Phila., III, p. 275, (Complete Writing II, 1859, p. 162.) Preocc.

1858. *Rhipiphorus sayi* Leconte, Jour. Acad. Nat. Sci. Phila. IV, p. 21.

1875. *Rhipiphorus octomaculatus sayi* Horn, Trans. Am. Ent. Soc., V, p. 123.

Horn considered this species as a variety of *octomaculatum* Gerstäcker; but for the reasons indicated below, it should be considered as a distinct species. The sexes are distinctly different in color, while in *octomaculatum* that is not the case. The legs in this species are concolorous and do not vary in color as is the case in the varieties of *octomaculatum*. The form of the apex of the tarsal segment differs entirely from that in *octomaculatum* and in general structure it is more delicate.

Head black in the males, red in females; antennae fuscous, first and second segment red. Pronotum red in both sexes; elytra of male testaceous, with base and tip black; sometimes an indistinct spot is present in the middle. Female antennae with three brownish black spots usually confluent with each other to form a curved line extending from base to apex. Thorax beneath, black in the males and dark brown in the females. Abdomen in the males black, in the females red. Legs in both sexes dark brown.

Vertex broadly truncate, occiput pubescent, with occipital suture present, this is sometimes indistinct, front surface sparsely punctate with median smooth line, clypeus more closely punctate. Pronotum punctured, posterior lobe acute, with a smooth elevated median line extending from its apex anteriorly. This is sometimes obsolete. Thorax beneath very densely punctured and pubescent. Hind tarsus with second segment shorter than third. The apices of the tarsi, especially of the second segment, are produced on both sides into lobe-like projections (see Pl. III, fig. 18).

Length 7 to 11 mm.

Distribution.—New Jersey, Pennsylvania, Delaware, District of Columbia, Virginia, North Carolina, Florida, Louisiana, Kansas, Missouri, Illinois, Arizona and California.

Say described this species as *bicolor* from Pennsylvania, and Leconte renamed it since that specific name has been used before by Castelnau.

The species is comparatively common, and is distributed throughout the Southern States from coast to coast. It is found from May to August.

Host.—*Elis* sp. One specimen of *M. sayi* Lec. with the cocoon from which it emerged, was sent to the U. S. National Museum from the Japanese Beetle Laboratory. Upon inquiry, Mr. Loren B. Smith, Senior Entomologist in Charge of that Laboratory, in a letter dated May 9, 1928, writes the following:

. . . I find by referring to our records that the Rhipiphorid beetle *Macrosiagon sayi* Lec. was reared from a cocoon of *Elis* which was collected at Centralia, Ill., April 20, 1921. Two species were found in that locality, namely *E. obscura* Say. and *E. quinquicincta* Fabr. It is not known from which one of these species the beetle was reared, although I presume it was *obscura*, since there were more of these in the collection. The rearing was done by Dr. T. H. Frison.

***Macrosiagon cruentum cruentum* (Germar)**

1824. *Rhipiphorus cruentus* Germar, Ins. Spec., Nov., 1, p. 168.

1855. *Rhipiphorus cruentus* Gerstäcker, Rhipiph. Col. Fam., p. 27.

1875. *Rhipiphorus cruentus* Horn, Trans. Am. Ent. Soc., v, p. 122 and 124.

1891. *Emenadia cruenta* Champion, Biol. Cent.-Am. Col., IV, Pt. 2, p. 357.

This species is sometimes confused with *dimidiatum* or *pectinatum* but it is easily distinguished from these as it is the only species which has the second tarsal segment longer than the third. The amount of red and black is variable. One species from Texas has the elytra entirely red. The abdomen of the male is usually black but sometimes red. The abdomen of the female is usually red but sometimes black. Some specimens have the abdomen partly red and black.

Head and thorax black, abdomen red or black, elytra red, with base and tip black. Wings brownish. Head oval, black, vertex broadly rounded, its front surface flat or very slightly concave, sparsely punctured and shining; frons and clypeus more densely punctured, the latter broadly truncate, or very slightly emarginate. Mandibles red at base, black at tip. First and second segments of antennae rufous, otherwise fuscous, processes acute at tip. Pronotum broad, slightly tapering roward front, punctured; posterior lobe convex with two slight concavities on each side. Sides of elytra straight, sutural margin curved sideward to form rounded tips. Pleural region of thorax punctured; second segment of hind tarsus longer than third and slender.

Length, 5 to 8 mm.

Distribution.—This species was described by Germar⁹ from North American specimens. Gerstäcker records it from Mexico. Horn states it is distributed from Georgia to California. Champion records it from Guanajuato, Mexico; specimens examined were from the following localities:

Virginia, North Carolina, Florida, Louisiana, Arkansas, Texas, Arizona, Utah and California.

Two other distinct varieties are distinguished in this species as follows:

⁹ According to W. Horn the Germar Collection of Coleoptera is partly in the Zoological Museum of Berlin, and in Deutsche Entomologische Institut (Mus.) Berlin-Dahlem.

Macrosiagon cruentum rufum (Leconte)1854. *Rhipiphorus rufus* Leconte, Proc. Acad. Nat. Sci. Phil., v, p. 225.1875. *Rhipiphorus cruentus rufus* Horn, Trans. Am. Ent. Soc., v, p. 125.

Head, pronotum and abdomen yellow, elytra yellow, tip often blackish.

Length, 5 to 7 mm.

Type.—Female; San Diego, California. [Leconte Collection.]*Plesiotype*.—Male; Isabella, California, June. [Frost Collection.]*Distribution*.—Other specimens examined were as follows:

CALIFORNIA: Isabella, June, [Frost Colln.], Tulare Co. and Pasadena, [Schaeffer Colln.].

This species is limited apparently to California but may be found in neighboring localities.

Macrosiagon cruentum horni new variety1875. *Rhipiphorus cruentus* var. Horn, Trans. Am. Ent. Soc., v, p. 125.

Horn described this variety, but did not call it by name. I think, however, because of the characteristics stated that it deserves a varietal name, which I give it in honor of its first describer, Dr. George H. Horn.

Head black, the pronotum rufo-testaceous, elytra with tip and base very narrowly black, male abdomen black, female abdomen red.

Length, 5 to 7 mm.

Type.—Female; Texas. [Horn Collection, A. N. S. P., No. 8136.]*Distribution*.—Specimens of this variety have also been examined from: Dummit County, Texas, [Leng Colln.], and San Diego, California, [Hubbard-Schwarz Colln.].**Macrosiagon limbatum** (Fabricius)1781. *Mordella limbata* Fabricius, Spec. Ins., 1, p. 332.1792. *Rhipiphorus limbatus* Fabricius, Entom. System., II, p. 112.1795. *Rhipiphorus limbatus* Olivier, Entom. Col., III, 65, p. 6.1801. *Rhipiphorus limbatus* Fabricius, Systema Eleuth., II, p. 121.1835. *Rhipiphorus limbatus* Say, Bost. Jour. Nat. Hist., I, p. 189.1855. *Rhipiphorus limbatus* Gerstäcker, Rhipiph. Col. Fam., p. 30.1859. *Rhipiphorus limbatus* Say, Complete Writings (Ed. Leconte), II, p. 660.1875. *Rhipiphorus limbatus* Horn, Trans. Am. Ent. Soc., v, pp. 122, 125.1891. *Emenadia limbata* Champion, Biol. Cent.-Am. Col., IV, pt. 2, p. 358.

Head yellow, vertex often black; clypeus often reddish; mandibles black, base yellow, antennae blackish, first and second segments yellow; pronotum yellow with discal black spot varying in size. Elytra usually black, sometimes pale,

with sides, suture and base narrowly black. Wings brown. Thorax yellow beneath, often variegated with black. Femora yellow with apex black; anterior tibia black, others yellow with apical half black, or often entirely black; tarsi black or annulated with yellow.

Head elongate, vertex rounded, glabrous; frons smooth, clypeus slightly punctured, apex broadly truncate or emarginate; labrum elongate, its apex rounded, lacinia long filiform, hairy; mandibles moderately curved. Pronotum elongate, slightly tapering forward, sparsely punctured, posterior lobe large and acute, hind angles prolonged and slightly covering the elytra. Elytra sparsely punctured, long, slightly tapering toward the end. Thorax sparsely punctured. Pleural sclerites very little convex, not bulging beyond lateral margin of pronotum; front coxae separated by prosternal spine, legs slender and long. Second segment of hind tarsus about half the length of the third segment, flat and shining above.

Length, 5 to 12 mm.

Distribution.—The native country of this species was not known to Fabricius. He described it, however, from a specimen taken from the same collection (Mus. D. Yeats) as *M. dimidiatum*—and the locality for the latter was given as North America.

Horn states the species is found from Pennsylvania to Texas. Champion records it from Mexico, Guatemala, Costa Rica and Panama. The specimens examined were from the following localities:

New Hampshire, Massachusetts, Connecticut, New York, New Jersey, Delaware, Pennsylvania, District of Columbia, Maryland, North Carolina, Virginia, West Virginia, Florida, Georgia, Texas, Arizona, Kansas, Arkansas and Iowa.

From the list of localities we see that the species is most common along the Atlantic coast although specimens have been taken as far west as Arkansas. The northern record of its distribution is New Hampshire and the southern is Panama.

The species is most common in July and August, and has been taken by sweeping, and upon the following plants: goat weed, Elder, *Solidago*, *Eupatorium*, *Spirae* and upon the Mint plants namely: *Pycnanthemum flexuosum*, *Monarda punctata* and *Monarda citriodora*.

Variation.—The species is comparatively common and widely distributed. Accordingly, the variations in the specimens are numerous. Say divided this species into three varieties, namely: variety a, with vertex black; variety b, elytra black, immaculate; and variety c, beneath, variegated with black. These varieties are not valid, since the amount of black on the individuals is extremely variable, and the varieties merge into one another.

Macrosiagon limbatum pulchrum new variety

Head, thorax and abdomen entirely reddish yellow; without any black spots. Elytra black. Body very shining. Elytra less dehiscent.

Length, 9 mm.

Type and Paratype.—Females; Black Mountains, North Carolina, (W. Beutenmuller, June). [Frank R. Mason Collection at the Academy of Natural Sciences of Philadelphia, no. 8137.]

Two females of this beautiful variety were taken by Mr. W. Beutenmuller.

Macrosiagon lineare Leconte

1866. *Rhipiphorus lineare* Leconte, New Spec. North Amer. Col., Smiths Misc. Coll., 6 p. 154

1875. *Rhipiphorus lineare* Horn, Trans. Am. Ent. Soc., v, p. 122, 125.

Specimens of *M. lineare* are often confused with those of *limbatum* Fabricius. The characteristics given in the key, however, and their short face and smaller size, should readily separate it from *limbatus*.

Head yellow-ferruginous, brown or black. Antennae fuscous, first and second segment reddish. Pronotum ferruginous, brown or black, elytra black, sometimes with a brownish tinge. Wings brownish. Thoracic sclerites brown, yellow or variegated; femora brown, tibia and tarsi variably variegated. Abdomen ferruginous or black, pygidium dark.

Narrow, subparallel. Head short, shining; vertex broadly rounded, smooth, frons shining, clypeus very slightly punctured, its front margin broadly rounded, labrum broad; mandibles entirely, or only at tip, black. Pronotum tapering very slightly toward apex, sparsely punctured; posterior lobe broad, slightly convex; hind angles of pronotum produced and acute. Elytra slightly depressed along the disc, gradually tapering and dehiscent only at the end. Thoracic sclerites sparsely punctured. Mesoepimeron and episternum of mesothorax flat, and not bulging beyond lateral margins of pronotum; anterior coxae separated by a prosternal spine; tibiae and tarsi variably variegated. Second segment of hind tarsi longer than one-half of the third, not flat nor shining above. Abdomen sparsely punctured.

Length, 4 to 6 mm.

Type.—Male; Kentucky. [Leconte Collection.]

Leconte described the species from one male specimen taken in Kentucky. One male and female now in the Charles Palm Collection, American Museum of Natural History, were collected in Southwest Arkansas. This male (Homotype) was compared with the type in the collection of Leconte, and is identical with it in all

respects except size and color. The type specimen is entirely dark and much smaller than the Arkansas Specimen, while the latter has thorax and abdomen red. The female (Plesiotype) from the same locality has been compared with the type and is identical with it, except in size and color and secondary sexual characteristics, its antennae being pectinate.

Other specimens examined were from Arizona, Huachuca Mountain, July, in the collections of Messrs. Notman, Leng and Schaeffer and from Alabama in the Collection of H. P. Loding.

Macrosiagon discicollis (Gerstäcker)

- 1855. *Rhipiphorus discicollis* Gerstäcker, Rhipiph. Col. Fam., p. 32.
- 1855. *Rhipiphorus mutilatus*, Gerstäcker, Rhipiph. Col. Fam., p. 32.
- 1855. *Rhipiphorus 4-maculatus*, Gerstäcker, Rhipiph. Col. Fam., p. 33.
- 1877. *Emenadia melanoptera*, Chevrolat, Bull. Soc. Ent. France, p. IX.
- 1889. *Emenadia vitraci*, Fleutiaux and Salle, Ann. Soc. Ent. France, IX, p. 432.
- 1891. *Emenadia discicollis* Champion, Biol. Cent.-Am., Col., IV, pt. 2, p. 358.

"Oblong, ovate rufo-ferruginous, head, antennae except base and legs, black; pronotum and elytra bluish black. Head suborbicular, smooth black, shining; its vertex little elevated, rounded above. Mandibles rufopiceous, palpi yellow; antennae black except its three basal segments yellow; thorax subtriangular, little longer than wide, strongly attenuated toward front, lateral sides inflexed, posterior angles acute; behind, obtusely triangular toward scutellar lobe, above convex, slightly punctate, glabrous, shining rufo-ferruginous, discoidal spots blue-black. Elytra little narrower than base of pronotum, more than half as long as base of thorax, sides whitened a little towards the middle, not attenuated toward the rear, with the apex subtruncate, internal angle rounded. Above, moderately convex with moderately thick and fine punctation; body below with blue markings, red, punctate, somewhat shining. Legs black, spines and claws ferruginous."

Length, 6 to 5 mm.

The above is a translation from the original description by Gerstäcker.

Distribution.—Gerstäcker described this species from Brazil, [Type in Zool. Mus. Berlin-Greifswald], while Champion records it from Mexico, Columbia, Antilles, Cuba, Porto Rico and Guadeloupe, (Plesiotypes), [British Museum].

Variation.—Upon the specimens taken from Central America, Champion states as follows: "We have received four female specimens of an *Emenadia* from Mexico agreeing very well with Gerstäcker's description of *E. discicollis*, and there is also a Mexican example of the same species in the British Museum. In three

Macrosiagon pectinatum (Fabricius)

- ¹⁰ The author feels that a further study is necessary before a key to the various varieties and races of this species can be arranged.

RHIPIPHORUS Bosc.

1792. *Rhipiphorus* Bosc., Jour. Hist. Nat., II, p. 293.
1818. *Myodes* Latreille, Nouv. Dic. d'Hist. Nat., ed. 2, XXV, p. 130.
1819. *Myodites* Latreille, Nouv. Dic. d'Hist. Nat., ed. 2, XXIX, p. 302 (not a).
1823. *Dorthesia* Say, Jour. Acad. Phil., III, p. 274.
1855. *Myodites* Gerstäcker, Rhipiph. Col. Fam., p. 15.
1859. *Myodites* Lacordaire, Hist. Ins. Col., V, p. 630.
1880. *Myodites* Leconte, Trans. Am. Ent. Soc., VIII, p. 210.
1892. *Myodites* Horn, Trans. Am. Ent. Soc., XIX, p. 48.
1891. *Rhipidophorus* Champion, Biol. Cent.-Am. Col., IV, p. 359.
1904. *Myodites* Pierce, Stud. Univ. Nebraska, IV, p. 157.
1920. *Myodites* Pierce, Ent. News, XXXI, p. 277.

Vertex elevated above anterior margin of pronotum. Eyes prominent, situated on sides of head, leaving a broad frons and clypeus. Mandibles prominent but bent inwardly. Antennae eleven segmented, often ten segmented in females, inserted above the eyes, one on each side of the vertex. Male antennae bilabellate, those of female monoflabellate, pectinate or deeply serrate, the first two segments without process. Pronotum broad, with no distinct lateral carina, pseudopleuron small and inconspicuous. Scutellum of mesonotum usually hidden under the posterior lobe of pronotum but may be seen when the insect is bent. Elytra very short, convex and scale-like; wings uncovered, and not folded, the metanotum and dorsal part of abdomen thus being left exposed. Metathorax well developed; seventh tergite of the abdomen in the female developed into a very conspicuous shield-like pygidium. The entire abdomen of the female is so bent that the pygidium is found on the ventral side of the body, and the ovipositor is directed obliquely forward. Legs short, first and last segment of hind tarsus usually larger than the others, third one smallest; claws in both sexes pectinate, but in the males the teeth on the claws are more numerous and finer. The length of the first segment of the hind tarsi varies with the species and serves as a good character for classification. The pygidium also differs in size and shape and serves for that purpose. Other characteristics used in classification are the shape of vertex, form of antennae, colors of abdomen, etc.

The genus may be separated into two main divisions. One group consists of those species in which the first segment of hind

tarsus is long, slightly thicker than the others and not at all obliquely truncate, while the other group consists of those species in which the first segment of hind tarsus is elevated, thicker than the others and obliquely truncate. There are, however, intermediate stages between the two, and we find species that cannot be classified distinctly in either.

In arranging the key for the species of this genus, we are confronted by another difficulty, namely, antigeny. In this genus the sexes differ from each other more than in the preceding genera, with the exception of *Rhipidius*. In some species the general color differs in both sexes, while in others the color is the same. The shape and proportional length of the tarsal segments, however, are similar in the two sexes and serve for identification of the same. Leconte and Pierce used the color characteristics of male and female together with structural differentiation in the same key, and this made it altogether very complicated. In order to avoid some difficulties, it was found most convenient to divide the genus into divisions based on the shape of the tarsal segments, and then into groups based on the color characteristics of the two sexes. In some cases the author placed the species of which one sex only is known, in the same group of its nearest allies. New discoveries may, therefore, cause some changes in the following classification.

Key to the Groups of Rhipiphorus

First segment of hind tarsus obliquely truncate and emarginate at tip; as a rule this segment is shorter than all others combined, and elevated.

1. Female abdomen black or brown, male abdomen of same color.
Group luteipennis
2. Female antennae 10 segmented, deeply serrate, processes subequal; female abdomen yellow, that of the known males black.....*Group scaber*
3. Female antennae 11 segmented, rami very long in female, decreasing in length toward apex. Female shining; abdomen straw-yellow variegated with brown-black, male black.....*Group vierecki*
4. Female abdomen for greatest part reddish-yellow; male abdomen the same as female.....*Group popenoei*

First segment of hind tarsus not obliquely truncate, very little thicker than the others, and as long as all others combined.

- Female abdomen partly yellow, partly brown; male abdomen (as far as known) like that of female.....*Group californicus*
 Female abdomen entirely brown; male as that of female.....*Group fasciatus*

First segment of hind tarsus as long as all others but a little thicker, a little truncate and emarginate at apex.

Female abdomen orange-yellow, male unknown. *Group aurantus*

Group luteipennis

1. First segment of hind tarsus much longer and thicker than second. 2
First segment of hind tarsus only a trifle longer than second and very little thicker. Second segment much longer than third. Pl. IV, fig. 8t. . . *minimus*
2. Female antennae eleven segmented, elytra yellow, base brown-black (male not known). Pl. IV, fig. 1a. *calopterus*
Female antennae ten segmented. 3
3. Pygidium longer than broad, (male not known). Pl. IV, fig. 2p. . . *nevadicus*
Pygidium as long as broad, concave and shining. Pl. IV, fig. 3p. . *luteipennis*

To this group probably belongs *Rhipiphorus brevipes*.

Rhipiphorus luteipennis (Leconte)¹¹

1865. *Myodites luteipennis* Leconte, Proc. Acad. Nat. Sci. Phil., XVIII, p. 97.

1880. *Myodites luteipennis* Leconte, Trans. Am. Ent. Soc., VIII, p. 210.

1892. *Myodites luteipennis* Horn, Trans. Am. Ent. Soc., XIX, p. 48.

1904. *Myodites luteipennis* Pierce, Stud. Univ. Nebr., IV, p. 161.

1920. *Myodites luteipennis* Pierce, Ent. News, XXXI, p. 277.

The species may be separated from its allies by its smooth, concave and shining pygidium, antennal rami curved, and vertex broadly rounded and sparsely punctate.

Body black or brown, elytra dark amber yellow. Head large, vertex rounded, sparsely punctate, front wide and flat; slight concavity around vertex, clypeus slightly emarginate, antennae of male eleven segmented and of the same color as elytra, rami slightly curved and fuscous at tip. Antennae of female ten segmented pectinate, brown, first rami curved, and directed meso-anteriorly. The first five or six rami are subequal, the last few short. Pronotum sparsely punctate and pubescent along sides with two shining glabrous areas on both sides of disc. Base broadly rounded, truncate or slightly emarginate. Elytra shining fuscous, closely punctate at base, finely so along margins. Thorax beneath, and abdomen, sparsely pubescent, pygidium triangular, smoothly rounded at tip, punctate along dorsal margin, less so along sides and smooth and very shining on concave center. Front and second legs yellowish or brown yellow, hind legs brown. First segment of hind tarsus obliquely truncate and elevated but shorter than last one. Hind tibia distinctly longer than tarsus.

Length, 6 to 8 mm.

Type.—Female; New York. [Leconte Collection.]

¹¹ Csiki, in his catalogue, has erroneously placed this species in the genus *Macrosiagon* and consequently he renamed *M. luteipenne* M'Leay.

Distribution.—Leconte described this species from two females taken in New York. There is also a male in the Leconte Collection from Selma, Alabama. Other specimens examined were taken in:

MAINE: Wales, August (C. A. Frost). NEW JERSEY: Dunellen, Bear Swamp near Ramsey, September, [Schaeffer Colln.].

NEW YORK: Staten Island, August, (Leng), Mosholu, (Schaeffer); Richmond, August, (W. T. Davis); [A. M. N. H.].

Variation.—Two females, the one in the Schaeffer Collection from Mosholu, N. Y., and the one in the Frost Collection from Wales, Maine, are light brown, and the pygidium is more shining and concave than in the others; the one from Wales, however, was collected *in Coito* with a normal male, which does not differ from the other males; there is therefore no doubt that the two females are merely a light-colored form of *luteipennis*.

***Rhipiphorus nevadicus* Leconte.**

1880. *Myodites nevadicus* Leconte, Trans. Am. Ent. Soc. VIII, p. 210. 211.

1892. *Myodites nevadicus* Horn, Trans. Am. Ent. Soc., XIX, p. 48.

1904. *Myodites nevadicus* Pierce, Stud. Univ. Nebr., IV, p. 157.

1920. *Myodites nevadicus* Pierce, Ent. News., XXXI, p. 277.

The vertex of *Rh. nevadicus* is similar to the vertex of *luteipennis*, but the species may be easily separated by the form of the pygidium, which is elongate in *nevadicus* and broader and more concave in *luteipennis*.

Brown, shining, elytra amber yellow. Head wider than long, vertex broadly rounded and sparsely but distinctly punctate, front flat or very slightly concave, sparsely pubescent. Antennae curved, 10 segmented, pectinate, rami subequal except last two that are shorter. Pronotum rounded at base, punctate and slightly pubescent along base, sides and center of disc, the anterior part is smooth and glabrous. Elytra sparsely and very finely punctate. Wings hyaline with anterior margin and band brownish. Abdomen more densely pubescent, margins of segments slightly darker, pygidium much longer than wide, rounded at tip, punctate and pubescent along sides; slightly concave and smooth in center. Under side of body more densely pubescent, first segment of hind tarsus obliquely truncate, but slightly thicker than others, and about as long as fourth segment; longer than the second and third combined. Hind tibia and first tarsal segment very finely transversely ridged along dorsal edge.

Length, 4 to 7 mm.

Holotype.—Female; Western Nevada. [Leconte Collection.]

Plesiotype or *Topotype*.—Female; Nevada. [Horn Collection.]

The description above was made from the Holotype. The specimen in the Horn Collection taken in Nevada is identical with the type; and the drawing of the pygidium was made from this specimen, while the outline of the hind tarsus was made from the type in the Leconte Collection. The writer believes that the specimen in the Horn Collection is a true topotype since they both have the same kind of labels, and was given to Leconte by Horn. The locality label of this specimen has a red marking at its left hand side which probably indicates that it was collected in the western part of the state.

Rhipiphorus calopterus new species.

This species may be confused with species of group *fasciatus* because of the similarity in the color of the elytra, but it belongs, however, in a different group. Species of group *fasciatus* have the first segment of hind tarsus long and thin, while *Rh. calopterus* has it short and thick. From *nevadicus* it may be separated by the form of the pygidium, being longer than wide in *nevadicus* and shorter in *calopterus*. From *luteipennis* it may be separated by the antennae, the rami being long, curved and subequal in *luteipennis*, and short, straight and decreasing in length in *calopterus*. In addition to this the antenna of the latter has eleven segments, while the others have only ten.

Brown. Head and pronotum blackish; front femora with a yellowish tinge in front; elytra at base amber yellow, basal third brown, shining; wings brown, tips hyaline. Head broad, vertex broadly rounded, finely but sparsely punctate, front finely pubescent, coarsely punctate with a small median excavation in front of vertex. Antennae of female 11-segmented, pectinate, brown, processes decrease in length toward apex, first ramus longest, much shorter than the length of the eyes. Pronotum about as broad at base as long, rounded, and slightly truncate at base, finely pubescent and densely punctate with smooth glabrous area extending from disc to both sides. Elytra coarsely punctate, especially near base, humeri distinct, smooth and shining. Wings brown, tips hyaline. Under side of body sparsely pubescent, punctate, pygidium coarsely but sparsely punctate at apex, but finely and densely punctate at its dorsal angles. Apex broadly rounded, almost truncate, convex, with a small concavity at anterior margin.

First segment of hind tarsus shorter than fourth, about as long as second and third together, but thicker and obliquely truncate at apex.

Length, 5.5 mm.

Monotype.—Female; Paris, Maine, July, (C. A. Frost). [Frost Collection.]

Rhipiphorus minimus (Pierce)

1904. *Myodites minimus* Pierce, Stud. Univ. Nebr., IV, p. 159.

1920. *Myodites minimus* Pierce, Ent. News, XXXI, p. 278.

Head and thorax black, abdomen dark brownish, antennae with stalk brown, rami light brown tipped with brownish. Elytra, anterior and median legs color of antennae, posterior darker. Wings hyaline, clouded at middle with brown.

Head depressed, rather coarsely and unevenly punctate, clad with very sparse, whitish pubescence; 11-jointed, very finely punctate throughout, vertex between the antennae elevated, rounded, not carinate. Pronotum very unevenly and coarsely punctate with pubescence very sparse at base and near anterior margin; glabrous shining along sides and disc; disc not carinate and but slightly and very broadly grooved toward apex. Mesothorax with scutellum concealed; apical half coarsely punctate; posterior margin straight. Metathorax sparsely punctate; postscutellum shining, glabrous, laterally converging, apically truncate. Abdomen coarsely, sparsely, unevenly punctate; finely but sparsely pubescent. Body sparsely punctate, pubescent beneath. Elytra sparsely and shallowly punctate. Posterior tarsus with the first joint not remarkably elongate, as long as second and third joints together, but not equaling the length of fourth, apically thickened, twice as thick as succeeding joints, obliquely truncate, and emarginate behind; second joint over twice as long as third; claws as long as second joint, pectinate.

Length, 4 mm.

Type.—Male; Belmont, Nebraska. [U. S. National Museum, No. 8256.]

The type has been examined and no characteristics were found that were not mentioned in the original description and therefore it was quoted above with some changes. It was found necessary however, to make a more detailed drawing of the hind tarsus, than the one Pierce presented.

Rhipiphorus brevipes new species

The species may be distinguished from other allies by its short legs and tarsi. Pl. IV, fig. 13.

Male: Black-brown, antennae yellowish, tips darker, legs brownish-yellow, bases of femora black-brown. Elytra amber yellow, extreme base brown.

Vertex rounded, frons with two elevations between bases of antennae, clypeus elevated, emarginate and red at tip. Pronotum pubescent, two glabrous areas near base distinct, median line depressed near base. Elytra punctate, base glabrous. Median line of mesoscutellum not furrowed, smooth and elevated. Tergites pubescent, second tergite smooth, first pubescent with glabrous area in middle, third tergite pubescent on sides only. Seventh tergite with smooth areas on both sides. Pygidium (eighth tergite) pubescent with dorsal margin smooth. Legs short and compact, very robust, first segment of hind tarsus very short and thick, about as long as fourth segment, obliquely truncate and emarginate, tips lobate.

Length 4 mm.

Monotype.—Male; Rio Balsas, (Wickham). Mexico. [Museum of Comparative Zoology.]

Group scaber

1. Pygidium in the female entirely brown or dark brown.....2
Pygidium in the female entirely, or for the greatest part yellow.....4
2. First tergite only with brown median spot; the rest are entirely yellow.

neomexicanus

- Three or four tergites with brown median spots.....3
3. First segment of hind tarsus elevated, truncate, and shorter than all others combined. Species so far taken in Nebraska only.....*solidaginis*
First segment of hind tarsus less elevated, about as long as fourth segment.
So far taken only in New Mexico and Colorado.*scaber*
4. Tip of pygidium brown, first segment of hind tarsus shorter than all others combined*semiflavus*
Entire pygidium yellow, first segment of hind tarsus delicate, and although truncate and emarginate, very little thicker, and distinctly longer than fourth.

nomiae

Rhipiphorus scaber (Leconte)

1852. *Myodites scaber* Leconte, Proc. Acad. Nat. Sci. Phila., v, p. 67.
1855. *Myodites scaber* Gerstäcker, Rhipiph. Col. Fam., p. 17.
1865. *Myodites scaber* Leconte, Proc. Acad. Nat. Sci. Phil., xviii, p. 96.
1880. *Myodites scaber* Leconte, Trans. Am. Ent. Soc., viii, p. 210.
1892. *Myodites scaber* Horn, Trans. Am. Ent. Soc., xix, p. 48.
1904. *Myodites scaber* Pierce, Stud. Univ. Nebr., iv, p. 183.
1920. *Myodites scaber* Pierce, Ent. News, xxxi, pp. 278 and 280.

Rh. scaber is very similar to *Rh. solidaginis* Pierce, and it is hard to separate the two. Pierce distinguished them by various characteristics but his comparison was made with a female "supposedly" of the species *scaber* Leconte, and some noteworthy errors enter into his comparison. In the first place, *Rh. scaber* has brown-black spots on the tergites the same as *Rh. solidaginis*, and the pygidium of both is very similar. The only distinct difference which may be observed is in the hind tarsi, and since it would be practically impossible to separate the two from description only, it was advisable to place the figures of the tarsi beside each other for comparison. In addition, the fact that *Rh. solidaginis* so far has been collected only in the salt basin in Nebraska and *scaber* only in the arid regions of Arizona, Colorado and New Mexico may be of assistance in separating them.

Head and thorax black. Abdomen yellow; first segment, one spot on each of

MEM. AM. ENT. SOC., 6.

the following two or three tergites, pygidium and legs dark reddish-brown, tarsi paler. Elytra pale yellow, apical half of wings brownish, tips hyaline.

Head punctate, pubescent. Vertex rounded, finely punctate, epicranial suture slightly distinct, two distinct tubercles in front, one at base of each antennae with a deep excavation between the two, clypeus slightly emarginate. Antennae of female 10 segmented, about the length of head from vertex to clypeus; brownish, with the base of first process yellowish. Pronotum broadly rounded at tip, gradually tapering toward front, densely punctate and pubescent, with distinct narrow median line which broadens on disc into a small glabrous area, and with two small glabrous areas on each side. Elytra finely, indistinctly punctate. Abdomen finely punctured and sparsely pubescent, pygidium gradually tapering toward tip, about as long as broad, coarsely and uniformly punctate, with two very small concave smooth areas on sides. First segment of hind tarsus longer, slightly thicker than the others, obliquely truncate and emarginate at apex.

Length, 9 mm.

Holotype.—Female; New Mexico? (Woodhouse). [Leconte Collection.]

Plesiotype.—Female; Littleton, Colorado, June. [Frost Collection.]

Distribution.—Leconte described the species from one female specimen collected by Dr. Woodhouse, probably along Zuni River Creek boundary between New Mexico and Arizona. The following are his remarks about this species.

"A very imperfect specimen from the Creek boundary, which is distinguished from another Southern species having a yellow abdomen, by its much larger size, more punctured head and thorax, and immaculate black feet. I am inclined to believe that the color of the abdomen is a sexual character as in the European *M. subdipterus*."

The locality indicated is probably along the Zuni River as we learn from the account of Dr. Woodhouse himself. The type is in poor condition and lacks the antennae. The specimen before me from Littleton, Colorado, agrees perfectly with the type in the Leconte Collection except that the epicranial suture is not distinct as in the type. The description above was made from the type and from the above-mentioned specimen. Another female in the U. S. National Museum from LaCruces, New Mexico, Sept., agrees well with the description.

Rhipiphorus solidaginis (Pierce)

1902. *Myodites solidaginis* Pierce, Can. Ent., xxxiv, p. 293.
1904. *Myodites solidaginis* Pierce, Stud. Univ. Nebr., p. 183.
1905. *Myodites solidaginis* Silvestri, Redia, III, p. 323.
1920. *Myodites solidaginis* Pierce, Ent. News, xxxi, pp. 278 and 280.

Male black, antennae, elytra and legs yellow; tips of antennae and joints between tibia and femora fuscous. Female—head and thorax black, thorax, often black-brown, abdomen reddish yellow; spots on tergites and pygidium brown, often red brown; femora and tibia brown, although the latter may be variegated with yellow, tarsi yellow brown, antennae brownish, first process yellowish. Vertex broadly rounded, finely punctate, pubescent, frons coarsely punctate and slightly concave between the eyes, clypeus finely punctate. Antennae 10-segmented, processes subequal. Pronotum broadly rounded and slightly truncate at base, coarsely and densely punctate and pubescent. Median carina at basal half and two smooth glabrous areas on either side. Distance between the two posterior areas equal to about half that between the anterior ones. Elytra irregularly punctate; scutellum punctate, divided by a median carina. Abdomen finely and sparsely punctate, second and third tergites smooth and glabrous. Pygidium of female and also the seventh tergite of male densely and coarsely punctate with two glabrous areas on both sides of center. First segment of hind tarsus elevated obliquely, truncate and emarginate at tip, as long as last segment.

Length, 9 to 10 mm.

Holotype.—Male; Lincoln, Nebraska, July 29. [U. S. National Museum, No. 8254].

Allotype.—Female; Lincoln, Nebraska, July 29. [U. S. National Museum.]

Distribution.—Pierce records this species from: Nebraska:—Pine Ridge, July; Lincoln, July 29, August 30; West Point, Aug. 3. The Holotype, Allotype and several paratypes upon which these records are based are in the collection of the U. S. National Museum; paratypes are also in the Casey Collection and in the Collection of the Academy of Natural Sciences of Philadelphia. In addition to these, specimens were examined as follows:

NEBRASKA: "Neb.," [Schaeffer Colln.], [Leng Colln.], [Palm Colln.], [A. M. N. H.], Lincoln (Salt Basin), [Notman Colln.], Aug. 22, (Shoemaker), [Leng Colln.].

The only localities this species has been taken in, are Salt Basin in Nebraska or similar topographic places. The restriction of this species to this locality is due to the fact that its host, *Epinomia triangulifera* Vachel, is very abundant in those localities. Pierce explains also that the abundance of the species may be due to the fact that the host makes its nest in the neighborhood

of the plant upon which the triunguloid larvae feed in their earlier stages.

Rhipiphorus neomexicanus new species.

Rh. neomexicanus is closely allied to *Rh. scaber* and *Rh. solidaginis*. The male of *neomexicanus* may be distinguished from *solidaginis* in having the smooth areas on the tergites larger and more distinct, and the seventh tergite larger and opaque. The female of this species may be distinguished in having all tergites, except first two, without brown median spots. In addition, the segments of the hind tarsus differ as is shown in Plate IV, figs. 10, 11 and 12.

Male entirely black, legs, antennae and elytra yellow, tips of femora and tibia with a brownish tinge, tips of rami slightly fuscous. Vertex elevated and acute, frons flat and punctate with a small excavation between the bases of antennae, clypeus broadly truncate. Pronotum rounded at base, depressed on both sides to produce a median carina near base, entire surface is regularly punctate, with two small glabrous areas on each side of the carina. The distance between the two posterior areas is about half the distance of the two anterior areas. Elytra very finely and sparsely punctate. The second tergite and the anterior portion of third tergite glabrous, other tergites pubescent with two distinct smooth areas on the sides. The seventh tergite as broad as the two preceding together, and the smooth areas very distinct and larger than those in the other tergites. First segment of hind tarsus as long as third and fourth together, obliquely truncate and emarginate at tip.

Female head and thorax black or brownish-black. Abdomen reddish-yellow, femora brown, tibia and tarsi yellowish-brown; pygidium in greatest part brown with a yellowish tinge in the center. Elytra yellowish hyaline; wings with a smoky band in the middle. Vertex less elevated than in male, more rounded and with distinct occipital suture.

Length, 7 to 8.5 mm.

Holotype.—Male; Albuquerque, (River plain), New Mexico, August, 1921 (Rehn and Hebard). [Academy of Natural Sciences of Philadelphia, No. 8135].

Allotype.—Female; same data as type. [Academy of Natural Sciences of Philadelphia.]

Distribution.—Besides the type and allotype there is a female (paratype) in Leng's Collection also from Albuquerque.

Rhipiphorus semiflavus (Leconte)

1865. *Myodites semiflavus* Leconte, Proc. Acad. Nat. Sci. Phil., XVIII, p. 97.
1880. *Myodites semiflavus* Leconte, Trans. Am. Ent. Soc., XIX, p. 210.
1892. *Myodites semiflavus* Horn, Trans. Am. Ent. Soc., XIX, p. 48.
1904. *Myodites semiflavus* Pierce, Stud. Univ. Nebr., IV, p. 161.
1920. *Myodites semiflavus* Pierce, Ent. News, XXXI, p. 278.

"Black, finely less densely punctate, vertex obtuse, conical, apex, without carina; base of thorax round without dorsal median line; elytra shining, smooth on sides; humeral celli slightly dark, obscure, abdomen yellow, sparsely finely punctate, apex piceous, legs testaceous variegated. .30.

"Maryland, one specimen given by Rev. J. G. Morris. The antennae are wanting, the anterior feet are entirely testaceous with the base of the thighs dusky; the middle thighs are dusky, and the tibia and tarsi testaceous; the hind feet are entirely dusky, the wings have a broad smoky band near the tip."

Length, 7.5 mm.

Type.—Female; Maryland. [Leconte Collection.]

The above is a translation of the original description by Leconte, and his remarks. The type is indeed a poor specimen, and no additional notes were made from it. I had no specimens that were conspecific with it and also in the collections loaned to me later on, I find nothing that agrees with this description.

Rhipiphorus nomiae new species

This species may be distinguished from the others of this group in having the first segment of the hind tarsus thick and long as the fourth, but obliquely truncate and emarginate at tip. In addition the female is of a chocolate brown, the pygidium is entirely yellow and, in general, the species is much smaller and more delicate than the others.

Male. Head and thorax black, abdomen brownish-black. Antennae straw yellow, tips brown; legs yellow, coxa both ends of femora and tibia brownish. Elytra hyaline-yellow with a brownish tinge at base. Vertex prominent, with a carina and a distinct excavation. Pronotum punctate, sides not pubescent, disc sparsely so; base slightly truncate, with two depressions in front of it, elytra broad, punctate on sides; seventh tergite roughly punctate opaque, with two round smooth areas on side. Pygidium finer and denser punctate and opaque. Wings with a brownish tinge behind middle near costa. Hind tarsus with first segment slender and slightly longer than fourth, but shorter than all segments combined; it is very little stouter than the others but obliquely truncate and emarginate at tip.

Female differs from the male in color. Head and thorax chocolate brown. Abdomen and the pygidium entirely yellow. Wings more brownish; in one female entirely brown. Legs brown, with tarsi partly yellowish. Antennae 10-segmented; 8 rami short, subequal in length. Vertex less prominent, but with epicranial suture; pygidium almost uniformly distinctly punctate.

Length, 6 mm.

MEM. AM. ENT. SOC., 6.

Holotype.—Male; Selma, Alabama, (Hubbard and Schwarz). [U. S. N. M., No. 41865.]

Allotype.—Female; Selma, Alabama, (Hubbard and Schwarz). [U. S. N. M.].

Paratypes.—One female with same data as type; [U. S. N. M.]. One female; "Ala," (C. F. Baker). [U. S. N. M.].

Regarding the specimens upon which this species is based, we may note a report by Dr. Leconte¹² as follows: "Mr. Schwarz collected at Selma, Alabama, a species of *Myodites*, Parasitic on *Nomia nevadensis* Cresson. The abdomen in the female is yellow, and in the male black." This female is the allotype of *Rh. nomiae*, and has a label of Dr. Schwarz, indicating its parasitism upon *Nomia*. From this label we learn also, that the name "*Myodites nomeæ*" was given to this species, but was not published. I retain, therefore, this name. Upon investigation, Mr. H. S. Barber found that the specimen of *Nomia* which Dr. Schwarz collected, and upon which the report by Leconte was based, has since become the type of *Nomia pattoni* Cockerell.

Group vierecki

Rhipiphorus vierecki (Fall)

1907. *Myodites vierecki* Fall, Trans. Am. Ent. Soc., xxxi, p. 259.

1920. *Myodites vierecki*, Pierce, Ent. News. xxxi, p. 279.

1920. *Myodites knausi* Pierce, Ent. News. xxxi, p. 279.

Female: Head and thorax black or brownish-black. Pronotum black or dark brown, with sides and base light brown or yellowish, or entirely black but extreme margins with a trace of yellow. Elytra yellow with extreme base brownish. Abdomen straw yellow. The following parts in abdomen are dark brown or black; first five tergites, tip of pygidium, first five pleurites, fourth, fifth, sixth and seventh sternites, especially at their median area. Legs pale yellow, joints brown. Head finely punctate, sparsely pubescent. Vertex rounded, not carinate, frons, slightly concave in middle with slight convex areas on sides of this concavity. Antennae 11-segmented, about as long as head, rami very long, diminishing in length toward apex. First ramus about half the length of the entire antennae, last ramus as long as the three preceding segments together. Pronotum smooth and glabrous on disc, sparsely punctate and pubescent on sides and front, more closely punctate at base. Disc of pronotum with a distinct concavity in middle and two behind it near base. Base broadly rounded, slightly emarginate at tip. Meso-scutellum glabrous in middle and densely pubescent on both sides. Abdomen very sparsely pubescent, punctuation almost indistinct. Pygidium longer than

¹² Trans. Am. Ent. Soc., viii, Proc., p. xxiii.

broad, dorsal angles usually depressed, otherwise entirely convex. First segment of hind tarsus slightly shorter than all others combined, straight, and obliquely truncate at apex.

Male: "Length, 9 mm. Similar to the female, with the following exceptions: antennae honey-yellow, bi-flabellate, with the tips of the rami about even. The abdomen is black with the base and apex of the first ventral segment yellow, and the prepygidial area yellow, but with the pygidium black."

Length, 9 to 11 mm.

Type.—Female; Florence, Arizona. [Fall Collection.]

Distribution.—Fall records the species from Alamogordo, New Mexico, and Florence, Arizona. Pierce records it from St. George, Utah, June 10, 1919, altitude 2800 feet, and Hurricane, June 14 at altitude 3200. (Knaus). The specimens examined by the author were as follows:

Eight paratypes of *Vierecki* Fall, all females, Alamogordo, New Mexico, May–April, and Florence, Arizona, May, in the collection of the Academy of Natural Sciences of Philadelphia and one female paratype of *Myodites Knausi* Pierce, in the Mason Collection, Academy of Natural Sciences of Philadelphia.

Variation.—The descriptions of both Fall and Pierce show that *Rh. vierecki* Fall, and *Rh. knausi* Pierce are one species. The paratypes examined also show that both authors described the same species. *Rh. vierecki* Fall, because of its priority, should be considered the proper name, and *Rh. knausi* a synonym. Pierce, in his key (1920), distinguishes the two by the characteristics of the males; he knew the male of his species but did not know the male of the species Fall described and his distinction between the two therefore is very obscure. Pierce, in his description, states also that the female antennae are ten segmented with nine rami, in other words, the second segment is in this case with a process. As far as the present writer knows, having studied this genus and allied genera and families, such can not be the case; as a matter of fact, the antennae of the female *vierecki* has eleven segments, the second being very small, closely united to the first and therefore inconspicuous. In cases where the female of a *Rhipiphorus* has only ten segments, it is the last one that disappears. *Rh. vierecki* has longer antennal rami than the other allied species; in addition to this it may be distinguished from the others by the color, shape of pygidium, and hind tarsi.

Group popenoei

1. Tergites brownish, with distinct carina. Female not known.....**rex**
Tergites as well as sternites reddish-yellow.....2
2. Elytra fuscous.....**flaviventris**
Elytra red-yellow. Pronotum shining.....3
3. Pronotum black, pygidium of female brown-black. (Male not known).

laevicollis

Pronotum with reddish tinge along sides. Pygidium of female red-yellow.

popenoei**Rhipiphorus popenoei** (Leconte)

- 1880. *Myodites popenoei* Leconte, Trans. Am. Ent. Soc., VIII, p. 210.
- 1892. *Myodites popenoei* Horn, Trans. Am. Ent. Soc., XIX, p. 48.
- 1904. *Myodites popenoei* Pierce, Stud. Univ. Nebr., IV, p. 161.
- 1920. *Myodites popenoei* Pierce, Ent. News, XXXI, p. 278.

Head, thorax, anterior part of pronotum, sides and median line, as well as median line at tip of pygidium brownish black or brown. Otherwise red-yellow. Legs yellow, coxae and proximal end of femora brown. Vertex rounded, front with distinct median excavation in front of vertex. Clypeus yellowish, emarginate and shining. Maxillary palpi yellow. Antennae of female brownish-black, slightly pale at base, rami subequal, and moderately long. Pronotum finely punctured at base, very sparsely along lateral margins, glabrous on disc where there is a distinct excavated median line. Base broadly rounded and but little broader than anterior margin. Elytra punctured, but smooth along humeri.

Length, 8.5 mm.

Type.—Female; Colorado. [Leconte Collection.]*Allo-plesiotype*.—Male; Palmerlee, Arizona, August, (N. Banks). [Leng Collection.]

The above description was made from the type in the Leconte Collection. The male in the Leng Collection, agrees very well with the above description and the type. It differs, however, in the following: The pronotum is entirely black with a reddish tinge at hind angles. Hind femora and part of hind tibia brownish-black, otherwise legs and tarsi as described above. Pygidium (8th tergite) black, two spots on the 7th tergite and first sternite brownish. In addition to the above, the following should be mentioned: Antennae with rami curled longer than head, and blackish-brown. First segment of hind tarsi thicker than the others, obliquely truncate and emarginate, and as long as the two following, together; second segment slightly shorter than fourth.

Rhipiphorus flaviventris (Champion)

1891. *Rhipidophorus flaviventris* Champion, Biol. Cent.-Am., Col., IV, pt. 2, p. 361.

This species, according to Champion, may be separated from *Rh. rex* by having its tergites yellow, and from *popenoei* and *laevicollis* by having piceous elytra.

"Length, $8\frac{1}{2}$ mm. (♂)."

Type.—Male; Cerro Zunil, Guatemala. [British Museum.]

Rhipiphorus laevicollis (Champion)

1891. *Rhipidophorus laevicollis* Champion, Biol. Cent.-Am., Col., IV, pt. 2, p. 360.

From the original description it would seem that this species is nearly related to *Rh. popenoei*, but may be separated by the color of thorax, which, according to Champion, is entirely black, while tinged with red in *popenoei* and by other minor characteristics stated in the descriptions.

"Length, 9 mm."

Type.—Female; Mexico. [British Museum.]

Rhipiphorus rex (Champion)

1891. *Rhipidophorus rex* Champion, Biol. Cent.-Am., Col. IV, pt. 2, p. 360.

This species may be separated from the other allied species by its carinate tergites.

"Length, 10 mm."

Holotype.—Mexico. [British Museum.]

*Group aurantus***Rhipiphorus aurantus** new species

Rh. aurantus differs from *Rh. mutchleri* and *Rh. simplex* in having no markings along the abdominal segments; from the other species that have a reddish-yellow abdomen, it may be separated by the form of the hind tarsus and the antennae.

Very robust. Head and prothorax black, abdomen red-yellow, first tergite brown, pygidium red-yellow with the apex and an arched line projecting toward dorsum brownish, legs brown, tarsi yellowish-brown, wings smoky. Vertex broadly rounded, slightly carinate, closely punctate; frons concave, coarsely punctate above, convex and finer punctate below. Clypeus broadly rounded, with slight emargination. Antennae short, 10 segmented, rami long, 1.5 subequal, from 5 to 8 reducing in length. Pronotum finely and uniformly punctate, median line distinct and more depressed and broad on middle disc, no distinct glabrous areas on the sides of it. Scutellum bi-lobed, a median carina dividing it into

two distinctly concave and finely punctate areas. Elytra broad at base, narrowly rounded at apex, sutural margin emarginate. Sides of metascutum sparsely punctate, abdomen broad, sides parallel, first tergite finely punctate. Second tergite smooth and glabrous, others coarsely punctate with a small smooth glabrous area on each side and in the middle. Under surface of thorax and abdomen punctate and pubescent. Pygidium coarsely punctate with two concave smooth glabrous areas in the middle. Legs comparatively short and strong, hind tibia slightly curved and distinctly longer than tarsus. First segment of hind tarsus about as long as all others together, very little thicker, but distinctly truncate and emarginate at tip.

Length, 10 mm.

Monotype.—Female; Tarrant Co., Texas, Aug. 17, 1902 (Hooker). [U. S. National Museum, No. 41864.]

The hind tarsi of this species are of a form which may be considered as an intermediate stage between those which have the first segment broad, short, and obliquely truncate; and those which have the first segment as long as all others combined. In this case the first segment of the hind tarsus is broad and obliquely truncate at apex, but is as long as all the others combined.

Group californicus

1. Main color of abdomen brown, tergites and sternites with yellowish tinge.

californicus

Main color of abdomen yellow with brownish markings. 2

2. First tergites with brown markings, last tergites and main color of pygidium yellow. Male not known. **mutchleri**

Last tergites and pygidium brown, first tergites yellow. **simplex**

Rhipiphorus californicus (Leconte)

1880. *Myodites californicus* Leconte, Trans. Am. Ent. Soc., VIII, pp. 210-211.

1892. *Myodites californicus* Horn, Trans. Am. Ent. Soc., XIX, p. 48.

1904. *Myodites californicus* Pierce, Stud. Univ. Nebr. IV, p. 162.

1920. *Myodites californicus* Pierce, Ent. News, XXXI, p. 278.

Leconte, in his description of the species, has failed to mention that the dorsal segments of the abdomen are yellowish. This characteristic, although it varies in individuals, helps to identify it, and distinguish it from other allied species.

Head and thorax black or brown-black, elytra entirely yellow, abdomen brown, ventral segments paler, dorsal segments yellowish. Head pubescent, vertex conic, front flat or slightly concave, antennae 10-segmented, dark brown, pectinate, shorter than head, rami compact and decreasing in length toward apex. Pronotum broad and rounded at base, punctate, pubescent, with smooth areas on both sides

of distinct median line. Elytra finely, very sparsely punctate. Wings hyaline, very faintly fasciate; abdomen shining, sparsely and finely pubescent; pygidium very shining, finely punctate and pubescent along margins. Legs brown, tarsi fuscous; first segment of hind tarsi as long as all others combined.

Length, 5 to 6.5 mm.

Holotype.—Female. California. [Leconte Collection.]

Alloplesiotype.—Male; California. [Schaeffer Collection.]

Distribution.—This species is found along the Pacific Coast. There is one female in the Leng Collection from Soda Springs, Washington. The male specimen in the Schaeffer Collection agrees very well with the type of *californicus* in color and form and is no doubt its male. It has the vertex more pointed, middle and hind femora and hind tibia pale brown, front legs and all tarsi and antennae straw yellow, thorax dark brown; this male was taken in California. There is one specimen (Homotype) in the Leconte Collection which is placed alongside the type of *Rh. nevadicus*, and labeled "*nevadicus*" but is without doubt wrongly determined, as upon examination and comparison I find this specimen to be a true *californicus*. It was taken in Washington Territory.

***Rhipiphorus mutchleri* new species**

The nearest ally of this species is *Rh. californicus*. It differs from that in having the dominant color of the abdomen yellow, whereas in *californicus* it is brown: the tibiae of *Rh. mutchleri* are curved and broad; and in general it is a larger species than *Rh. californicus*.

Head and thorax black, abdomen and elytra yellowish-red, legs, tip of pygidium and some small areas along dorsal margins of sternites and spots on first two or three tergites brownish-black; front legs and all tarsi yellow, legs otherwise brownish. Head punctate, sparsely pubescent, vertex rounded, punctate, with suture or small carina; front slightly concave, clypeus truncate or slightly emarginate. Antennae 10-segmented, short, pectinate, rami decreasing in length toward apex. Pronotum punctate, with smooth median line and two shining areas on each side, base broadly rounded. Elytra broad, entirely yellow, shining, finely punctate. Wings hyaline, with smoky band along the middle. Pygidium broad, triangular, punctate along sides, smooth and usually concave in middle, although this concavity may be obsolete. First segment of hind tarsus as long as the others combined and slightly thicker than the others.

Length, 6 to 7.5 mm.

Holotype.—Female, Ormsby County, Nevada, July, (Baker). [American Museum of Natural History.]

Distribution.—The description was made from five females collected by Baker, Ormsby Co., Nevada. Four of these, including the Holotype, are from the Charles Palm Collection, American Museum of Natural History. One is in the U. S. National Museum, Washington, No. 41866, and one female in the Schaeffer Collection labeled "Cal."

Variation.—The amount of brownish-black along the dorsal margin of the sternites varies in the individuals. In some the spots are confluent with each other. In others they are small. In some individuals only the first two tergites have brown patches while in others four or five are marked with brown. The color of the legs is not of great specific value since it varies in individual specimens.

It gives me much pleasure to name this species in honor of Mr. Andrew J. Mutchler who has always been ready to offer helpful suggestions and advice regarding this paper in the course of its preparation.

***Rhipiphorus simplex* (Champion)**

1891. *Rhipidophorus simplex* Champion, Biol. Cent.-Am., Col., IV, pt. 2, p. 263.

This species may be distinguished from *Rh. mutchleri* by its brown pygidium and brown patches on the last tergite. In *Rh. mutchleri* the pygidium is in great part yellow, and the first tergites are with brown spots, the latter being entirely yellow.

Head and prothorax black, abdomen reddish-yellow, pygidium, entire 6th tergite and small patches on other tergites brownish; elytra yellow with extreme base and small patch at apex brownish-yellow, femora, tips of middle and hind tibia dark brown, apical half of front femora and tibia with basal halves of middle and hind tibia and tarsi yellowish, antennae yellowish-brown. Wings hyaline-yellow, subcosta brown-black, with smoky area at its end. Vertex very slightly elevated, its anterior face distinctly excavated, frons very finely punctured and pubescent. Antennae 10-segmented, shorter than head and twisted, rami short and subequal in length. Pronotum finely pubescent, with a median line at its anterior half, and one oblique glabrous area on either side of disc near the middle, and one on either side of disc near the base; the distance between the two posterior areas slightly smaller than that between the anterior ones. Elytra finely punctate, their apices shining. Thorax beneath finely and densely pubescent, abdomen more sparsely so. Pygidium "heart-shaped," concave, shining, very sparsely pubescent,

indistinctly punctate. Hind tibia longer than tarsus, first segment of hind tarsus straight, as long as others combined and slightly thicker.

Length, 6.5 mm.

Type.—Female; Ventannes in Durango, Mexico, (Forrer). [British Museum.]

Plesiotype.—Female; La Providencia Obispo, Guatemala, (M. Ronillard). [U. S. National Museum.]

The above description was made from the plesiotype in the U. S. National Museum.

Variation.—Two females in the Schaeffer Collection collected in Brownsville, Texas, agree in all respects with the description and the specimen from Guatemala but differ as follows: The abdomen is yellow but the following parts are brown; pygidium, 6th and 5th tergite in their entire width, a broad patch on the fourth tergite, sides of last two sternites and in one of them a small spot on third tergite. Legs are usually darker, wings with a smoky band along the entire width, and base of elytra reddish-brown.

*Group fasciatus*¹³

1. Wings smoky 2
 Wings hyaline 5
2. Wings smoky brown to the tip; elytra for greatest part blackish; vertex elevated.
 *zeschi* and *schwarzi*
 Wings hyaline with smoky band 3
3. Elytra piceous, abdomen with yellowish membrane between first tergites. . *niger*
 Elytra yellow 4
4. Elytra entirely yellow *tuberculatus*
 Elytra yellow, base dark brown *fasciatus*
5. Elytra piceous with yellowish markings. *washi*, *hyalinus* and *stylopides*
 Elytra yellow—with small brownish spot *iridescens*

Rhipiphorus hyalinus (Champion)

1891. *Rhipidophorus hyalinus* Champion, Biol. Cent.-Am., Col., IV, pt. 2, p. 363.

Champion remarks upon this as follows: "This is much smaller than any of the other species here described, and is readily separ-

¹³ In this group are included those species in which both sexes are entirely brown or black. Although the author has studied the types of Leconte, and has examined several specimens, he feels uncertain about the validity of the species included in this group. He, therefore, leaves the entire group unaltered, until further study may throw more light upon it. The key is based upon the description, since most of the species included were not available for examination nor could be identified from the original description.

able from all of them by its hyaline wings. The vertex has a short compressed tubercle in the middle. The head is exceedingly broad. The rami of the antennae are very slender. *R. hyalinus* agrees in some respects with Leconte's description¹⁴ of the North-American *R. stylopides* (Newm.), but it is evidently distinct from that species."

"Length, $2\frac{3}{4}$ mm."

Type.—Cordova, Mexico. [British Museum.]

***Rhipiphorus iridescens* new species**

This species differs from *hyalinus*, the pronotum having no median line and being differently sculptured; also the elytra in *Rh. iridescens* are yellowish while brownish in *hyalinus*. It differs from *stylopides* in color of elytra and from *walshi* and others in size, color of elytra and color of wings.

Blackish; antennae fuscous, elytra pale with base and patch at sutural margin near apex brownish, femora brownish, tibia and tarsi slightly paler. Wings hyaline, iridescent; costa hyaline, or slightly fuscous.

Frons flat, vertex small, acute, and tuberculate, with small erect whitish hair. Clypeus slightly emarginate. Pronotum roughly punctate with two oblique, smooth areas on the sides, connected with each other on the disc. Base rounded and slightly truncate. Elytra rounded at apex, punctate on sides only. Tergites, with the exception of first and second and part of third, roughly punctate, with very short hair. 7th tergite with two small depressions but not smooth; pygidium (8th tergite in the male) smooth and glabrous on dorsal margin, punctate and clad with erect pubescent. Hind tarsus with first segment as long as the others combined, thin and straight.

Female like male; differs from it only in secondary sexual characteristics as follows: Vertex less prominent but carinate; antennae 10-segmented, with 8 rami. Third ramus slightly longer than others, the last three are fused, pygidium (7th tergite in female) elongate, acutely rounded, concave and smooth in center.

Length, 4 mm.

Holotype.—Male; El Paso, Texas, July 11, 1917, (Jos. Bequaert). [American Museum of Natural History.]

Allotopotype.—Female; same data as holotype. [American Museum of Natural History.]

¹⁴ Proc. Acad. Phil. xvii. p. 97.

Rhipiphorus walshi (Leconte)

1865. *Myodites walshi* Leconte, Proc. Acad. Nat. Sci. Phila., XVIII, p. 97.
1880. *Myodites walshi* Leconte, Trans. Am. Ent. Soc., VIII, p. 210.
1892. *Myodites walshi* Horn, Trans. Am. Ent. Soc., XIX, p. 48.
1904. *Myodites walshi* Pierce, Stud. Univ. Nebr., IV, p. 162.
1920. *Myodites walshi* Pierce, Ent. News, XXXI, p. 278.

Antennal rami little curled and slightly darker at apex. Median line slightly distinct at base, and in addition to the two larger oblique smooth areas on both sides of disc, there are two smaller glabrous areas near base; two such areas are also on each of the tergites from the fifth to the seventh. The first tergite is entirely smooth, while the second to sixth have a smooth glabrous area in the middle. The mesoscutellum is rugulose and with a distinct median carina; the elytra are rather finely rugulose and not punctate, base fuscous, apex amber yellow with a fuscous spot.

Length, 5 mm.

Holotype.—Male; Illinois. [Leconte Collection.]

Distribution.—Illinois, New Jersey, New York, North Carolina.

I have before me one male from Hewitt, New Jersey, which agrees very well with the type. The above additional description is made from this Homotype:

Rhipiphorus stylopides (Newman)

1838. *Myodites stylopides* Newman, Ent. Mag., v, p. 376.
1880. *Myodites stylopides* Leconte, Trans. Am. Ent. Soc., VIII, p. 210.
1892. *Myodites stylopides* Horn, Trans. Am. Ent. Soc. XIX, p. 48.
1904. *Myodites stylopides* Pierce, Stud. Univ. Nebr., IV, p. 162.
1920. *Myodites stylopides*, Pierce, Ent. News, XXXI, p. 278.

Many different specimens from different localities agree with the short description of Newman, and it is hard to say which is the true *stylopides*.

Length, 3.5 mm.

Type.—Unknown; Alton, Illinois.

Rhipiphorus tuberculatus (Champion)

1891. *Rhipidophorus tuberculatus* Champion, Biol. Cent.-Am., Col., IV, pt. 2, p. 362.

Champion remarks upon this species as follows: "This species differs from all the others here described by the strongly raised, very stout, blunt tubercle on the vertex in the male sex, this tubercle being replaced in the female by an angular elevation. The abdomen is thickly and finely punctured. The angular elevation on the vertex of the female will easily distinguish *R. tuberculatus* from the same sex of the closely allied *R. simplex*; the latter, moreover, has an angular prominence beneath the point

of insertion of each antenna, of which there is no trace in *R. tuberculatus*."

"Length, $4\frac{1}{2}$ to $5\frac{1}{2}$ mm. (σ ♀.)"

Holotype.—Male; Atoyac in Vera Cruz, Mexico. [British Museum.]

Allotopotype.—Female. [British Museum.]

***Rhipiphorus niger* (Waterhouse)**

1875. *Myodites niger* Waterhouse, Cist. Ent., I, p. 369.

1891. *Rhipidophorus niger* Champion, Biol. Cent.-Am., Col., IV, pt. 2, p. 369.

"Length, $5\frac{1}{4}$ mm."

Type.—Female; Dueñas, Panzos, Guatemala, [British Museum.]

Plesiotype.—Male; Orizaba, Mexico, (Champion). [British Museum.]

***Rhipiphorus zeschi* (Leconte)**

1880. *Myodites zeschi* Leconte, Trans. Am. Ent. Soc., VIII, pp. 210-211.

1881. *Myodites zeschi* Leconte, Bull. Buff. Soc., IV, p. 28.

1892. *Myodites zeschi* Horn, Trans. Am. Ent. Soc., XIX, p. 48.

1904. *Myodites zeschi* Pierce, Stud. Univ. Nebr. IV, p. 162.

1920. *Myodites zeschi* Pierce, Ent. News, XXXI, p. 278.

Leconte expressed his opinion that this may be the male of *Rh. schwarzi*, and he described it as a new species only because of the distant locality it was taken in. Later authors sank this in synonymy with *Rh. schwarzi*. I do not know whether this is justified or not; the best way this may be settled is by comparing two that were caught *in coito* and see whether they agree with the types of Leconte. I therefore consider this as a valid species for the present.

Length, 6.5 mm.

Type.—Male; Buffalo, New York. [Leconte Collection.]

***Rhipiphorus schwarzi* (Leconte)**

1880. *Myodites schwarzi* Leconte, Trans. Am. Ent. Soc., VIII, pp. 210-211 and Proc., p. XXIII.

1892. *Myodites schwarzi* Horn, Trans. Am. Ent. Soc., XIX, p. 48.

1904. *Myodites schwarzi* Pierce, Stud. Univ. Neb. IV, p. 162.

1920. *Myodites schwarzi* Pierce, Ent. News, XXXI, p. 278.

The best characteristics to distinguish this from *walshi* are as follows: *schwarzi* has the elytra entirely blackish-brown with a reddish patch near the suture, while *walshi* has the base only

blackish. The wings in *schwarzi* are smoky black to the apex, whereas they are hyaline, slightly smoky, in *walshi*. In general this latter is a smaller and more delicate species.

Length, 6 mm.

Type.—Male; Sumter County, Florida, [Leconte Collection.]

One female (Homotype) from Monticello, Florida, in the collection of the American Museum of Natural History, agrees very well with the type.

Host recorded.—*Augochlora pura* Say.

Rhipiphorus fasciatus (Say)

1823. *Dortheia fasciata* Say, Jour. Acad. Phila., III, p. 274.

1855. *Myodites fasciatus* Gerstäcker, Rhipiph. Col. Fam., p. 17.

1880. *Myodites fasciatus* Leconte, Trans. Am. Ent. Soc., VIII, p. 210.

1892. *Myodites fasciatus* Horn, Trans. Am. Ent. Soc., XIX, p. 48.

1904. *Myodites fasciatus* Pierce, Stud. Univ. Nebr., IV, p. 162.

1920. *Myodites fasciatus* Pierce, Ent. News., XXXI, p. 278.

variety:

1904. *Myodites fasciatus brunea* Pierce, Stud. Univ. Nebr., IV, p. 162.

In the collections the author has studied, various specimens bear the label "*M. fasciatus* Say," but it is still a question as to which of those is the real species of Say described from "Missouri."

Length, 8 mm.

Doubtful Species

Rhipiphorus flavicornis Say

1823. *Dortheia flavicornia* Say, Jour. Acad. Phil., III, p. 274.

"Black, antennae bright yellow, elytra dark piceous with a common pale spot. Pa."

Rhipiphorus americanus Guérin

1835. *Myodites americanus* Guérin, Gen. Ins., fasc. I, n. 2, t. 2.

"Nigra, scabra, parce pilosa; os ferruginea elytrorum apicis albidii; metolae hyaline iridescentes, costa fusca. N. Am."

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EXPLANATION OF PLATES

PLATE I.

Pelectoma (P. flavipes).

- Fig. 1 A.—Side view of head and prothorax.
Fig. 1 B.—Front view of head (male).
Fig. 1 C.—Antennae of female.

Trigonodera (T. schaefferi).

- Fig. 2 A.—Side view of head and prothorax.
Fig. 2 B.—Front view of head (male).
Fig. 2 C.—Antennae of female.

Toposcopus (T. wrighti).

- Fig. 3 A.—Side view of head and prothorax.
Fig. 3 B.—Front view of head (male).
Fig. 3 C.—Antennae of female.

Rhipidius (sp.?).

- Fig. 4 A.—Side view of head and prothorax.
Fig. 4 B.—Front view of head.

Macrosiagon (M. dimidiatum).

- Fig. 5 A.—Side view of head and prothorax.
Fig. 5 B.—Front view of head (female).
Fig. 5 C.—Antennae: a, female; b, male.

Rhipiphorus (R. soligaginis).

- Fig. 6 A.—Side view of head and prothorax.
Fig. 6 B.—Front view of head (female).
Fig. 6 C.—Antennae: a, female; b, male.

PLATE II.

- Fig. 1 M.—Male genitalia of *Pelecotoma (P. flavipes)*.
l. lateral view; d. dorsal view.
Fig. 2 M.—Male genitalia of *Trigonodera (sp.)*.
Fig. 2 F.—Female genitalia of *Trigonodera (sp.)*.
l. lateral view; d. dorsal view; v. ventral view.
Fig. 3 M.—Male genitalia of *Toposcopus (T. wrighti)*.
l. lateral view; v. ventral view.
Fig. 5 M.—Male genitalia of *Macrosiagon (M. limbatum)*.
l. lateral view; d. dorsal view.

- Fig. 5 F.—Female genitalia of *Macrosiagon* (*M. dimidiatum*).
l. lateral view of ovipositor in the tube; *d.* dorsal view of ovipositor with the tube removed.
- Fig. 6 M.—Male genitalia of *Rhipiphorus* (*R. solidaginis*).
l. lateral view; *d.* dorsal view.
- Fig. 6 F.—Female genitalia of *Rhipiphorus* (*R. solidaginis*).
d. dorsal view: (upper figure) with the ovipositor protruding; (lower figure) the ovipositor is shown in the tube and portion of the eighth tergite is cut off.
- Fig. 7 M.—Male genitalia of *Evaniocera* (*E. dafouri*).
- Fig. 7 F.—Female genitalia of *Evaniocera* (*E. dafouri*).
l. lateral view; *d.* dorsal view; *v.* ventral view.

PLATE III.

Trigonodera (sp.).

- Fig. 2 W.—Wing.

Rhipidius (sp.).

- Fig. 4—Female.
 Fig. 4 A'.—Female: side view of head and prothorax.
 Fig. 4 B'.—Female: front view of head.
 Fig. 4 V.—Male: side view of metathorax and abdomen.
 Fig. 4 W.—Male: wing.

Macrosiagon (*M. dimidiatum*).

- Fig. 5 Vv.—Abdomen: section at base, showing first tergite (*It*) and first sternite (*Is*).
 Fig. 5 Vl.—Lateral view of entire abdomen.
 Fig. 5 W.—Wing.

Rhipiphorus (*R. solidaginis*).

- Fig. 6 Vv.—Abdomen of female: ventral view showing ventral position of the seventh tergite (*7t*).
 Fig. 6 Vl.—Lateral view of female abdomen.
 Fig. 6 W.—Wing.

Evaniocera.

- Fig. 7 W.—Wing.

Macrosiagon fernaldi.

- Fig. 14 B.—Front view of head of male.
 Fig. 14 a.—Antennae of female.

Macrosiagon flavipenne.

- Fig. 15 a.—Antennae of female.

Macrosiagon octomaculatum.

Fig. 16 O.—Occiput, showing suture.

Fig. 16 t.—Lateral and dorsal views of hind tarsus.

Macrosiagon pectinatum.

Fig. 17 O.—Occiput.

Macrosiagon sayi.

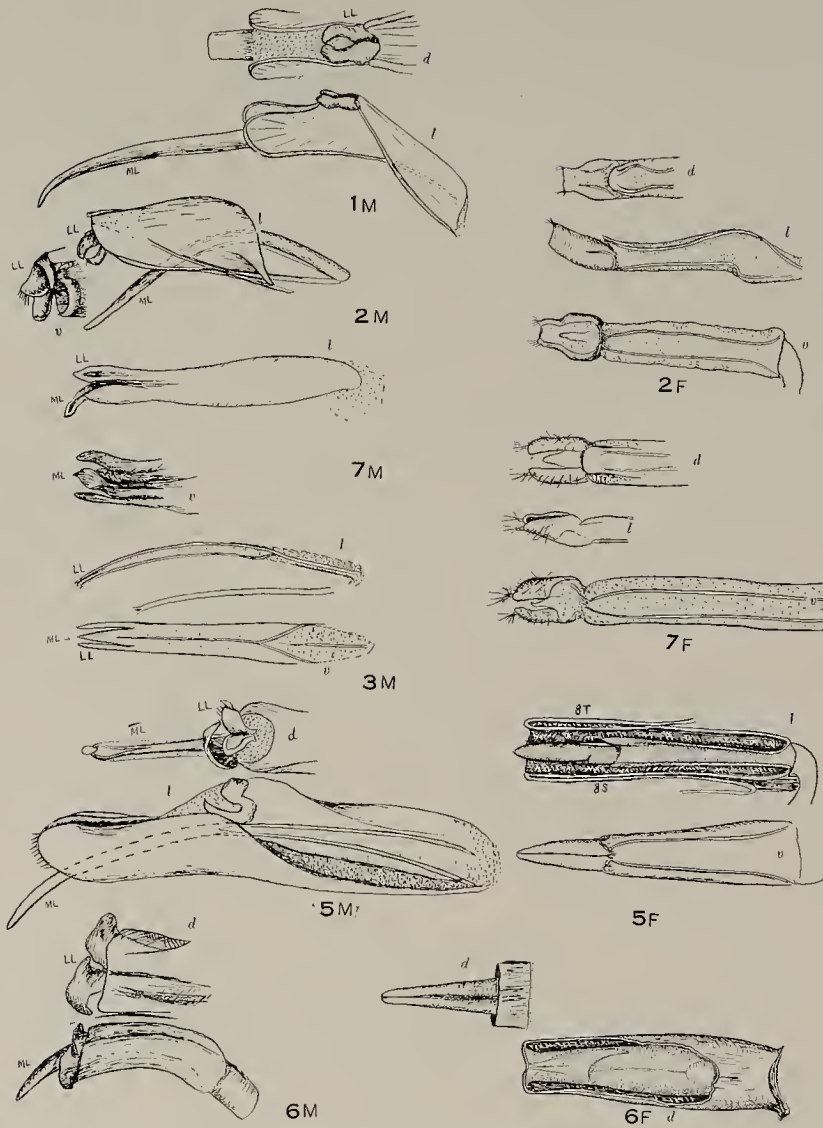
Fig. 18 t.—Lateral and dorsal views of hind tarsus.

PLATE IV.

- Fig. 1 a.—*Rhipiphorus calopterus*. Female antennae.
 Fig. 1 p.—*Rhipiphorus caloptera*. Pygidium.
 Fig. 1 t.—*Rhipiphorus calopterus*. Lateral view of hind tibia and tarsus.
 Fig. 2 p.—*Rhipiphorus nevadicus*. Pygidium.
 Fig. 2 t.—*Rhipiphorus nevadicus*. Dorsal and lateral view of hind tarsus.
 Fig. 3 a.—*Rhipiphorus luteipenne*. Female antenna.
 Fig. 3 p.—*Rhipiphorus luteipenne*. Pygidium.
 Fig. 4 p.—*Rhipiphorus mutchleri*. Pygidium.
 Fig. 4 t.—*Rhipiphorus mutchleri*. Lateral view of hind tarsus.
 Fig. 5 t.—*Rhipiphorus californicus*. Lateral view of hind tarsus.
 Fig. 6 p.—*Rhipiphorus aurantus*. Pygidium.
 Fig. 6 t.—*Rhipiphorus aurantus*. Lateral view of hind tibia and tarsus.
 Fig. 7 p.—*Rhipiphorus vierecki*. Pygidium.
 Fig. 7 t.—*Rhipiphorus vierecki*. Lateral view of hind tibia and tarsus.
 Fig. 8 t.—*Rhipiphorus minimus*. Lateral view of hind tarsus.
 Fig. 9 t.—*Rhipiphorus nomiae*. Lateral view of hind tarsus.
 Fig. 10 t.—*Rhipiphorus solidaginis*. Dorsal and lateral views of hind tarsus.
 Fig. 11 t.—*Rhipiphorus scaber*. Dorsal and lateral views of hind tarsus.
 Fig. 12 t.—*Rhipiphorus neomexicanus*. Dorsal and lateral views of hind tarsus.
 Fig. 13 t.—*Rhipiphorus brevipes*. Dorsal and lateral views of hind tarsus.



RIVNAY—AMERICAN RHIPIPHORIDAE



RIVNAY—AMERICAN RHIPIPHORIDAE



RIVNAY—AMERICAN RHIPIPHORIDAE

INDEX

Names quoted in synonymy are given in *italics*.

- | | |
|--|---|
| <p><i>abdominale</i> (Rhipiphorus) 25</p> <p><i>acutipenne</i> (Macrosiagon) 32</p> <p><i>ambiguus</i> (Rhipiphorus) 40</p> <p><i>americanus</i> (Rhipiphorus) 63</p> <p><i>aurantus</i> (Rhipiphorus) 55</p>
<p><i>bicolor</i> (Rhipiphorus) 34</p> <p><i>bifoveatum</i> (Macrosiagon) 28</p> <p><i>bivittata</i> (Trigonodera) 20</p> <p><i>brevipes</i> (Rhipiphorus) 46</p>
<p><i>californicus</i> (Rhipiphorus) 56</p> <p><i>calopterus</i> (Rhipiphorus) 45</p> <p><i>carinipenne</i> (Macrosiagon) 30</p> <p><i>Caspyria</i> 16</p> <p><i>cruentum</i> (Macrosiagon) 35</p>
<p><i>Dorthesia</i> 41</p> <p><i>dimidiatum</i> (Macrosiagon) 30</p> <p><i>discicollis</i> (Macrosiagon) 39</p> <p><i>dubium</i> (Rhipiphorus) 40</p>
<p><i>Emenadia</i> 23</p> <p><i>Evaniocerinae</i> 13</p> <p><i>excavatum</i> (Macrosiagon) 29</p>
<p><i>fasciata</i> (Dorthesia) 63</p> <p><i>fasciatus</i> (Rhipiphorus) 63</p> <p><i>fasciatus</i> (Rhipiphorus) 40</p> <p><i>fernaldum</i> (Macrosiagon) 26</p> <p><i>flavicornis</i> (Rhipiphorus) 63</p> <p><i>flavipenne</i> (Macrosiagon) 25</p> <p><i>flavipes</i> (Pelecotoma) 15</p> <p><i>flaviventris</i> (Rhipiphorus) 55</p>
<p><i>horni</i> (Macrosiagon) 36</p> <p><i>humeralus</i> (Rhipiphorus) 40</p> <p><i>hyalinus</i> (Rhipiphorus) 59</p> <p><i>impressus</i> (Rhipiphorus) 40</p> | <p><i>iridescens</i> (Rhipiphorus) 60</p>
<p><i>Kipiphorus</i> 5</p> <p><i>knausi</i> (Myodites) 52</p>
<p><i>laevicollis</i> (Rhipiphorus) 55</p> <p><i>leachii</i> (Trigonodera) 16</p> <p><i>lineata</i> (Trigonodera) 19</p> <p><i>limbatum</i> (Macrosiagon) 36</p> <p><i>lineare</i> (Macrosiagon) 28</p> <p><i>longipes</i> (Rhipiphorus) 40</p> <p><i>luteipennis</i> (Rhipiphorus) 43</p>
<p>Macrosiagon 23</p> <p><i>marginale</i> (Rhipiphorus) 30</p> <p><i>maritimum</i> (Macrosiagon) 33</p> <p><i>maxillosus</i> (Rhipiphorus) 40</p> <p><i>melanoptera</i> (Emenadia) 39</p> <p><i>minimus</i> (Rhipiphorus) 46</p> <p><i>mutchleri</i> (Rhipiphorus) 57</p> <p><i>mutilatus</i> (Rhipiphorus) 39</p> <p><i>Myodes</i> 41</p> <p><i>Myodites</i> 41</p> <p><i>Myoditini</i> 5</p>
<p><i>nebulosa</i> (Trigonodera) 19</p> <p><i>neomexicanus</i> (Rhipiphorus) 50</p> <p><i>nevadicus</i> (Rhipiphorus) 44</p> <p><i>niger</i> (Rhipiphorus) 62</p> <p><i>nigricorne</i> (Rhipiphorus) 40</p> <p><i>nigrus</i> (Rhipiphorus) 40</p> <p><i>nomiae</i> (Rhipiphorus) 51</p> <p><i>nubila</i> (Trigonodera) 17</p> <p><i>nubilus</i> (Pelecotomoides) 18</p>
<p><i>octomaculatum</i> (Macrosiagon) 32</p>
<p><i>paradoxus</i> (Metoecus) 4</p> <p><i>Pelecotoides</i> 16</p> |
|--|---|

Pelecotoma	14	schwarzi (Rhipiphorus)	62
Pelecotominae	13	semiflavus (Rhipiphorus)	51
<i>Pelecotomoides</i>	16	<i>sexmaculata</i> (Mordella)	40
pectinatum (Macrosiagon)	40	simplex (Rhipiphorus)	58
popenoei (Rhipiphorus)	54	solidaginis (Rhipiphorus)	49
Ptilaphorini	5	stylopides (Rhipiphorus)	61
pulchrum (Macrosiagon)	38	subdipterus (Rhipiphorus)	4
<i>puncticeps</i> (Rhipiphorus)	32	<i>Symbius</i>	22
<i>4-maculatus</i> (Rhipiphorus)	39	<i>thoracicus</i> (Rhipiphorus)	40
rex (Rhipiphorus)	55	Toposcopus	20
Rhipidiinae	14	Trigonodera	16
Rhipidiini	5	<i>triste</i> (Rhipiphorus)	40
Rhipidius	22	tuberculatus (Rhipiphorus)	61
Rhipiphorinae	13	<i>varicolor</i> (Rhipiphorus)	40
Rhipiphorini	5	<i>ventrale</i> (Rhipiphorus)	40
Rhipiphorus	41	vierecki (Rhipiphorus)	52
rufum (Macrosiagon)	36	<i>vitraci</i> (Emenadia)	39
<i>sanguineolentus</i> (Rhipiphorus)	40	walshi (Rhipiphorus)	61
sayi (Macrosiagon)	34	wrighti (Toposcopus)	21
scaber (Rhipiphorus)	47	zeschi (Rhipiphorus)	62
schafferi (Trigonodera)	18		

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The thesis submitted by Mr. Ezekiel Rivnay
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