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A REVISION OF THE GENUS *COPRIS* MÜLLER OF THE WESTERN HEMISPHERE (COLEOPTERA, SCARABAEIDAE)

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INTRODUCTION

Copris Müller is a genus of principally Old World coprophagous scarabs represented in the New World primarily in North and Central America. The present work deals only with the adults of the Western Hemisphere species.

The name *Copris* is fairly old; it was coined by Geoffroy (1764) to include all those species in the Linnaean genus *Scarabaeus* characterized by the absence of a visible scutellum. However, since Geoffroy's work has been discarded for nomenclatorial purposes*, the first valid user of the name was Müller (1764), who included an indication but no species. The first valid inclusion of species was by Fourcroy (1785), who included ten species, the first of which was *lunaris* L. Fabricius did not adopt the name *Copris* until 1798 in the *Supplementum Entomologiae Systematicae*. Thereafter the name was in wide use but the first valid type designation appears to be that of Curtis (1832), who designated *Scarabaeus lunaris* Linnaeus as the type of the genus.

Following Olivier's (1790) very broad concept of the genus (including even many scutellate dung beetles) numerous groups were separated off as independent genera and by the end of the first third of the 19th century the name *Copris* had become restricted to a fairly homogeneous assemblage. In 1837 Hope proposed the first of several further subdivisions, in which he was followed by Burmeister (1846) and Erichson (1847). These subdivisions Lacordaire (1856) did not accept, preferring to go back to the broader concept. Nevertheless, the genera and subgenera proposed by Hope, Burmeister, and Erichson subsequently became largely accepted and it was the latter author who formulated the restricted concept of *Copris* which exists, in largely unmodified form, today, although several additional small genera have been separated off since. Recently Balthasar (1958) divided the genus into four subgenera (one of which is *Litocopris* Waterhouse, 1891).

* Opinions and declarations rendered by the International Commission on Zoological Nomenclature, Vol. 4, Opinion 228, 1954.

All the American species belong to the subgenus *Copris* as understood by Balthasar.

There have been very few attempts at any revisional study of the large genus *Copris* and these have been restricted to relatively small geographical areas. The American species of the genus have been investigated very perfunctorily from two geographical vantage points—the United States and Central Mexico—with no attempt, until now, at coordinating the results. Fortunately, the two areas are sufficiently distinct zoogeographically that a minimum of synonymization has resulted. All the literature consists of scattered new species descriptions with four exceptions: Harold (1869), while describing most of the Mexican species, presented a key to them with short discussions of means of distinguishing them; Horn (1873) presented a key and descriptions of the four United States species known at the time; Bates (1887–1889), in the *Biologia Centrali Americana*, reviewed the Mexican and Central American species known to him; and Schaeffer (1906) presented a short but quite usable key to the United States species known at that time. In his review, Bates used only Harold's names, even though he was looking at several undescribed species which he attempted to fit into Harold's descriptions. As a result, the range extensions given by Bates for Harold's species, repeated in all subsequent catalogues and lists, are largely erroneous. There followed some individual species descriptions and Gillet (1911), in the *Coleopterorum Catalogus*, lists 16 species and two "varieties" for the Western Hemisphere. Thereafter there were several more species descriptions. The Leng Catalogue and Supplement (1920–1948) list eight species for the United States and Canada, while Blackwelder (1944) lists 12 species and two varieties for America exclusive of these two countries, of which one species and one variety are listed as common to both areas. Subsequently Pereira and d'Andretta (1955) synonymized one name, Matthews and Halffter (1959) described five new species and synonymized one name, and Matthews (1959) described one additional species and elevated one variety to species rank, presenting a key to the males of the Mexican species.

There were until now, therefore, 24 species and one variety known from the Western Hemisphere. The present work describes one new species and three new subspecies, elevates the one remaining variety to species rank, lowers two species to subspecies level, synonymizes two names and resurrects one, bringing the total to 23 species and five subspecies known for this hemisphere at present.

In the world as a whole the genus at present contains approximately 160 described species which are distributed about as follows among the zoogeographical regions (with some species counted twice): Ethiopian—77, Oriental—46, Palaearctic—27, Neartic—16, Neotropical—8. It does not occur in Madagascar or in Australia. The northern limits of the genus in the Eastern Hemisphere appear to coincide approximately with the 50th parallel (Kolbe, 1905), except that one species occurs very locally in southern England. Of the Coprini, this is by far the most boreal of the genera, all the others being rather strictly tropical (except *Synapsis*).

In the Western Hemisphere (map, fig. 1) *Copris* is represented in the United States east of the 100th meridian, in all of Mexico and U. S. territory immediately bordering on Mexico (except California), and in all of Central America to Panama. In South America it is represented by a single species from North and Central America occurring in the mountains of Colombia and Ecuador. It is absent from the Antilles and the Galapagos Islands. One species has been introduced by man into Hawaii.

The American forms are distributed by countries as follows:

CANADA: *f. fricator* (F.).

UNITED STATES: *arizonensis* Sch., *f. fricator* (F.), *f. cartwrighti* Rob., *gopheri* Hubb., *howdeni* M. and H., *incertus* Say, *inemarginatus* Blatch., *l. lecontei* n. sp., *minutus* Dru., *r. remotus* Lec.

MEXICO: *arizonensis* Sch., *armatus* Har., *boucardi* Har., *costaricensis dolichocerus* n. subsp., *halfpteri* Matt., *incertus* Say, *k. klugi* Har., *k. sierrensis* n. subsp., *laeviceps* Har., *l. lecontei* n. sp., *l. isthmiensis* n. subsp., *lugubris* Boh., *megasoma* M. and H., *mexicanus* M. and H., *moechus* Lec., *rebouchei* Har., *r. remotus* Lec. *r. dicyrtus* M. and H., *sallei* Har.

GUATEMALA: *aspericollis* Gill., *boucardi* Har., *costaricensis dolichocerus* n. subsp., *laeviceps* Har., *lugubris* Boh.

BELIZE: *laeviceps* Har., *lugubris* Boh.

EL SALVADOR: *boucardi* Har., *lugubris* Boh.

HONDURAS: *laeviceps* Har., *lugubris* Boh.

NICARAGUA: *lugubris* Boh.

COSTA RICA: *c. costaricensis* Gahan, *incertus* Say, *laeviceps* Har., *lugubris* Boh., *subpunctatus* Gill.

PANAMA: *c. costaricensis* Gahan, *lugubris* Boh., *subpunctatus* Gill.

COLOMBIA: *incertus* Say.

ECUADOR: *incertus* Say.

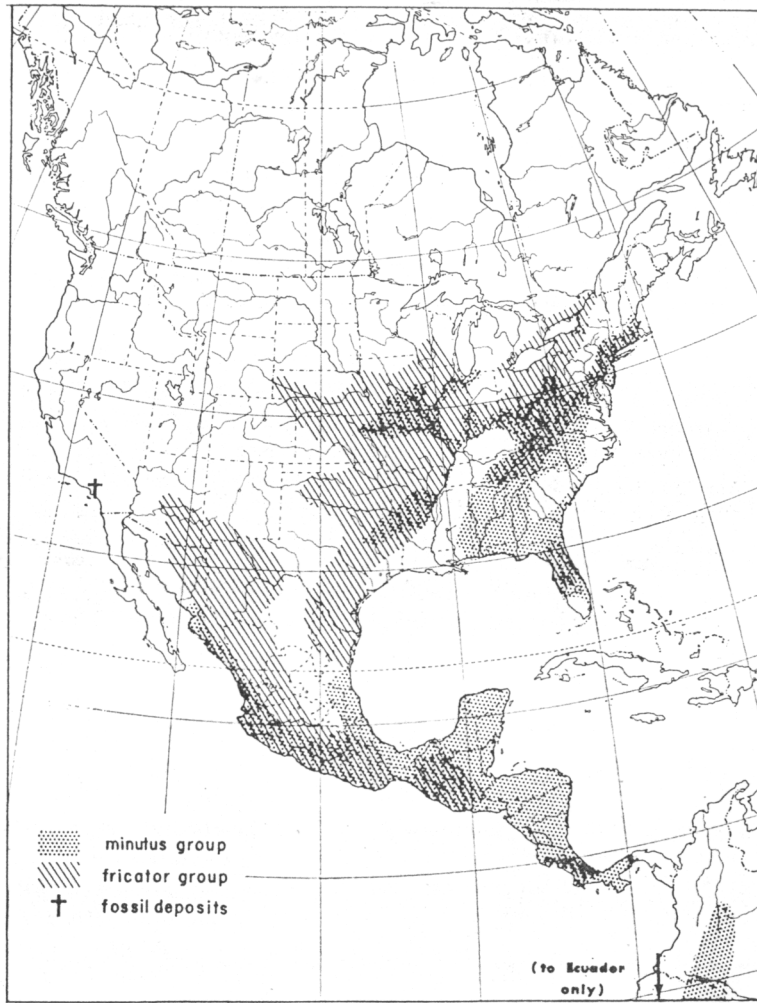


Fig. 1. The apparent distribution, based on material in collections, of the genus *Copris* in the Western Hemisphere.

The present study was based on the collections of several institutions and individuals and was supplemented by field excursions into certain critical areas from which adequate material was found to be lacking.

The methods used were those standard to taxonomic procedure. An attempt was made to investigate cryptic characters for use in classification by examining one specimen of both sexes of each species in minute detail, dissecting it to its minimum component parts and examining all interior as well as exterior surfaces. In this manner the possible taxonomic significance of the mouthparts, antennae, wing venation, dorsal abdominal surface, metendosternite, male genitalia and female spermathecum was investigated. The results were disappointingly negative; although some characters, such as the male genital capsule, reflected species differences to a slight extent, these could be much more easily seen using external features. Consequently, the use of cryptic characters was abandoned and the study was confined to those external "classical" characters familiar to investigators for centuries.

In the descriptions, characters cited in the group and complex descriptions are not repeated under the species.

In the present classification the use of the male armament has been avoided completely in arriving at a natural system. However, the male armament, when developed, provides one of the easiest ways of identifying a species quickly; for this purpose facies illustrations have been provided on plates IV-VII and the first key to the species is based largely on male secondary sexual ornamentation. It is recommended that, if a series includes some major males, the first key be used for determination. However, all forms of both sexes should key through the second key.

With regard to the geographical localities cited on labels, some judicious elimination has proved necessary. If a locality written on a label appeared to be unreliable for any reason, it was disregarded. A certain amount of difficulty was experienced in locating many Mexican and Central American localities on a map. It would greatly facilitate the work of future investigators if collectors in these areas would confine themselves to citing localities which are listed in the Index to the Map of Hispanic America, 1:1,000,000 (1943, 1944). In Central America, the Department in which a town is located is essential information. In the "material examined" section, localities for which the department or state was given but which could not be found on any map are preceded by a question mark. Additional pertinent

information not provided on the label, such as the altitude, was added to the citation in brackets. Information added to the Champion localities was obtained from Champion (1907).

In the case of certain groups of insects, such as the present one, much useful biological information can be gleaned from the data on labels if the collector includes a word about how the insect was collected. The only collector in this group who has consistently done this is the late F. Nevermann of Costa Rica.

All illustrations are by the author. The facies illustrations (plates IV-VII) showing the male armament were drawn by eye with the aid of proportional dividers. These illustrations are meant to show only the overall aspect of the forebody of a major male of each species and a general indication of the distribution of simple and complex punctures. Such details as the distribution of setae and the proportions of the mouthparts are only roughly indicated and not meant to be exact. The mouthparts and genitalia illustrated were mounted on slides and projected on paper with a standard projector. All other illustrations except the nest diagrams were done with the aid of an ocular grid and cross-lined paper. The nest diagrams were redrawn from field sketches and measurements.

A total of 3,400 specimens was examined, including the holotypes of 14 names. Many of the Mexican species were described by the Baron de Harold. Harold's types are presumed to be in the Paris Museum, but I was unable to obtain verification from that institution. Fortunately, Harold's descriptions, although short, are excellent and little doubt remains in my mind as to which of his names belongs to which species.

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MORPHOLOGY

The morphology of the adult Scarabaeinae has been the subject of some investigations. Hardenberg (1907) presented an excellent discussion of the mouthparts of *Pinotus carolinus* (L.), *Copris fricator* (F.), *Canthon pilularius* (L.), and several other Coprini, plus many other scarabs. Mohr (1930) compared the external morphology of *Canthon pilularius* (L.) with that of an aphodiine and a geotrupine. Halffter (1952) discussed aspects of the external morphology of *Phanaeus quadridens* Say. Pereira and Martínez (1956) presented illustrations of the mouthparts and genitalia of many Canthonini and Matthews and Halffter (1959) discussed the external morphology of a species of *Copris*. For purposes of comparison, frequent mention is made below of some of these papers and of one on a melolonthine (*Amphimallon majalis* Razoumowski) by Butt (1944) because of the detail in which the morphology of this species is there treated.

The following discussion is confined to those features of the external morphology of adult *Copris* which are of taxonomic significance, i.e. which may serve to distinguish the genus from others closely related or which vary among the species.

MICROSCULPTURE

The interpunctural surfaces are generally quite smooth in the American species except in *fricator* and *howdeni*, where the surfaces show a very fine shagreening.

The punctures are of two basic types which in turn vary importantly among the species groups and complexes:

1. Simple punctures. This term refers to simple surface depressions which have no raised areas within them and which usually have indistinct edges. They are found on the dorsal head surface and on the convex portions of the pronotum and elytra in all species.

2. Complex punctures. These are of varying type but always show a raised area within them and sharp edges. The raised area may or may not bear a seta; in the former case the puncture is said to be setigerous or umbilical and setigerous; in the latter it is said to be simply umbilical or, if very large, annular.

The following areas show round setigerous punctures with the seta more or less erect (fig. 23): along the posterior margin of the inner, smooth area of the proepimeron, on the sternellum, the mesosternum, the mesepimeron, occasionally the median lobe of the metasternum and the median coxae, and the abdominal sterna.

All other areas with setigerous punctures show a reniform type (fig. 21), which is a setigerous puncture one side of which has been pushed in with the result that the seta appears to issue from the side of the puncture and is recumbent, being directed away from the pushed-in edge.

The following areas normally show round or oval umbilical punctures which are not setigerous (figs. 20, 22): the dorsal surface of the genae, the frontal area behind the horn, all depressions on the pronotum and the pygidial surface.

Finally, some species complexes show a remarkable modification of the inside surface of the punctures, which is distinctly granulate (when seen at above 90× magnification) (figs. 20, 21). This type of surface is seen inside all complex punctures, of whatever type, which are large enough to show the inner surface, on both the dorsal and ventral body surfaces. Punctures of this type are said to be granular and occur throughout the *minutus* species group, recurring in the *fricator* group only to a lesser extent in the *rebouchei* complex.

HEAD

The cephalic taxonomic characters which are not self-explanatory are the following:

Posterior oblique carina.—This is a carina on the dorsal surface which runs from just behind the eye obliquely inward towards the base of the horn. When present, it is usually very sharp immediately near the eye and then stops abruptly, being continued

inward and forward by a raised ridge of varying sharpness (fig. 25, poc).

Transverse occipital groove.—Running very near the edge of the dorsal portion of the occipital margin is a groove bearing short, closely set setae (figs. 24, 25, tog). This groove may be complete across the entire occipital margin, or it may be divided into three approximately equal parts with the lateral ones displaced slightly forward (fig. 25). Occasionally the median section is missing.

Transverse occipital carina.—This is a carina of varying sharpness which runs in front of and closely parallels the transverse occipital groove (fig. 24, toc). It is found only in the *incertus* complex.

Immediately behind the front margin of the head dorsally is a row of seta tufts which are most conspicuous medially but which extend for varying distances laterally and posteriorly, sometimes extending onto the genae. The extent of this row of tufts apparently varies significantly among the species, but this character was not used in the classification because of the difficulty of seeing the setae in worn specimens.

The mouth cavity is rectangular in shape and is margined with a very broad, smooth margin which is anteriorly drawn out into a point. The shape of the mouth cavity differs somewhat in different coprine genera.

MOUTHPARTS

The mouthparts of *Copris* and all other Scarabaeinae are quite remarkable for their modification of a basically primitive type towards very highly sensory and membranous appendages (plate II). A good description of the mouthparts of *Copris fricator* (F.) (= *C. anaglypticus* Say) is given by Hardenberg (1907). Since the mouthparts do not appear to provide useful taxonomic characters at the species level in this genus, they will not be further discussed here.

PROTHORAX

The prothoracic taxonomic characters which are not self-explanatory are the following:

Lateral pronotal carina.—This is a carina which runs from an anterior point on the pronotal lateral margin upwards and backwards to pass just under the lateral fossa, after which it disappears. It is absent in the *minutus* group.

Prosternal-proepisternal suture (fig. 26. pp).—This is the suture between the anterior portion of the prosternum and the pleuron. In the *incertus* complex it appears carinate because of a deep depression of the pleural surface immediately next to it.

Pleural elements.—The interpretation of the lower surface of the prothorax adopted here differs radically from that of many coleopterists (who call the entire lower surface the sternum) and that of Butt for *Amphimallon*, but agrees with that of Mohr and Halffter. Butt considers the lateral portions of the lower surface as parts of the pronotum, which is therefore believed to join directly with the sternum with a resultant complete inflection of the pleural elements, which Butt considers to be represented only by a tiny sclerite fused to the dorsolateral wall of the pronotum on the inside.

In my opinion, it is more logical to assume merely that the sutures delimiting the pleural sclerites, seen in the primitive Coleoptera, have become completely fused and effaced in order to reinforce the prothorax. This would mean that most of the under surface lateral to the sternum in scarabs is made up of pleural elements fused together.

On this pleural area in *Copris* there is seen a distinct oblique carina running from the coxal cavity outward (fig. 26, pc). This carina is absent in many coprines and other scarabs and may be assumed to be a secondary modification evolved to further reinforce the prothorax. For the purposes of convenience, the area anterior to this carina is called the proepisternum, and that posterior to it is called the proepimeron. However, it should be understood that these areas do not in all probability correspond to the true morphological sclerites called by these names.

The longitudinal proepimeral carina.—The proepimeron in *Copris* and a few closely allied genera bears another characteristic carina which arises perpendicularly from the posterior proepimeral margin and quickly fades out (fig. 26, 1pc). This carina serves to partly delimit a densely, setigerously punctate outer area of the proepimeron from an almost smooth inner one (except in *C. minutus*).

PTEROTHORAX

Very few taxonomic characters have been found in the pterothorax and all are self-explanatory. The proportions and shapes of the sclerites do not differ among the American species of *Copris*.

ELYTRA

There are ten distinct elytral striae in the genus *Copris*, of which the ninth is practically always present only for its posterior half and lies very close to the tenth. The eighth stria is of great taxonomic importance and may be present merely as a short segment near the middle of the sides, in which case it is said to be obsolescent, as a line more or less interrupted posteriorly at the hind angles, in which case it is said to be incomplete, or as a complete, uninterrupted line.

LEGS

The general shape and proportion of the legs in *Copris* may be seen in fig. 26. There is one strong spur terminally on the anterior tibia, called the forespur, the shape of which is of great taxonomic significance.

The fore coxae are elongated cylinders very deeply sunk into the prothorax (fig. 27). They are rigidly pivoted at the two opposite ends of this cylinder such that the only possible movement is a rotation. The outer pivot consists of a knob formed by an invagination of the pronotal surface, called the lateral fossa of the pronotum.

The median coxae are oriented parallel to the body axis and widely separated. Their ventral (visible) surfaces are longitudinally obtusely carinate. The area exterior to this carina is called the outer face of the median coxa.

The arrangement of setae on the middle and hind tibiae was found to be of taxonomic significance with regard to two sets of setae, as follows:

Ventral seta tufts, also called distal seta tufts (fig. 49, st).—These terms refer to a row of tufts on the lower surface of the tibiae. The tibia is seen to be quadrate in cross section with a row of teeth and setae running down each ridge forming the corners. The ventral seta tufts are situated along the middle of the ventral face between the usual ridge setae and are usually confined to the distal end.

Supplementary setae (fig. 50, ss).—These are confined to the *incertus* complex and consist of an oblique row of very few, indistinct setae near the distal end of the dorsal tibial surface.

The tarsi are unmodified and always present. Each segment is somewhat expanded distally and gradually diminishes in size apically. There is some variation in the comparative width of

the tarsal segments in different species, but this character was not used in the taxonomy. The tarsal claws are small, parallel, and equally developed, with a small plate-like empodium at their base.

ABDOMEN

The only taxonomic characters on the abdomen involve the pygidium, which may be incompletely margined ventrally. The visible sternites are six in number and do not merge together along the ventral mid-line.

The tergites of segments VII and VIII are of particular interest because they make up the ventral portion of the stridulatory apparatus. The dorsal portion of tergite VIII (the propygidium) is heavily sclerotized and bears a deep longitudinal groove medially. This groove firmly holds the down-turned median edges of the elytra in repose. The actual stridulatory surface is not on this segment, however, but on the preceding one, where it consists of a finely sclerotized median area bearing some extremely fine transverse ridges. These ridges rub against some similar ridges or teeth on the elytral ribs when the abdomen is moved against the inside elytral surface, the groove on tergite VIII serving to keep the two parts in line.

Both sexes of every species of *Copris* I have examined show this apparatus and all those which I have collected in the field could be induced to squeak. For a discussion of stridulation in the lamellicornia the reader is referred to Arrow (1904).

GENITALIA

On the whole, the male genitalia in this genus are not of any use in determining the species, at least as far as their gross aspect is concerned. The possibility that the internal sac may bear taxonomic characters was not examined.

SEXUAL DIMORPHISM

The phenomenon of sexual dimorphism in the lamellicorn beetles has been the subject of much speculation but, unfortunately, little organized investigation. Darwin (1871) used the scarabs as examples for his celebrated theory of sexual selection. Since then the diversity and possible uses of the horns or enlarged mandibles in the lamellicorns have been discussed in numerous works. It is

not the purpose of this discussion to review this voluminous literature; for a recent survey the reader is referred to Arrow (1951). For some of the theoretical implications of horn allometry in the scarabs see Huxley (1932) and Paulian (1935). An excellent recent quantitative survey of horn allometry in a single dynastine species is presented by Bowden (1959).

However, no one has examined the nature of the variation in horn size among related species of a single genus. It is the purpose of this survey to examine intra- and interspecific variation in horn size and general qualitative differences in armament among all the American species of *Copris*.

THE SEXUAL ARMAMENT IN *Copris*

Nearly all the males of the American species display armament of a single type: there is one horn arising from the middle of the frontoclypeal suture on the head and the pronotum bears four forwardly directed prominences in a transverse row (plates IV-VII). The median two of these prominences are variable in shape (blunt, acute, or truncated) and sometimes merge into a single process. The lateral pronotal prominences are always strongly compressed and acute when developed.

The females typically bear a transverse crest on the frontoclypeal suture of the head. This crest is low and truncate apically, transversely oval and slightly excavate in dorsal view, and its sides converge apically, are parallel, or diverge, depending on the species or degree of development. The pronotum of the female does not bear any corniform prominences but does bear a median transverse carina (sometimes interrupted medially) and a small tumosity to either side of this carina. In the species descriptions female armament of this type is simply described as "normal for the genus."

Following the established custom among scarabaeidists I have called specimens (male or female) showing very little or no development in sexual armament "minor" individuals, and those showing strong development "major". It should on no account be inferred that these are clear-cut categories, but rather that they represent the two extremes of a spectrum of variation. Alternately I have called these specimens poorly developed and well developed, respectively.

The following exceptions to the above descriptions of armament are seen in the American species:

In the *minutus* group, the female head horn (or crest) is narrow, high, and rather corniform but still apically truncate in the *incertus* complex, completely corniform (apically acute) in the *minutus* complex. In the latter complex, in fact, it is very difficult to distinguish between the sexes, since the pronotal armament is often scarcely developed. The *incertus* complex is further distinguished by the presence of a corniform tubercle on the frons of the male behind the head horn.

In the species *halffteri* Matthews an extraordinary reversal has taken place: the male has acquired female armament. This phenomenon must not be confused with the similarity to females shown by very minor males of many species. In *halffteri* the males I have seen are well developed and show strong armament, but this is always of an exaggerated female type (fig. 77) which few females of any species ever achieve, because they are seldom so developed. This species is apparently very localized and shows strong affinities with a common and widespread species (*C. rebouchei* Harold), from which it evidently evolved. It is interesting that this form, which is most certainly a separate species, is completely sympatric with its parent species, both having been found in the same pile of cow dung.

INTRASPECIFIC VARIATION IN HORN HEIGHT

The measurements used in the following analysis represent the height of the male head horn from the edge of the clypeus to the tip of the horn in direct front view. This is compared with the maximum length of the hind femur in ventral view. The measurements were carried out with an ocular micrometer at $9\times$ magnification, the units used being one micrometer unit or .097 mm in this case. Since only ratios are dealt with, the measurements were not converted to millimeters. For calculating curvilinear regression lines, a constant factor was subtracted from each measurement of horn height to insure that the horn itself, and not also the height of the frons, was being taken into consideration. This factor was taken as the height from the clypeal edge to the tip of the frontal protuberance in the least developed specimens (those with no horn as such) of the species involved.

The mathematical interpretations of the curves obtained were taken to be either the "simple heterogony" formula of Huxley (1932) ($y = bx^k$, where y represents the magnitude of the differentially growing organ—in this case, the horn, x represents the magnitude of the animal or some reference structure—the femur, and b

Table I. Regression of Male Cephalic Horn Height (y) on Length of Hind Femur (x) in 14 Species of *Copris*.
 1 unit = .097 mm

No.	Species from smallest to largest	Regression y = ax + b' or log y = k log x + log b	Origins of deviations (x, y)	Mean horn to femur ratio (\bar{y}/\bar{x})	Number of individuals measured (N)
1	<i>minutus</i>	log y = 9.40 log x - 12.967	30.41, 15.42	.507	203
2	<i>incertus</i>	log y = 10.57 log x - 16.192	41.50, 17.13	.413	35
3	<i>costaricensis</i>	y = 4.36x - 150.21 (y = 9.99x - 345.65)	42.67, 35.83 37.67, 30.67	.840 .814	6 3
4	<i>reboucheti</i>	y = 4.93x - 166.59	42.42, 42.54	1.003	24
5	<i>remotus</i>	y = 3.95x - 278.35	42.83, 42.42	.990	12
6	<i>lecontet</i>	y = 3.99x - 147.38 (y = 3.08x - 89.94)	44.65, 30.77 43.00, 42.50	.689 .988	48 4
7	<i>lugubris</i>	y = 5.33x - 207.34	46.77, 41.94	.897	95
8	<i>kiugi</i>	y = 4.14x - 150.59	48.17, 48.83	1.104	24
9	<i>fricator</i>	y = 5.86x - 251.28	48.50, 32.93	.679	16
10	<i>moechus</i>	log y = 15.9 log x - 24.294 log y = 20.13 log x - 32.982 (y = 2.63x - 88.02)	49.10, 21.83 50.12, 30.34 54.29, 54.76	.445	68
11	<i>arizonensis</i>	combined: y = 3.88x - 151.59	52.90, 48.70	.921	60
12	<i>boucardi</i>	y = 5.20x - 251.94	54.35, 59.29	1.091	17
13	<i>armatus</i>	y = 6.29x - 325.59	59.22, 56.00	.946	9
14	<i>subpunctatus</i>	y = 4.40x - 471.39	60.11, 52.50 62.86, 57.14	.873 .909	18 14

Average of a except those in parentheses: 4.70

Average: .825
Total 656

and k are constants) or a simple linear relationship ($y = ax + b'$) such as that found by Bowden (1959), whichever seemed to fit best. These different interpretations are of no real significance, in my opinion, the linear curve probably being merely the top part of a power function curve. In the case of *C. moechus*, it seems that both a power function and a linear curve fit the data (fig. 4 and table I), with the break occurring near the middle.

It may be objected that the material measured here was taken from museum collections and therefore not collected under proper statistical sampling procedure. To this it should be pointed out that we are concerned here with the positions of curves only, not with their slope or the positions of their origins of deviation (the common mean of the two variables). It should, theoretically, make no difference *where* along a common curve a sample is taken; the subsequent plotting of these samples should reveal the position of the curve.

One of the main purposes of this study is to determine whether significant differences can be found in horn development patterns within a single species and to analyze the nature of these differences if they occur. When plotted on a graph, the data points representing horn height to femoral length ratios for an intraspecific grouping, such as a population or geographical race, could differ from those representing another grouping, or the rest of the species, in two quite different respects: 1) they could fall along only a section of a common species curve, that is to say, a race may fall near the bottom of the curve, another near the top, etc. or 2) much more significantly, one or more populations may fall along a recognizably different curve, thus showing a different allometric relationship with at least a different value of b .

Individual populations could not be examined in this respect since they were almost never represented in sufficient numbers. With regard to geographical groupings, however, significant differences were found within five of the 14 species examined. In *minutus* (Drury) (fig. 2) specimens from a relatively small area of the range, represented by Mobile and Montgomery, Ala. and Clarksville, Fla. (in the Florida panhandle), are seen to fall almost entirely along the extreme upper portion of the curve (open circles) with little overlap with the rest of the species (dots). Mysteriously, two specimens from this area fall near the bottom of the species curve. It will be noted, however, that all specimens from this area give every appearance of falling along the common species curve. Visually these specimens are conspicuous for their great size and horn development.

minutus

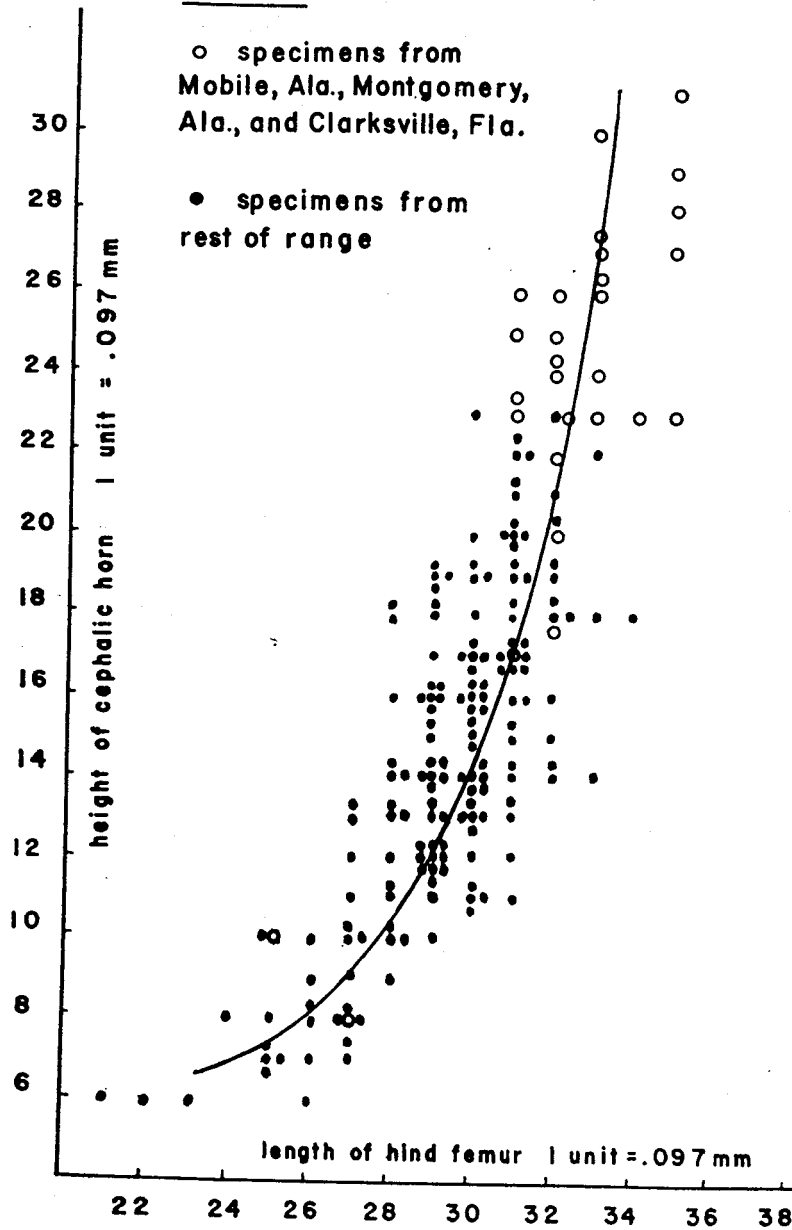


Fig. 2. *C. minutus* (Drury). Plot of horn height (y) against femoral length (x); $k = 9.40$ for random 25% sample ($N = 53$). For this and the following figures refer to text and table I for explanations of the symbols used.

In *fricator* (F.), on the other hand (fig. 3), specimens from a wide geographical area in the southwestern portion of the range (open circles) are all grouped in the lower part of the common curve. Visually these specimens also stand out, but in this case for their hornless condition and small size. Here, however, there is a suggestion that these specimens fall along a slightly different curve situated higher than the common species curve.

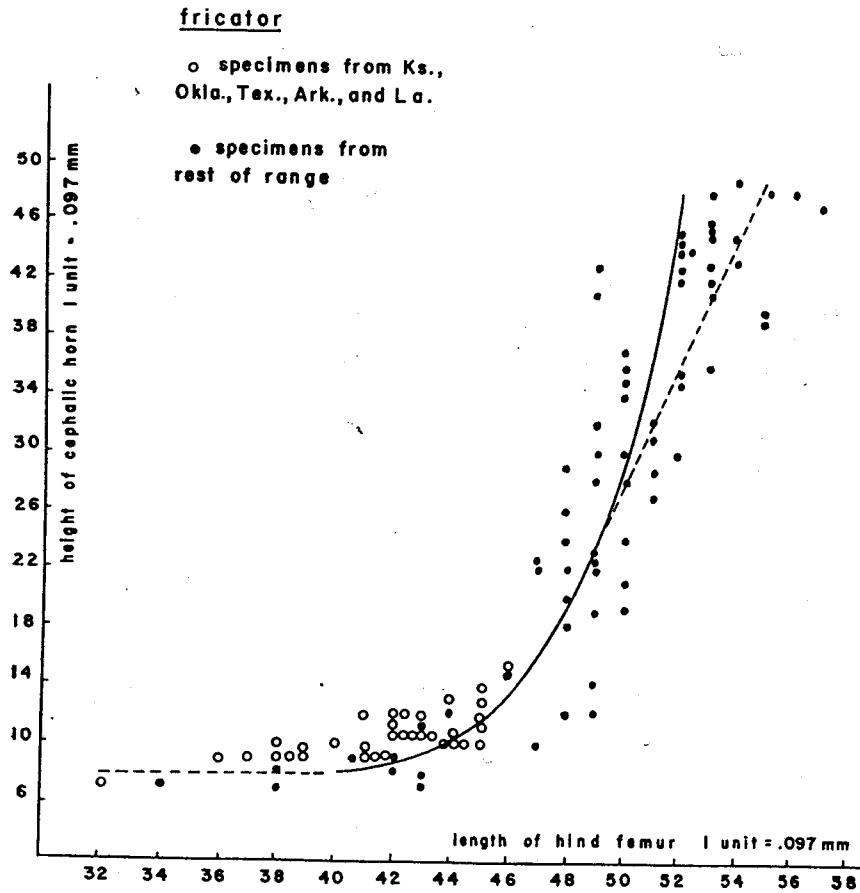


Fig. 3. *C. fricator* (F.), $k = 15.09$ for $x = 42$ to 50 . Interrupted lines estimated.

The previous two examples of geographical variation come under category (1) above. The geographical race falls along a special part of the common species curve, with little or no evidence for any different allometric relationship.

The most interesting and significant type of variation is the one in which a geographical grouping falls along a totally different curve from the one which characterizes the rest of the species. This is unmistakably seen in three species of the genus (figs. 6-8). In the first (*klugi* Harold), when the data from specimens originating in the Sierra Madre Occidental are plotted, they are seen to fall along a line which is significantly to the right of those from the rest of the species, originating in the Transverse Volcanic Range. The degree of significant separation may be judged by noting the extent of overlap of the 95% confidence intervals shown. Visually this difference is expressed by the northern specimens possessing consistently shorter horns for their size, in comparison with the southern form, but this difference is so slight as to be all but undetectable to the eye. This is in sharp contrast to the visually conspicuous but much less important difference in category (1) above.

This shift in the position of the relationship curve in different geographical groupings is much more strongly accentuated in two additional species: in *costaricensis* Gahan, comparing specimens from Chiapas with those from Costa Rica (fig. 7), and in *lecontei* n. sp., comparing specimens from north and south of Cabo Corrientes on the west coast of Mexico (fig. 8). For each of these three species there are therefore two separate relationship curves (table I).

In the last three examples the differences in allometric relationship are reflected in morphological differences only in the first species (*klugi*). Here the northern specimens consistently show a faint sclerotized diagonal band on the male parameres; this band is absent in the southern form. In the other two species I could detect practically no morphological differences between the geographical groupings thus separated by their horn relationships. Hence, this procedure gives us a taxonomic tool of some sensitivity in the horned scarabs. It should further be noted that even if different geographical groups or different species fall along different curves the slopes of these curves are approximately the same, allowing for sampling error and bearing in mind the very small samples in some cases.

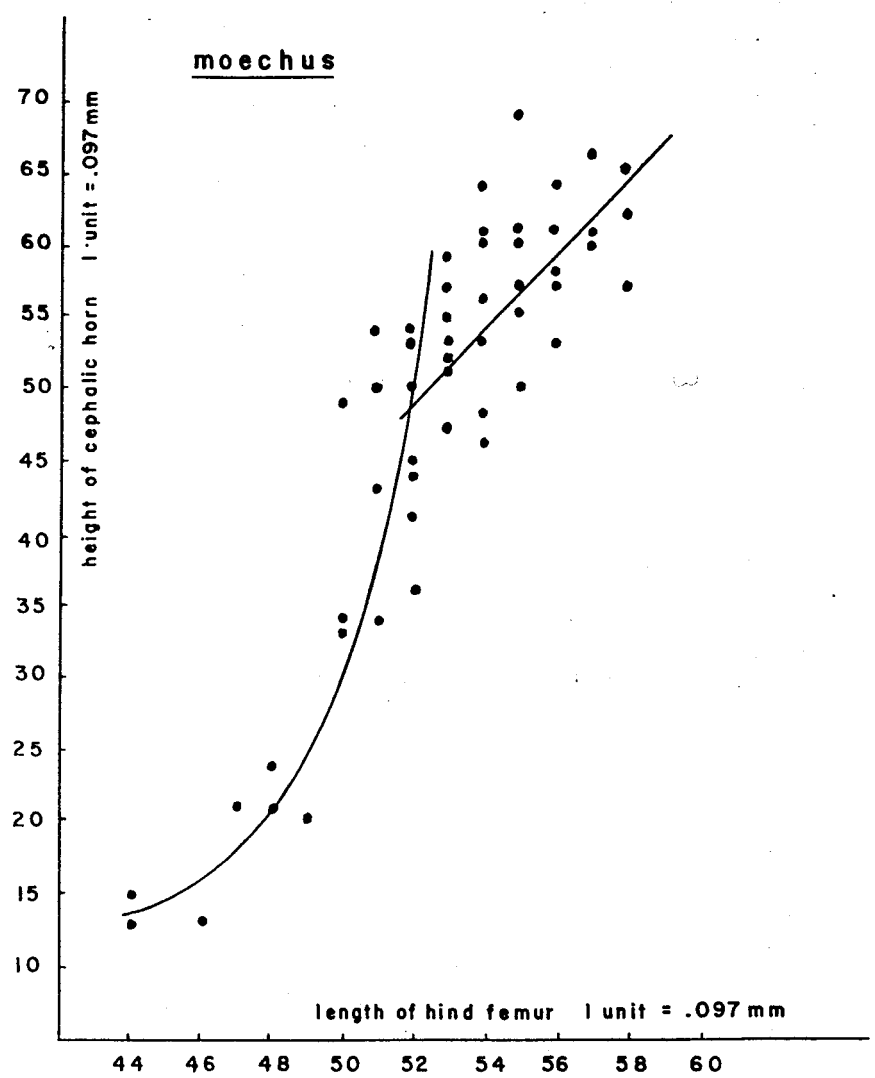


Fig. 4. *C. moechus* Lec., $k = 20.13$ for $x = 44$ to 52 ; $a = 2.63$ for $x = 52$ to 58 .

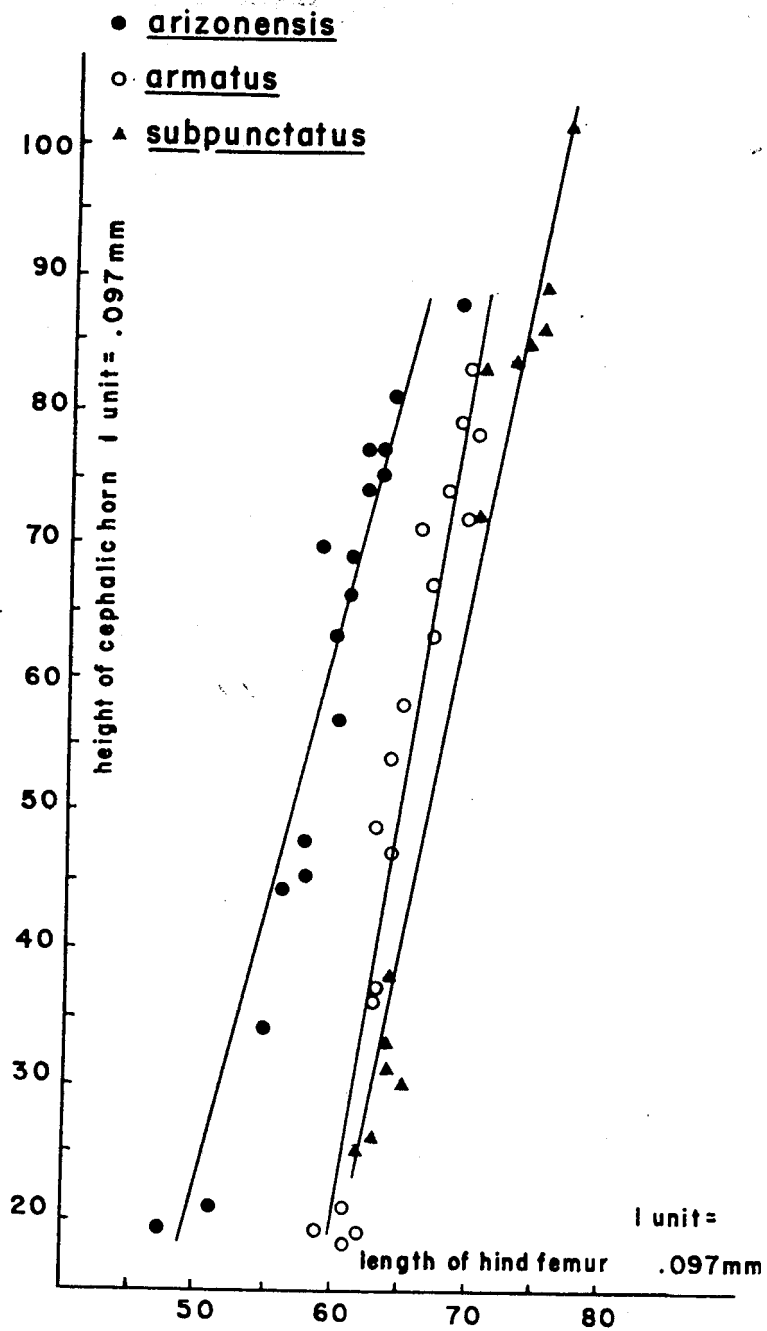


Fig. 5. *C. arizonensis* Schaeff, *C. armatus* Har., and *C. subpunctatus* Gillet, $a = 3.88, 6.29,$ and 4.40 respectively.

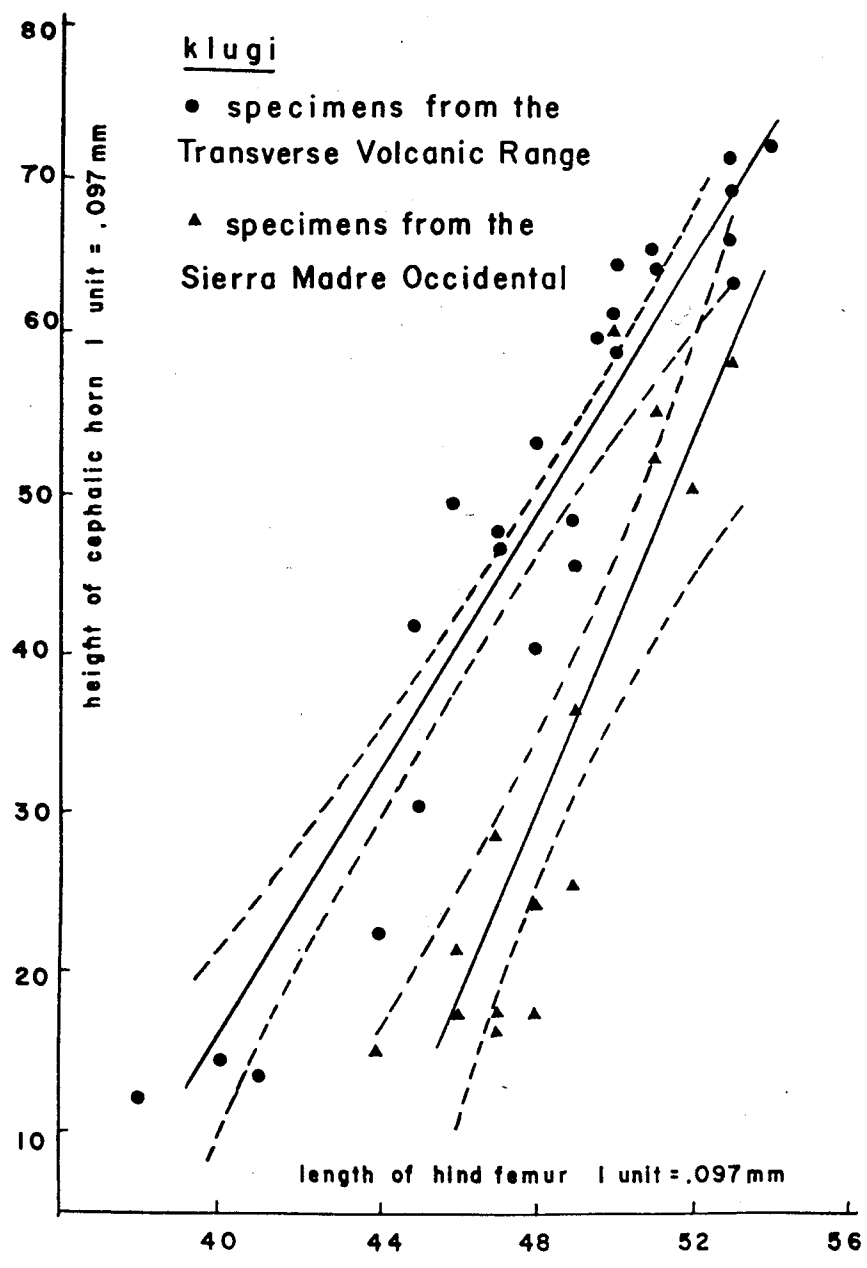


Fig. 6. *C. klugi* Har., $a = 4.14$ for Transverse Volcanic Range, 5.86 for Sierra Madre Occidental. Interrupted lines indicate 95% confidence intervals for regression lines.

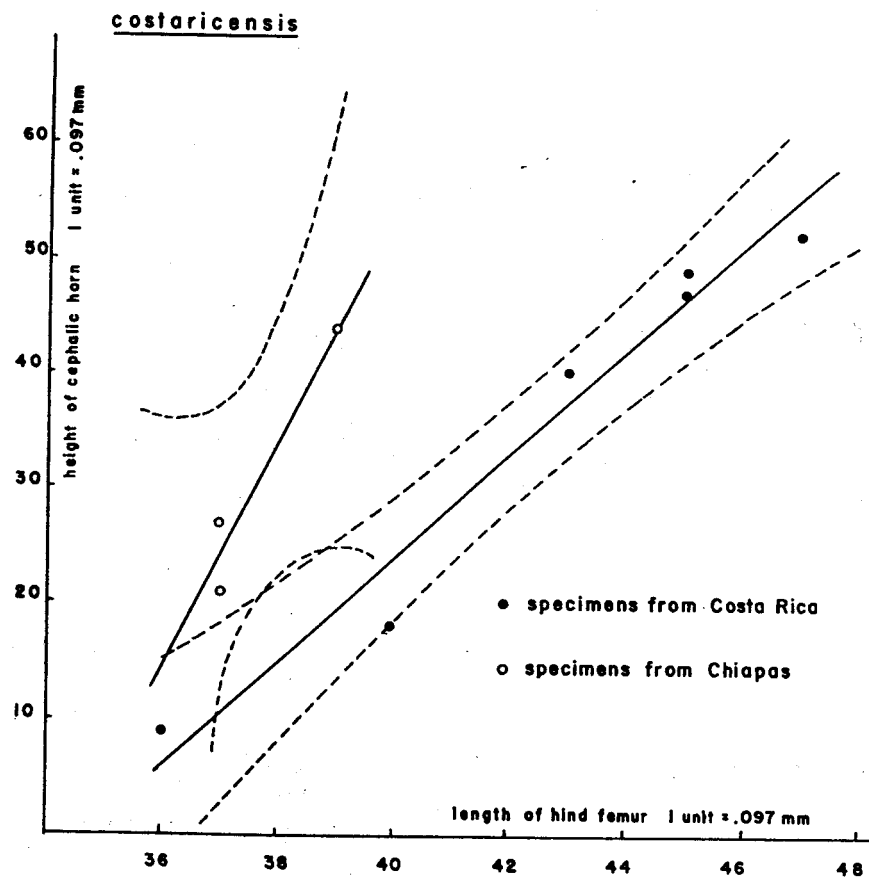


Fig. 7. *C. costaricensis* Gahan, $a = 4.36$ for Costa Rica, 9.99 for Chiapas. Interrupted lines indicate 95% confidence intervals for regression lines.

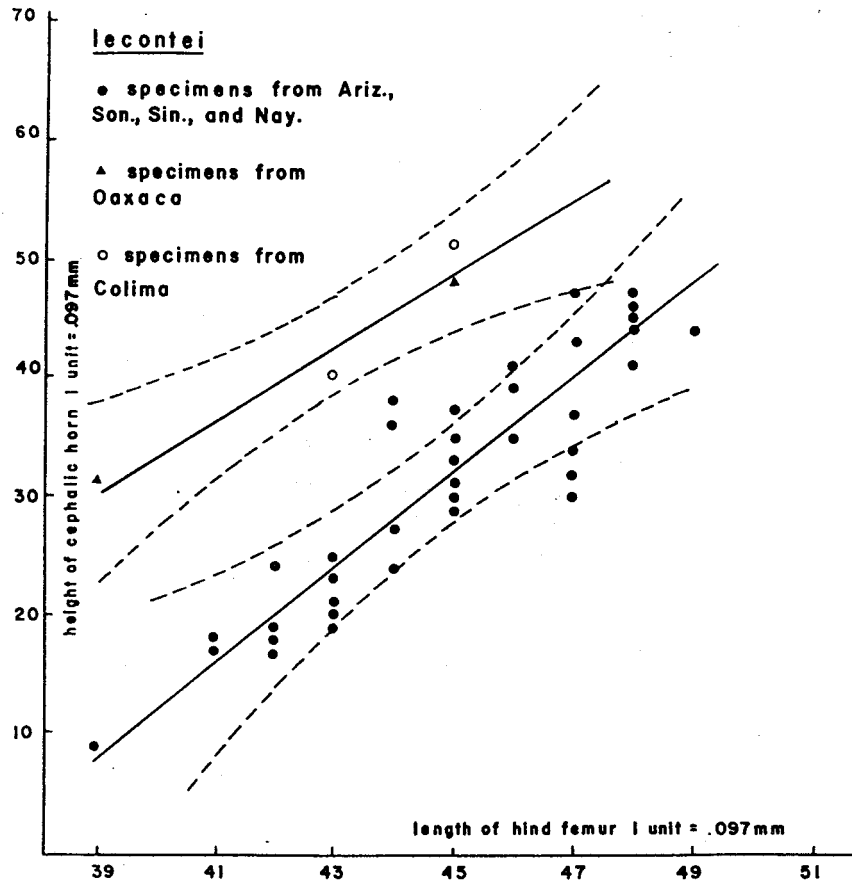


Fig. 8. *C. lecontei* n. sp., $a = 3.99$ for Arizona to Nayarit, 3.08 for Oaxaca and Colima. Interrupted lines indicate 95% confidence intervals for regression lines.

INTERSPECIFIC VARIATION IN HORN HEIGHT

It is not our purpose here to discuss the interesting theoretical implications of the species curve distributions. It should merely be noted in passing that the "rule of Lameere and Smith" (Huxley, 1932, pp. 212-216) is not at all adhered to in *Copris* (contrary to what Paulian [1935] states) but that each species falls along a curve (or two curves) of its own and that these curves are re-

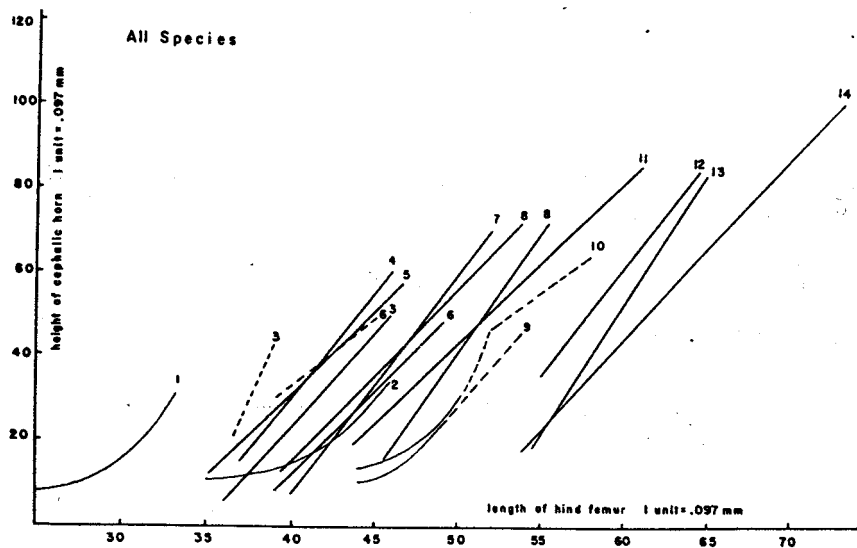


Fig. 9. Plot of horn height against femoral length; regression lines for all species measured. Interrupted lines are of relatively low reliability. Numbers refer to species as listed in table I.

markably parallel (fig. 9). This is expressed mathematically in the relatively constant value of a (averaging 4.76) in the linear formula $y = ax + b'$ (table I). The points of origin of deviations are nearly isometric (fig. 10). This shows that there is a constant *average* proportion of horn-to-body size in all the species regardless of size and a more or less constant degree of allometry. It seems probable that the allometric nature of the horn size relationship is of selective advantage to the species, perhaps to maintain some sort of dominance hierarchy in random assemblages at food sources for the purposes of pairing off.

There are no detectable consistent qualitative differences in horn shape or design between species to suggest in any way that the horn could have any species-recognition value. There are differences in horn design and these are very useful to the taxonomist, but these differences do not correlate with relationship or geographical distribution in any way (e.g., closely related sympatric species do not necessarily differ more strongly in horn design).

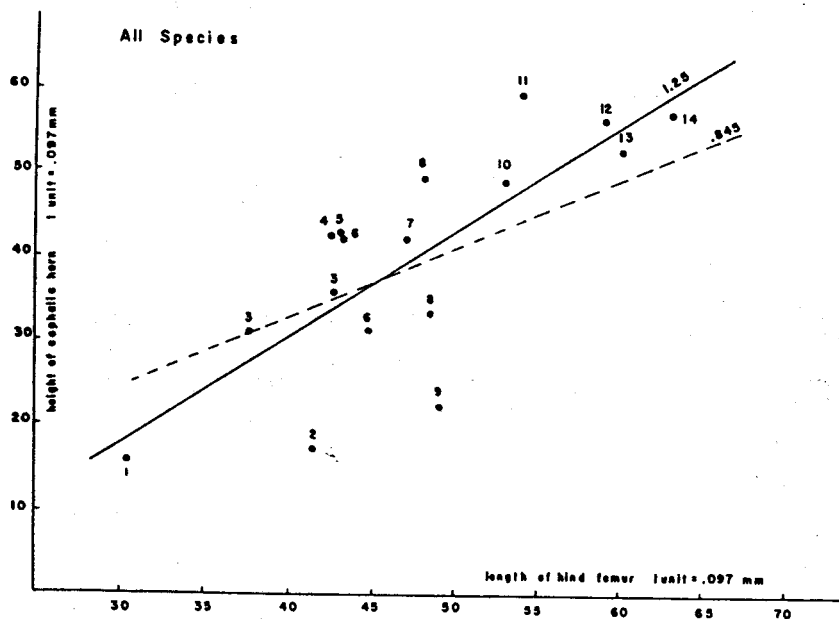


Fig. 10. Regression of mean height of head horn on mean length of hind femur for all species. Solid line represents regression of \bar{y} on \bar{x} ; interrupted line represents the line of constant proportionality (isometry). Further explanation in text. Numbers refer to species as listed in table I.

BIOLOGY

Notes on the nesting habits of five American species have been published. These will be briefly summarized below together with notes on the results of my own field observations on four species.

The available data indicate that the majority of the species of the genus feed on mammal dung, the only known exception being that of *C. gopheri* Hubbard, which feeds on the dung of the

Florida Gopher Tortoise. Aside from this, there is no evidence to indicate that any preference is shown for the dung of any particular species or type of feeder. There are scattered records of individuals occurring at carrion (these are mentioned in the systematic section under the particular species involved), but it must be borne in mind that these could be attracted to the gut contents of the carcass. There are a very few records of individuals coming to traps baited with fermenting malt, mushrooms, decaying meat, and fruit.

Insofar as I have been able to determine, the nidification behavior of the American species differs only in detail from that of *Copris hispanus* (L.) in Europe, as discussed by Fabre (1918), Siyazov (1914), and Lengerken (1954).

It appears, therefore, that biological differences between species generally do not reside in the nature of the food consumed or in the basic aspects of nidification. We may therefore expect that such differences are to be found in ecological tolerances to such factors as humidity, temperature, and so forth, so that the genus may be able to exploit the available dung food in all possible environments. One example of this may be provided by the habitat preferences shown by the two closely related species *incertus* Say and *lugubris* Boheman. The former is typical of the humid tropical forest fauna of the more elevated portions of the Veracruz region, exemplified by Jalapa and Fortín de las Flores, whereas the latter, in this region and in Oaxaca, is restricted to the open areas—the clearings in the forest and the sandy areas immediately along the sea coast (Gonzalo Halffter, personal communication).

There follow brief accounts of the nidification of seven American species the habits of which are at least partly known.

Copris fricator (Fabricius)

From my own observations in the Blue Ridge Mountains in May, 1959, the following outline of the life history of this species emerges.

Nidification is preceded by a period of adult feeding in the spring. Feeding always involves the digging of a small, shallow individual burrow about 4 cm. long beneath or beside a pile of cow dung. The burrow is filled with dung before feeding, the beetle grabbing small "armfulls" of dung and backing into the hole. Each individual of both sexes digs its own burrow independently.

Nidification begins towards the end of May in North Carolina and usually involves a pair of beetles of each sex acting in co-

operation, although the female may begin the nest alone. Of 13 nests I uncovered in various stages of construction and provisioning, seven contained a male as well as the female. Of six later nests uncovered, containing completed brood ovoids, a male was present in only one, showing that the male usually departs after construction and provisioning is completed.

The completed nest is a large oval underground chamber located under the dung pile and with the measurements indicated in table II. The floor of the chamber is 5-12 cm. below the ground surface and is connected to the surface by a short passageway just wide enough to admit one beetle; this passageway is left open to the outside (fig. 82). Initially the nest is nearly filled by one large "cake" of dung which is "tended" by the female or pair wandering repeatedly over its surface. After an unknown period, the female begins cutting and shaping the brood ovoids from the dung cake (figs. 83-86). These measure about 2.5 cm. in diameter with one slightly longer vertical axis at the top of which is located a small spherical cavity containing one egg. The female evidently lays the egg and completes the ovoid before starting on the next one. The total number of ovoids seen in completed field nests varies from three to five. The larva on hatching begins to consume the inside of the ovoid, storing excrement in the characteristic coprine "hump" (an outpouching of the mid-gut). Emergence of adults in captivity from these ovoids completed in late May took place between 14 and 25 July. The continuous presence of the female in the nest was proved necessary to maintain the smooth, unblemished contours of the outside of the ovoids. Ovoids kept apart from the female soon became heavily overgrown with fungi and molds.

Lindquist (1933) indicates that the beetles overwinter singly as adults in very deep vertical burrows devoid of dung.

Ritcher (1945) described the third-stage larva of this species (under the name *tullius* Olivier).

Copris remotus Leconte

Lindquist (1935) gave an excellent account of the nesting habits of this species near Uvalde, Texas. Some of his numerical data are summarized in table II.

The points in which the nidification of this species appears to differ from that of *C. fricator* just discussed are as follows. The female apparently digs and provisions the nest alone; provisioning, with cow dung, takes one or two days. Each brood ovoid takes two

Table II. Summary of Data on the Nidification of Nine Species of *Copris*.

Species	Place	Source	Average dimensions of chamber (cm)	Average depth of bottom of chamber (cm)	Tunnel plugged	Number of brood-ovoids per nest	Average size of ovoids (cm)	Participation of male
<i>hispanus</i>	Provence	Fabre	10-12 x 6	20	Yes	Up to 5	4.0 x 3.4 x 3.4	to end of provisioning
"	Dalmatia	von Lengerken	9 x 7.5 x 6.5	14.5	Yes	Up to 5	4.0 x 3.6 x 3.3	to end of provisioning
"	Central Asia	Siyazov	8 x 7 x 5	70	Yes	±5	4.5 x 4 x 4	to making of first ovoid
<i>lunaris</i>	captivity	Fabre	15 x 6	?	?	7-8	?	throughout
<i>fricator</i>	Kansas	Lindquist	3.79 x 2.8	9.78	?	?	?	?
"	NC, Va.	original	5.7 x 5 x 3.7	8.83	No	3-5	2.63 x 2.37 x 2.33	to start of ovoid formation
<i>remotus</i>	Texas	Lindquist	5 x 7.5 x 2.5	?	Yes	1-8	2.5 x 2	none?
<i>aspericollis</i>	Guatemala	original	8 x 7 x 6	15	Yes?	(av. 4-6)	?	at least to end of provisioning
<i>minutus</i>	Virginia	original	?	7	?	4	?	?
"	Kentucky	Ritcher	?	?	?	2-3	1.4 x 1.35	throughout?
<i>gopheri</i>	Florida	Hubbard	?	10-12.5 (beneath tortoise gallery)	?	1?	?	?
<i>lugubris</i>	Nicaragua	original	7.6 x 4.8 x 3.6	12.7	Yes	?	?	at least to end of provisioning
<i>incertus</i>	N. Zealand	Thomas	?	?	No?	2-7	1.8-2.5 diam.	to start of ovoid formation

to three days to construct and there may be up to eight ovoids per nest. The female plugs the ingress passageway with soil.

Under laboratory conditions embryonic development takes 5-10 days, the first instar 2-4 days, the second 2-5 days, the third 13-17 days, the pupa 12-37 days, for a total of 38-69 (average 49) days to complete development from hatching to adulthood. Eggs are obtained from 20 March to 10 October.

A reared female lived 644 days in captivity. Several females laid eggs over two seasons. Lindquist was able to get up to 12 nests from one female, with a total of 41 eggs. The normal appears to be 3-4 broods annually.

Copris aspericollis Gillet

I uncovered three burrows of this species under cow dung near Guatemala City on 22 July 1958. Two consisted merely of short burrows containing one female each and no dung. The third consisted of a chamber containing a dung cake and a male and female pair. No ingress tunnel could be detected, suggesting that it had been blocked with soil. Evidently, nidification in this species involves the participation of both sexes.

Copris minutus (Drury)

The only available data on this common species is provided by Ritche (1945), who found larvae in balls of dung associated with one or two adults in a brood chamber, the number of balls being two or three. The nests are dug several inches deep in the soil under cow dung. Measurements are given in table II. The adults are usually found in the chambers with the ovoids even after the larvae have pupated. Third-stage larvae were found in April and June, pupae in July. Ritche described the full-grown larva.

I found one nest of this species in the Blue Ridge Mountains of Virginia on 4 July, 1960, containing four brood ovoids and one female beetle.

Copris gopheri Hubbard

Hubbard's (1894) account is still the only one we have on this interesting species. He found nests in large numbers four or five inches below the floor of the nest chamber of the Gopher Tortoise near Crescent City, Florida. The brood ovoids are apparently made of tortoise dung. An important difference and apparently

unique feature of this species is that the larva, when pupating, constructs a cocoon of excrement around itself. This is apparently necessary because of the friable nature of the tortoise dung. The study of the biology of this species is made extremely difficult by the enormous depth of the tortoise burrows.

Copris lugubris Boheman

I was able to uncover six burrows of this species in Nicaragua on 27 and 28 July, 1958. The important features of the nests are diagrammed in figs. 87 and 88 and measurements are given in table II. Only the preliminary, or dung-cake, stage was seen. Important points are that the ingress tunnel is blocked with loose soil, there is usually a cavity *under* the dung cake (a unique feature), and the male always accompanies the female in this stage of nest construction (digging and provisioning).

Copris incertus Say

An excellent account of this species in New Zealand, where it was introduced, is given by Thomas (1960). His account is similar to that given above for *C. fricator*, but the following points are worth noting.

On one occasion, three days after dung was exposed to beetles six burrows were dug up, four containing a female each and two containing a male and female pair. The dung cake remains intact for several weeks in the field. The egg cavity is made and the egg laid directly in the dung cake *before* the brood ovoid is cut and shaped around it. The particular process of oviposition has not been observed in the other species. Two to seven ovoids are made per nest. Development from egg to adult takes 57-70 (average 62) days in captivity. The larva and pupa are figured.

It is to be noted that there is no cavity under the dung mass as is seen in the very closely related *C. lugubris*, but that the spaces are over and around the mass, as in the other species seen.

Additional biological data taken from the labels attached to the collected material used in this revision are presented in the systematic section under the particular species involved.

The genus *Copris* Müller is completely isolated taxonomically from any other New World genus of Coprini and can easily be distinguished by the characters mentioned in the diagnosis. In the Old World, however, it shows close affinities with a number of genera, among which we may mention particularly *Pseudopedaria* Felsche (Africa), *Coptodactyla* Burmeister and *Arrowianella* Paulian (Australia). The customary grouping of coprine genera into "subtribes" (ending in the termination -ides) after Gillet (1911) is in my opinion so artificial that it should be abandoned.

The genus *Copris* has been recently divided into four subgenera (Balthasar, 1958), all the American species falling into the subgenus *Copris s. str.* A study of the American species, however, reveals a sharp division into two groups which would merit subgeneric distinction if the genus were purely American. As it is, it is more probable that this division represents a double invasion of North America by two ancestral Asian species, since it is not reflected in the Old World fauna. It is impossible, therefore, to erect formal categories for these two subdivisions; they have been treated as "groups" in the present work, each being named after the earliest described included species. Each of these groups are further divisible into subgroups, here called "complexes", of species which fall naturally together. There are seven such complexes, each containing a few species, some of which are extremely closely related and most of which are distributed in geographical "chains" (allopatrically).

Figure 11 summarizes the relationships of the species as interpreted here. In the *fricator* group, the *armatus* complex is considered the most primitive as it contains large, morphologically unmodified species (with the full complement of elytral striae, simple anterolateral angles, typical puncturation, etc.). It will be noted that the geographical distribution of the groups suggests that the center of evolution for the genus in the New World is the northern Mexican highland region and that species become more evolved as they radiate out from this center.

There is a further suggestion, derived from the close relationships between the species within the two groups, that the genus is at present rather actively speciating in the New World and may therefore be of rather recent immigration, probably from Asia via the Bering bridge. Certain Chinese species I have seen (undetermined) bear a striking similarity to *incertus* Say.

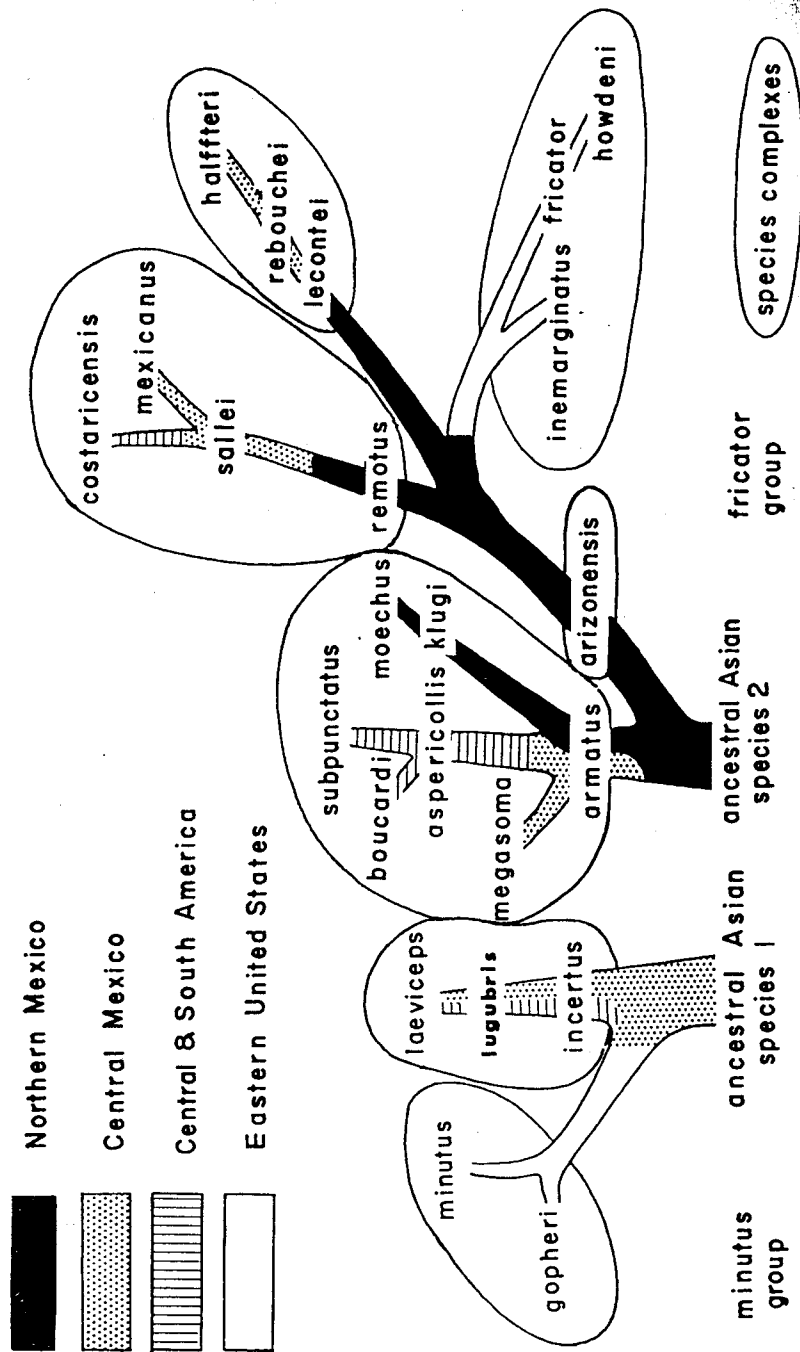


Fig. 11. Proposed relationships of the American species of *Copris*.

The fossil species *Copris pristinus* Pierce (1946), of the Upper Pleistocene (La Brea tar pits, California), is definitely a *Copris* and appears to be a true extinct species very close to *C. armatus* Harold but much larger, being in a size class with the giant *C. megasoma* Matthews and Halffter, which it also closely resembles. The latter two species are from central Mexico. I cannot place *C. pristinus* with greater accuracy at the moment, as I have not seen the original material.

Palaeocopris labreae Pierce, from the same deposits, cannot be placed anywhere at present and appears to be a composite of two genera.

GENUS *Copris* MÜLLER, 1764

Copris Müller, 1764, Fauna insectorum Fridrichsdalina, p. xi. Type, by subsequent designation, *Scarabaeus lunaris* Linnaeus (Curtis, 1832, British Entomology, pl. 414).

DIAGNOSIS. Head semicircular in outline, very strongly flattened, and completely margined above, its dorsal surface punctate, never wrinkled. Thorax below with a distinct oblique propleural carina and a longitudinal proepimeral carina (fig. 26, lpc, pc), a short transverse mesosternum with a median impunctate area, an obtusely angular meso-metasternal suture, and a parallel-sided median metasternal lobe devoid of long setae. Elytra with ten striae, of which at least eight are complete (including the one along the lateral carina). Abdomen with six visible sternites, all of which are distinct along the mid-line, not being fused together or overlapping. Fore tibia with four outer teeth or expansions, the proximal one very small. Hind tibia with a very prominent transverse carina close to the middle on its outer face.

KEY TO THE SPECIES OF THE GENUS *COPRIS* IN THE WESTERN HEMISPHERE BASED ON THE MAJOR MALES*

1. Male armed like a female, with a well developed, typical female head horn which is transverse, quadrate, and apically excavate (fig. 77); anterior margin of prosternum with a salient, bilobate median process (fig. 55). Guerrero *halffteri* Matthews.
- Male armed with a conical or slender horn; anterior margin of prosternum with a median process varying in shape but never bilobate, or without any median process 2.

* The following species, the males of which are hornless, are not included in this key: *howdeni* Matthews and Halffter, *inmarginatus* Blatchley, and *laeviceps* Harold. *C. sallei* Harold, of which I have seen only females, is also not included.

2. Median pronotal prominences, when present, transversely truncated; lateral pronotal carina absent; lateral pronotal inner margin evenly curved; pygidial margin incomplete, its edge effaced ventrally 3.
 Median pronotal prominences rounded or acute; lateral pronotal carina present; lateral pronotal margin sinuate or slightly angulate anteriorly 6.
3. Head with a horn-like tubercle behind the horn; forespur expanded distally, truncate (fig. 33); a tuft of long setae present on hind edge of median and posterior trochanters 4.
 Head with only one horn-like prominence; forespur acute or bluntly rounded; trochanters without setae 5.
4. Head horn arising approximately from middle of head surface; tubercle behind it erect or sometimes bent (never inclined forward (fig. 64); dorsal edges of median pronotal prominences, when seen from the front, sloping down laterally at an angle of about 45° from horizontal. S. Mexico and Central America *lugubris* Boheman.
 Head horn arising from before middle of head; tubercle behind horn inclined forward (fig. 63); dorsal edges of median pronotal prominences, when seen from the front, almost horizontal. Tamaulipas to Ecuador, Hawaii, New Zealand *incertus* Say
5. Pronotum and elytral striae coarsely punctate; clypeus contrastingly more finely punctate than rest of head; a segment of anterior portion of 9th elytral stria present and coarsely punctate; proepimeron fully punctate. Eastern U. S. *minutus* (Drury)
 Entire body very feebly punctate; elytral striae partially impunctate; 9th elytral stria present only posteriorly; proepimeron partly impunctate inwardly. Florida *gopheri* Hubbard
6. Anterolateral angles of pronotum with the point made salient by an inward curve or emargination of the margin immediately behind it; 8th elytral stria nearly always complete. Smaller beetles (10-18 mm in length) 7.
 Anterolateral angles of pronotum subquadrate, obtusely angled, or broadly rounded, occasionally acute in very highly developed specimens, never with a sharp inward curve of the margin immediately behind them. Larger beetles (14-29 mm in length) 13.
7. Pronotum uniformly very densely punctate, the punctures separated by a distance roughly equal to their diameter

- (fig. 66); elytral interstriae distinctly and profusely punctate; head horn almost straight, slightly transversely dilated at apex in well developed individuals. Central and Northeast U. S., Southeast Canada ... *f. fricator* (Fabricius)
- Pronotum not uniformly very densely punctate, the punctures separated by a distance equal to far more than their diameter on at least part of pronotum; elytral interstriae very finely punctate (appearing impunctate to the unaided eye) or quite impunctate. 8.
8. Median dorsal sulcus of pronotum and pronotal disc impunctate; median pronotal prominences laminar, well separated, with a deep depression between them, and parallel (fig. 76); pygidial margin incomplete, its inner border completely effaced ventrally (fig. 58); anterior prosternal margin with an acute, minute median tooth (fig. 54). Central Mexico *rebouchei* Harold.
- Median dorsal sulcus of pronotum punctate or, if impunctate, then anterior prosternal margin is without an acute median tooth and inner border of pygidial margin is completed ventrally by a close-set row of punctures (fig. 59) 9.
9. Pygidial margin incomplete, its inner border completely effaced ventrally; median pronotal prominences closely approximated, parallel in direction, in developed individuals tending to become merged into a single bifurcate process receiving the head horn (fig. 80); anterior margin of pronotum forming a minute, downwardly directed median point. Chiapas and Central America *costaricensis* Gahan
- Pygidial margin nearly always complete; median pronotal prominences never merging and otherwise not as above 10.
10. Male with well developed, divergent median pronotal prominences, but with either no trace of any lateral prominences (fig. 79), or these represented by tubercles. Tamaulipas *remotus dicyrtus* Matthews and Halffter.
- Male, if bearing well developed median pronotal prominences, also bears well developed, laminar lateral prominences 11.
11. Clypeal teeth obtuse, relatively approximated, the margin between them excised at a distinct angle without any median notch; hind angles of head quadrate; median dorsal sulcus of pronotum not contrasting with rest of disc in puncturation; disc usually moderately punctate (fig. 75). S. Arizona and W. Coast of Mexico to Tehuantepec *lecontei* n. sp.
- Clypeal teeth acute and remote, very small, the margin between them not appreciably excised, with or without a

- very shallow median notch; hind angles of head acute; median dorsal sulcus of pronotum coarsely umbilicopunctate in sharp contrast to the impunctate or very finely punctate elevated portions of disc 12.
12. Median pronotal prominences remote and slightly divergent (fig. 78); fovea abruptly bent in very near apex, where it forms a dull point (fig. 43). S. Texas, N. Nuevo León *r. remotus* Leconte.
 Median pronotal prominences very approximated, their outer edges converging forward (fig. 67); fovea curved inward and tapering near apex to a sharp point (fig. 44). Michoacán *mexicanus* Matthews and Halffter.
13. Clypeal emargination very shallow, wide, and arcuate, without a median notch; fovea curved inward and tapering to a sharp point (fig. 39); median pronotal prominences closely approximated to form a single bifurcate process in well developed individuals (fig. 68); entire surface of pronotum regularly and usually densely punctate; 8th elytral stria complete. S. Arizona and New Mexico, W. Texas Chihuahua *arizonensis* Schaeffer.
 Clypeal emargination broadly triangular, with a median notch, or absent; fovea rounded at the end or coming to a blunt point, curving downward a little but not inward appreciably; 8th elytral stria incomplete, disintegrating posteriorly or largely effaced 14.
14. Median prominences of pronotum with the apices well separated, their outside edges divergent in well developed individuals 15.
 Median prominences of pronotum closely approximated, their outside edges evenly convergent anteriorly 18.
15. Anterior face of pronotum sparsely to moderately punctate; clypeus devoid of teeth 16.
 Anterior face of pronotum coarsely granulate; clypeus obtusely bidentate 17.
16. Median pronotal prominences with the apices obliquely flattened, their lower surfaces flat or slightly concave; clypeus entire, without any median notch (fig. 70). Michoacán *megasoma* Matthews and Halffter.
 Median pronotal prominences conical, round in cross section; clypeus with a median notch (fig. 69). Central Mexico *armatus* Harold.
17. Elytral striae appearing distinctly punctate to the unaided eye; apices of median pronotal prominences conical, round in cross section (fig. 74). Guatemala. *aspericollis* Gillet.

Elytral striae appearing impunctate to the unaided eye, the punctures obsolescent; apices of median pronotal prominences pyramidal, their lower surfaces flattened or slightly excavate (fig. 72.). Costa Rica, Panamá

- subpunctatus* Gillet.
18. Anterior face of pronotum sparsely to moderately punctate (fig. 71). Central Mexico *klugi* Harold.
Anterior face of pronotum granulate or asperate, or if partly punctate, then very densely so, the punctures with raised edges, imparting an asperate appearance to the surface 19.
19. Apices of median pronotal prominences pyramidal, abruptly and sharply turned upward when seen from sides (fig. 73); head horn evenly tapering when seen from front. Chiapas and Central America *boucardi* Harold.
Apices of median pronotal prominences blunt or conical, directed forward or evenly curving slightly upward when seen from sides (fig. 81); head horn, when seen from front or rear, expanded distally into transverse knob. Chihuahua and Durango *moechus* Leconte.

KEY TO THE SPECIES OF THE GENUS COPRIS IN THE WESTERN
HEMISPHERE BASED ON THE MALES AND FEMALES

1. Lateral pronotal carina absent; lateral pronotal margin evenly curved; pygidial margin incomplete, the inner border effaced ventrally 2.
Lateral pronotal carina present; lateral pronotal margin sinuate or slightly angulate; pygidial margin complete or not 6.
2. Median and posterior trochanters with a tuft of long setae on the hind edge. Total length 13.5-19 mm 3.
Median and posterior trochanters without setae. Total length 8-13 mm 4.
3. ♂. (Forespur spatulate.) Occipital margin usually with a sharp transverse carina closely paralleling the marginal setigerous groove (fig. 24, toc). ♀. (Forespur tapering.) Anterior portion of pronotum without any transverse carina; very developed specimens with two low transverse gibbosities not followed by any intensification of the punctures. S. Mexico and Central America
lugubris Boheman.
- ♂. (Forespur spatulate.) Occipital margin usually with a dull transverse carina closely paralleling the marginal

- setigerous groove. ♀. (Forespur tapering.) Anterior portion of pronotum, even in the least developed specimens, with two indistinct transverse carinae which are rounded and, especially in developed specimens, sinuate, with the disc immediately behind them abruptly and contrastingly densely punctate. Tamaulipas to Ecuador, Hawaii, New Zealand *incertus* Say.
4. Lateral pronotal margin finely serrate just behind anterolateral angle; prosternal-proepisternal suture distinctly carinate; pronotum and head completely devoid of gibbosities in both sexes. S. Mexico and Central America *laeviceps* Harold.
Lateral pronotal margin not serrate; prosternal-proepisternal suture not carinate; pronotum sculptured or not; head usually with a horn-like process 5.
5. Pronotum and elytral striae coarsely punctate; a punctate segment of 9th elytral stria present at base of elytron; proepimeron entirely, evenly punctate; clypeus contrastingly more finely punctate than rest of head; forespur linear, rounded at the end (fig. 6). Eastern U. S.
minutus (Drury).
Entire body very finely punctate; elytral striae partly impunctate; proepimeron largely impunctate inside posterior longitudinal proepimeral carina; forespur crescent-shaped, curving outward (fig. 35). Florida *gopheri* Hubbard.
6. Anterolateral angles of pronotum with the point made salient by an inward curve or indentation of lateral margin immediately behind them (sometimes indistinct), the margin often sharply sinuate anteriorly; 8th elytral stria nearly always complete. Total length 10-18 mm 7.
Anterolateral angles of pronotum subquadrate, obtusely angled, or broadly rounded, never with a sharp inward curve of margin immediately behind them. Total length 14-29 mm 17.
7. Pronotum uniformly very densely punctate, without smooth areas except at the very apices of prominences, if any 8.
Pronotum with impunctate areas, or large areas with finer or sparser punctures than others 10.
8. Clypeal margin entire, slightly sinuate at most; elytral intervals appearing smooth, convex. Florida
inemarginatus Blatchley.
Clypeus distinctly emarginate; elytral intervals appearing distinctly punctate to the unaided eye, moderately convex or flat; elytral striae crenulate, the punctures obsolescent 9.

9. Elytral interstriae moderately punctate, convex, the punctures separated by a distance equal to 1-3 times their diameter. Central and N. E. U. S. *fricator* (Fabricius).
 Elytral interstriae more densely punctate, flat, the punctures separated by a distance about equal to their diameter; both sexes always completely devoid of pronotal prominences. Florida *howdeni* Matthews and Halffter.
10. Pygidial margin incomplete, its inner border completely effaced ventrally (fig. 58) 11.
 Pygidial margin complete, its inner border entirely engraved, or incomplete but with median portion of inner border represented by close-set punctures (fig. 59) 13.
11. Median longitudinal sulcus of pronotum coarsely punctate and deeply impressed; anterior margin of pronotum forming a minute, downwardly directed median tooth; median coxae with some coarse punctures on outer faces. Chiapas and Central America *costaricensis* Gahan.
 Median longitudinal sulcus of pronotum shallow and impunctate or finely punctate, the punctures never umbilical; anterior margin of pronotum not forming any median tooth 12.
12. Anterior margin of prosternum with a minute, acute median tooth (fig. 54); basal part of disc and median longitudinal sulcus of pronotum quite impunctate. Central Mexico
rebouchei Harold.
 Anterior margin of prosternum without any median tooth (fig. 53) or with a very low broad lobe which may be truncate or bidentate apically; basal part of disc and median longitudinal sulcus of pronotum finely punctate in northern specimens. S. Arizona and W. Coast of Mexico to Tehuantepec *lecontei* n. sp.
13. Anterior margin of prosternum with a salient median process which is bilobed at the apex (fig. 55); base and median longitudinal sulcus of pronotum quite impunctate; a deep depression between median pronotal prominences in both sexes; ♂ with a typical female head horn. Guerrero
halffteri Matthews.
 Anterior margin of prosternum without a salient, bilobed median process 14.
14. Forespur curved inward near the apex and tapering to a sharp point (figs. 40, 44) 15.
 Forespur straight and bluntly rounded at the apex, or abruptly bent inward very near apex and narrowing to a dull point (figs. 43, 45) 16.

15. Hind angles of head quadrate; ♂ with a broad triangular median emargination of clypeal margin; base of pronotum and median longitudinal sulcus finely punctate or impunctate, the puncturation gradually intensifying anteriorly. S. Arizona and W. Coast of Mexico to Tehuantepec *lecontei* n. sp.
 Hind angles of head acute; ♂ with a very shallow, barely perceptible emargination and two remote, minute teeth on clypeal margin; base of pronotum impunctate except for median longitudinal sulcus, which is coarsely umbilicopunctate. Michoacán *mexicanus* Matthews and Halffter.
16. Eighth elytral stria incomplete, effaced or at least partly disintegrating posteriorly; anterior pronotal margin with a minute, acute median tooth. Veracruz and Chiapas *sallei* Harold.
 Eighth elytral stria complete; anterior pronotal margin without any median tooth; ♂ with a very shallow, arcuate median emargination of clypeal margin; base of pronotum impunctate or finely punctate, becoming abruptly coarsely punctate anteriorly in the depressions. Texas, Nuevo León, Tamaulipas *remotus* Leconte.
17. Eighth elytral stria complete; pronotal puncturation rather dense, umbilical, usually becoming sparser posteriorly, never asperate or granulate on the anterior face; ♀ head horn usually widely expanded distally; ♂ with a very shallow, arcuate clypeal emargination and curved, acute forespurs (when not worn). S. Arizona and New Mexico, W. Texas, Chihuahua *arizonensis* Schaeffer.
 Eighth elytral stria incomplete, disintegrating posteriorly (sometimes almost complete); pronotal puncturation much less dense on disc; ♀ head horn either parallel-sided or narrowing apically; forespurs of both sexes straight and with blunt apices; ♂ clypeal emargination angular or absent 18.
18. Elytral striae appearing impunctate to the unaided eye, the punctures obsolescent, quite effaced on the 8th stria. Costa Rica, Panamá *subpunctatus* Gillet.
 Elytral striae appearing distinctly punctate to the unaided eye 19.
19. Clypeal margin entire, devoid of teeth or emargination; ventral surfaces of median and posterior femora impunctate. Total length 28-30 mm. Michoacán *megasoma* Matthews and Halffter.

- Clypeal margin with at least a small median notch, often also with two broad, low teeth or expansions; ventral surfaces of median and posterior femora with at least a few punctures distally. Size smaller, total length 14-25 mm 20.
20. ♂. Clypeal margin very broadly, shallowly emarginate, with two very small teeth (often worn); anterior face of pronotum entirely punctate, the punctures large, umbilical, and often dense, not accompanied by pronounced asperation. ♀. Anterior face of pronotum with at least a few umbilical punctures along anterior margin interspersed among the dense rugosities or granules of the surface. Central Mexico to Chihuahua, in the mountains *klugi* Harold.
- ♂. Clypeal margin with a small, acute median notch and no marginal expansions, or anterior face of pronotum granular, asperate, or both punctate and asperate. ♀. Anterior face of pronotum uniformly densely granular or sparsely to moderately asperate 21.
21. Clypeal margin with a small acute median notch and no salient teeth. ♂. Anterior face of pronotum punctate, with no rugosities. ♀. Anterior margin of prosternum usually with a quadrate median lobe; anterior face of pronotum sparsely to moderately asperate, never granulate. Central Mexico. *armatus* Harold.
- Clypeal margin with two low, indistinct expansions; anterior face of pronotum granulate, usually densely so 22.
22. Complete portion of 8th elytral stria fully punctate like the other striae; anterolateral angles of pronotum angulate, the angle very obtuse. Chihuahua, Durango
moechus Leconte.
- Complete portion of 8th elytral stria more feebly punctate than striae I-IV; anterolateral angles of pronotum broadly rounded (in undeveloped specimens). Chiapas and Central America 23.
23. Basal part of pronotal disc impunctate, shiny. Chiapas, Guatemala, El Salvador *boucardi* Harold.
- Basal part of pronotal disc profusely but shallowly punctate, dull. Guatemala *aspericollis* Gillet.

Group I. The *minutus* group.

Outer face of apical maxillary palpal segment convex. Lateral pronotal carina absent. Lateral pronotal margin evenly curved.

Male median pronotal prominences, when present, broadly transversely truncated. Complex punctures with minutely granular texture. Sternellum tending to be longitudinally carinate. Pygidial margin always incomplete. Male genital parameres slender, tapering to a fairly acute apex. Individuals are frequently incompletely pigmented. Five species.

Complex 1. The *incertus* complex.

Lateral pronotal margin finely and irregularly serrate just behind the anterolateral angles. Prosternal-proepisternal suture strongly carinate.

Three closely related species of tropical Mexico, Central America, and northeastern South America: *incertus* Say, *lugubris* Boheman and *laeviceps* Harold.

Copris incertus Say

Copris incerta Say, 1835, Boston Journ. Nat. Hist., I: 175 [type: Mexico; Museum of Comparative Zoology]; 1859, Complete Writings, ed. Le Conte, II: 649; Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 494 (key); Bates, 1887, Biol. Cent.-Amer., Coleop. II, 2, p. 55 (distr.); Heyne and Taschenberg, 1908, Die exotischen Käfer, p. 64 (descr.); Pereira and d'Andretta, 1955, Pap. av. Dep. Zool. Secr. Agric., S. Paulo, XII: 261-263 (descr. and syn.); Matthews, 1959, Ciencia XIX(6-7): 135 (key and distr.); Thomas, 1960, N.Z. Journ. Sci., III (1): 8-14 (biol. and distr.).

Copris prociidua Say, 1835, Boston Journ. Nat. Hist. I: 176 [type: Mexico; Museum of Comparative Zoology]; 1859, Complete Writings, ed. Le Conte, II: 649; Harold, 1859, Ann. Soc. Ent. France, ser. 4, IX: 495 (key); 1880, Stettiner Ent. Zeit. XLI: 27 (distr.); Blanchard, 1885, Trans. American Ent. Soc. XIII: 171 (distr.); Bates, 1887, Biol. Cent.-Amer., Coleop. II, 2, p. 54 (distr.); Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 255 (key); Williams, 1929, Proc. Hawaiian Ent. Soc. VII(2): 210, 227, 237 (distr.); Pereira and d'Andretta, 1955, Pap. av. Dep. Zool. Secr. Agric., S. Paulo, XII: 260-263 (distr. and syn.); Matthews, 1959, Ciencia XIX(6-7): 135 (key and distr.).

DESCRIPTION OF MALE. *Head*.—Armed or not. Clypeus bidentate, clypeal teeth not at all prominent, margin between them broadly, angularly emarginate with a slightly deeper V-shaped median notch not cutting through margin. Posterior angles of genae subquadrate or slightly obtuse. Upper surface of head rather densely punctate, the punctures simple except for those behind horn (between eyes), which are coarse and granular. Posterior oblique carina absent. Occipital margin with transverse setigerous groove intact and paralleled by an incomplete, dull carina, which is sometimes absent. Demarcation between gula and submentum usually broadly V-shaped, sometimes rounded. *Thorax*.—Pronotum armed or not. Anterolateral angles obtuse, lateral margin just behind them irregularly serrate. Lateral margin evenly arcuate. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus deep, coarsely punctured. Puncturation of pronotum as follows: sparsely and very finely punctate, or impunctate, on disc, becoming a little more densely and deeply punctate on anterolateral lobes and anterior declivities, the punctures here simple; grossly umbilico-punctate, the punctures granular, along entire submargin (sparser laterally and anteriorly), along dorsal longitudinal sulcus, and in lateral fossae. Anterior prosternal margin with a rounded median tooth; sternellum concave with an indistinct median longitudinal carina, moderately punctate. Median lobe of metasternum with no coarse punctures; median longitudinal groove complete. *Elytra*.—8th stria obsolescent, effaced at base and for median third of elytral length, present intact only for a short length near base and behind posterior angle; 9th stria arising from 10th about halfway down elytron; 10th complete or disintegrating temporarily for median third of elytral length. Striae moderately punctate, the punctures not deep, round, little wider than striae, separated by a distance equal to more than their diameter. Interstriae slightly convex, sparsely and very finely punctate, appearing smooth. *Abdomen*.—Pygidium punctate only dorsally, the punctures granular; pygidium incompletely margined, inner edge of margin being effaced ventrally. *Anterior legs*.—Ventral surface of femur with coarse setigerous punctures on posterior longitudinal half, finely punctate on anterior. Forespur expanded and truncated distally. *Middle legs*.—Coxa with some indistinct punctures along median carina. Trochanter with a tuft of long setae arising from posterior margin. Ventral surface of femur very finely punctate, appearing smooth, except for a few setigerous punctures at distal end in some specimens. Tibia below with one distal seta tuft, above with 1-3 supplementary setae distally. *Posterior legs*.—Trochanter with a tuft of long setae

arising from posterior margin. Ventral surface of femur without coarse punctures or with several coarse punctures at distal end. Tibia below with one distal seta tuft, above with 0-3 supplementary setae. *Total length*.—13.5-18.5 mm.

Male armament. The least developed male seen possessed neither a head horn nor any pronotal prominences. More developed specimens bear a slightly curved, tapering clypeal horn which is situated forward of the middle of the head (the more developed the horn the more anteriorly it is located), and an acute tubercle just behind it which is strongly inclined forward, almost recumbent (fig. 63). The median pronotal prominences are very low, approximated, and broadly, transversely truncated. The upper edges of the truncated faces, when seen from the front, are practically on a horizontal plane. The lateral pronotal prominences are low, conical, and directed upwards. The males never achieve a very high degree of secondary sexual development (compared to *lugubris*).

DESCRIPTION OF FEMALE. Similar to male, but differing in armament and in the following features: clypeal teeth more prominent, rounded, approximated, the notch between them deeper, more rounded; forespur not expanded distally, tapering to a blunt point; pronotum anteriorly more densely punctate; median and posterior tibiae with more seta tufts distally below (1-3) and more supplementary setae above (2-4). *Total length*.—13.5-18.5 mm.

Female armament. Head sometimes devoid of a horn in small specimens, with only an acute transverse cariniform process, but usually bearing a narrow transverse horn which is truncated and excavate apically. Median pronotal prominences quite different from the male's, indistinctly transversely carinate, the carinae visible even in undeveloped specimens close to the anterior margin. In large specimens these carinae are sinuate, their anterior faces moderately punctate, the disc behind them abruptly and contrastingly densely punctate. Lateral pronotal prominences absent.

DISTRIBUTION. Fig. 12. This species has a remarkably extended distribution which appears to be made up of isolated populations. It is represented in numerous localities in the tropical forest of eastern Mexico north of Veracruz and in Yucatán at altitudes of 150-1360 m. (500-4500 ft.). It does not occur along the coast itself where it is replaced by the closely related *C. lugubris* Boh. To the south the species disappears completely (in collections) to show up again among some specimens collected by Nevermann on the lower reaches of the Reventazón in Costa Rica, where it appears to occur in association with *C. laeviceps* Harold. Thence it disappears again and we do not find it until we reach the Cordilleras of Colombia and Ecuador, where it occurs at altitudes of 1050-1800

m. (3500–5800 ft.). Blanchard and Horn mention this species (under the name *prociduus*) as occurring in Texas, but I have seen no reliable records to support this and in view of the nature of its habitat in Mexico I consider it highly unlikely that it occurs in the United States (other than in Hawaii), except perhaps as an occasional stray. Blanchard further mentions having seen a specimen from Guatemala.

In addition to the localities cited below, Pereira and d'Andretta

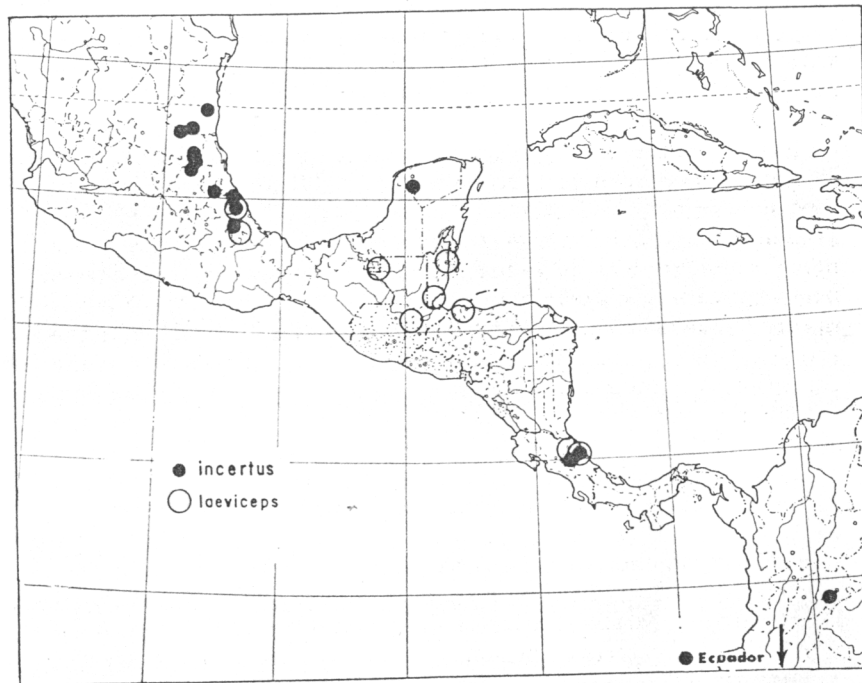


Fig. 12. Distribution of the *incertus* complex, I. Base map reproduced by permission of the University of Chicago.

give five additional Colombian, six additional Ecuadorean, and five additional Hawaiian localities which certainly refer to this species.

This species has been introduced into some Pacific islands in order to reduce the amount of exposed cow dung, which serves as a breeding medium for several species of flies. It has become successfully established in Hawaii, Western Samoa, and New Zealand (Thomas, 1960).

BIOLOGY. Recorded from cow dung in Mexico and New Zealand and cow and horse dung in Hawaii. Nevermann in Costa Rica found it under human dung, in dried wood, and in undergrowth at night. There is one Hawaiian record of its occurrence on *Opuntia* cactus attacked by *Fusarium* disease. Nidification is discussed previously.

REMARKS. I have examined three specimens from the Say material in the Harris collection at the Museum of Comparative Zoology which agree with Say's original description of *incerta*. All are females (Say's description was that of a female, as he suspected), two of them simply bear one very small label each with the number "51" on it while the third bears three labels: an old handwritten one with "*incerta* Say" and "Mexico" written on it, a newer handwritten one (Harris's?) with "type Mexico" on it, and likewise a very small one with the printed number "51". The latter specimen is here designated as lectotype of *incertus* Say.

This same collection also contains a single specimen bearing the name *prociua*. It is a male of the same species and agrees perfectly with Say's original description. It also bears three labels saying "*prociua* Say" and "Mexico", "type Mexico", and the number "53". Since this is the only male of this species in the collection, it is here considered to be the holotype of *prociuus* Say.

All these specimens belong to the same species and since the female was described first, this species (which has hitherto been called *prociuus* or *incertus* var. *prociuus*) must now bear the name *incertus*—engendering considerable nomenclatorial confusion, because the name *incertus* has consistently been applied to a closely related, very abundant species here considered as *lugubris* Boheman.

The separation of this species from the closely related *lugubris* Boheman and *laeviceps* Harold is discussed under the remarks pertaining to those two species.

MATERIAL EXAMINED. 99 males, 106 females, including lectotype.

UNITED STATES: *Hawaii:* Mapulchu, Molokai; Maui.

MEXICO: *Hidalgo:* Chapulhuacán; *Puebla:* Necaxa; San Diego; Mesa de San Diego; Villa Juárez; *San Luis Potosí:* El Salto; Huichihuyan, 20 mi N Tamazunchale; Tamazunchale; *Tamaulipas:* 3 mi NW Acuña; Quintero; *Veracruz:* Banderilla; Barranca de Metlac; Córdoba; Fortín; Jalapa; Laguna de Tamihaua, 20 km N Tuxpan; Martínez de la Torre; Orizaba. *Yucatán:* Uxmal.

COSTA RICA: *Cartago:* Turrialba, 800 m (Schild), 1 ♂ (USNM); 31 May 1951 (O. L. Cartwright), 1 ♂ (USNM). *Limón:* Hamburgfarm, Reventazón, Plain of Limón, 21 Jul. 1931, 27 Jul. 1935, 21 May 1936 (F. Nevermann), 4 ♂♂, 6 ♀♀ (USNM).

COLOMBIA: *Cundinamarca*: Fusagasugá, 1800 m, 9 Sep. 1942 (F. J. Otoyá), 6 ♂♂, 2 ♀♀ (USNM); 8 May 1946 (E. A. Chapin), 3 ♂♂, 2 ♀♀ (USNM).

ECUADOR: *Guayas*: Naranjal (F. Campos R.), 1 ♀ (USNM); *Los Ríos*: 21 Apr. 1938 (W. MacIntyre), 1 ♂ (OLC); *location undetermined*: Paramba, 3500 ft, Mar. 1897 (Rosenberg), 1 ♂ (BM); Lita, 1 ♂ (BM); San Rafael (F. Campos R.), 1 ♂ (USNM).

Copris lugubris Boheman

Copris lugubris Boheman, 1858, *Eugenies Resa*, *Coleop.*, p. 42 [type: Galapagos I.; Naturhistoriska Riksmuseum, Stockholm]; Waterhouse, 1877, *Proc. Zool. Soc. London* V: 82; Linell, 1898, *Proc. United States Nat. Mus.* XXI: 258; Felsche, 1901, *Deutsche Ent. Zeitschr.*, p. 145; Mutchler, 1925, *Zoologica* V(20): 237; Van Dyke, 1953, *Coleoptera of the Galapagos Islands*, p. 122; Pereira and d'Andretta, 1955, *Pap. av. Dep. Zool. Secr. Agric. S. Paulo*, XII: 261 (synon.).

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus bidentate, clypeal teeth relatively prominent, margin between them shallowly, angularly emarginate without any median notch. Posterior angles of genae subquadrate or obtuse. Upper surface of head largely impunctate basally, becoming moderately punctate on flattened portions and horn, punctures simple; in small specimens there are some granular punctures between the eyes. Posterior oblique carina obsolescent. Occipital margin with transverse setigerous groove complete, closely preceded by a sharp transverse carina which may be complete or interrupted at middle. Demarcation between gula and submentum a deep arc, usually with a median V-shaped area. *Thorax*.—Pronotum armed or not. Anterolateral angles obtuse, the lateral margin just behind them irregularly serrate. Lateral margin rather evenly arcuate without any pronounced angulation. Anterior margin of pronotum not forming any median point or angulation. Median longitudinal sulcus deep, coarsely punctured. Puncturation of pronotum as follows: sparsely and finely punctate on disc becoming a little more densely and deeply punctate on anterolateral surfaces and anterior declivity, the punctures simple here; grossly punctate, the punctures umbilical and granular, only along hind submargin (and occasionally along fore submargin), along the dorsal sulcus, and in the lateral fossae. Anterior prosternal margin with a prominent, rounded

median tooth; sternellum somewhat concave but with an indistinct median longitudinal carina, moderately punctate. Median lobe of metasternum very finely punctate, with no coarse punctures; median longitudinal groove very indistinct anteriorly. *Elytra*.—8th stria obsolescent, effaced at base and median third of elytron, present integrally only for a short length near base and apically; 9th stria arising at anterior third of elytral length and continuing distally; 10th stria complete. Striae indistinctly punctate, the punctures not deep, round, little wider than stria, separated by a distance equal to more than their diameter over most of stria length. Interstriae very slightly convex, sparsely and very finely punctate, appearing smooth. *Abdomen*.—Pygidium moderately punctate dorsally, the punctures granular, becoming sparser ventrally; margin incomplete, effaced ventrally. *Anterior legs*.—Ventral surface of femur entirely punctate, the punctures coarser and setigerous on posterior longitudinal half. Forespur rather straight, expanded and truncate at apex (fig. 33). *Middle legs*.—Coxa faintly punctate along median carina. Trochanter with a single tuft of long setae arising from posterior edge. Ventral surface of femur sparsely and very finely punctate, usually with a few setigerous punctures distally. Tibia below with a single distal seta tuft, above without supplementary setae. *Posterior legs*.—Trochanter with a single tuft of long setae arising from posterior edge. Ventral surface of femur very sparsely and finely punctate. Tibia below with a single distal seta tuft, above usually without supplementary setae apically, sometimes with one or two. *Total length*.—13.5–18 mm.

Male armament. The least developed male seen possessed a head horn, albeit a very low one, on the posterior part of the clypeus and a barely evident tubercle close behind it. The pronotum showed traces of median prominences in the form of two approximated transverse tumosities and not a trace of any lateral prominences. With further development, the head horn elongates, becoming gently arcuate and slightly dilated apically in the most developed specimens. The horn is situated at about the middle of the head. Behind it is a prominent tubercle which is either erect or bent forward, but never inclined forward (fig. 64). The median pronotal prominences are broadly transversely truncate, closely approximate, their outer edges converging anteriorly in dorsal view. The upper edges of the truncated faces, when seen from the front, are very strongly sloping down to the sides at about a 45° angle from the horizontal or more. The lateral prominences are laminate, directed forward and upward, and parallel to the longitudinal axis when viewed from above.

DESCRIPTION OF FEMALE. Similar to the male, but differing in armament and in the following features: clypeal teeth more prominent and approximated, with a V-shaped median notch in margin between them. Forespur not expanded and truncate distally, narrowing slightly to a rounded apex. Pronotum anteriorly more densely punctate. Hind tibia above with 2-4 supplementary setae distally (fig. 50). *Total length*.—14-19 mm.

Female armament. Many females are completely unarmed, with only a short transverse carina on the head. The head horn,

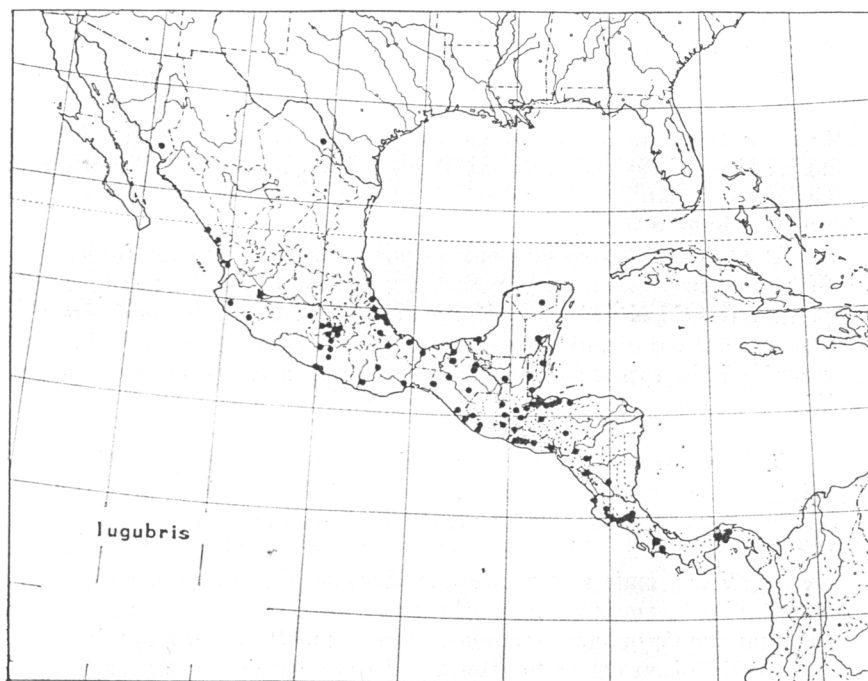


Fig. 13. Distribution of the *incertus* complex, II. Base map reproduced by permission of the University of Chicago.

when developed, is much less transverse than is usual in the genus and is often quite high and narrow; it is excavate on the posterior surface. The median pronotal prominences in developed specimens are like those of a minor male, that is, low rounded tumosities; the lateral ones are absent. There is never an abrupt intensification of the dorsal pronotal puncturation just behind the median tumosities.

DISTRIBUTION. Fig. 13. Widely distributed throughout Southern Mexico and Central America to the Panama Canal at all altitudes up to 1500 m. (4500 ft.). In the northern part of its range it extends up along the coastline on both sides of Mexico, occurring along the Gulf Coast in the sandy area just behind the sea beach. A single specimen was taken surprisingly far inland in northern Coahuila and might be a stray. It has been recorded from Colombia, Ecuador and Hawaii, but I have seen no reliably labelled specimens from these areas and I believe all these records refer to the closely related *C. incertus* Say.

BIOLÓGY. Some aspects of nidification have been discussed previously. The collected specimens bear the following data: at light, under cow dung, in a banana trap, in dead calf, on avocado. I have collected it under burro dung and human faeces. It appears to be most frequently collected at light. In Central America it is active throughout the year. In Central Mexico it is one of the only two species of coprophages occasionally encountered above ground during the dry season (G. Halffter, oral communication).

REMARKS. This species has long gone under the name *incertus* Say. In the remarks under the species now bearing that name I pointed out that Say's types in the Museum of Comparative Zoology show that he did not have any specimens of this species. I have examined the type of *C. lugubris* Boheman in the Naturhistoriska Riksmuseet, Stockholm, and have found it to be this species. *C. lugubris* is therefore its valid name.

C. lugubris may be told from *incertus*, to which it is closely related, by a number of characters in both sexes. Specific distinction is shown beyond doubt by the differences in the male secondary sexual characters, which never show intermediacy between the two forms. The female also shows very distinct differences in pronotal sculpturing (compare descriptions of female armament) and, because of the frequent occurrence of minor males in both species, it is actually often easier to separate the two species on the basis of the females. Additional, less reliable, differences are seen in the male genital parameres (which bear a minute dorsal hook at the apex in *incertus* (fig. 61) but not in *lugubris*) and, to a lesser extent, in the occipital margin of the head, which in *lugubris* usually bears a sharp transverse carina, whereas in *incertus* this carina is usually dull or absent altogether.

MATERIAL EXAMINED. 303 males, 360 females.

MEXICO. *Campeche*: Ciudad del Carmen; *Chiapas*: Comitán; El Vergel (Volcán Soconusco); Escuintla; ?Finca "La Isla"; La Esperanza (Tapachula region); Las Cruces; Ocosingo; Pacific slope Cordilleras; Palenque; ?San José; ?Sta. Julia; Suchiate; Tapa-

chula; Tuxtla Gutierrez; *Coahuila*: 10 mi. S. Allende; *Colima*: Colima; Volcán de Colima; *Distrito Federal*: México; *Guerrero*: Acapulco; Acuitlapán (nr. Cacahuamilpa); Balsas; Cacahuamilpa; Chilpancingo; 22 mi. N. Chilpancingo; El Margues, 28 km. W. Acapulco; Iguala; 3 mi. N. Mexcala; Taxco; Teloloapan; *Jalisco*: Chapala; Purificación; *Mexico*: Río San Jerónimo, 10 km. NE. Cacahuamilpa; Tenancingo; ?Tenayuca; Tonatico; *Michoacán*: San José Purua; *Morelos*: Cuautla; Cuernavaca; 10 mi. S. Cuernavaca; Jojutla; ?Oaxtepec; Yautepec; *Nayarit*: Tepic; 17 mi. NW. Tepic; *Oaxaca*: Amapa; Ixcatlán (W. of Tuxtepec); Oaxaca; 25 km. S. Oaxaca; Panixtlahuaca; Soyaltepec (N. of Tuxtepec); Tehuantepec; ?Valerio Trujano; *Quintana Roo*: Bacalar; *Sinaloa*: Escuinapa; Mazatlán; *Sonora*: Río Mayo; *Tabasco*: Teapa; Villahermosa; *Veracruz*: Atoyac; Coatepec; Cotaxtla; La Gloria, Cardel; Lake Catemaco; Minatitlán; Papantla; Presidio; Puente Nacional; Pureza, 5th R.R. station Veracruz to Jalapa; San Andrés Tuxtla; San Carlos; San Martín, San Andrés Tuxtla; Tecolutla; Tlapacoyan; Tres Zapotes; Veracruz; *Yucatán*: Chichen Itzá.

GUATEMALA: *Alta Vera Paz*: Cacao Trece Aguas; Cobán; San Miguel Tucurú; *Baja Vera Paz*: Rabinal; San Jerónimo; *Chiquimula*: Chiquimula; *Guatemala*: Guatemala City; San José de Pinula; *Izabal*: Cayuga; Los Amates; *Jutiapa*: Laguna Atescatempa; *Petén*: La Libertad; ?Pacomón; *San Marcos*: San Marcos; *Suchitepéquez*: ?Finca El Cipres; Mocá; Variedades; *Zacapa*: Zacapa; *location undetermined*: Jacobo.

BELIZE: Belize; Benque Viejo; San Antonio; Punta Gorda.

EL SALVADOR: *La Libertad*: Santa Tecla; *La Unión*: La Unión; *San Salvador*: San Salvador; *San Vicente*: 49 Km. E. San Salvador; *Sonsonate*: Izalco; Sonsonate.

HONDURAS: *Atlántida*: La Ceiba; Tela; *Copán*: Copán; *Morazán*: Esc. Agr. Pan. Zamorano; *Santa Bárbara*: Choloma; Quimistán; *Tegucigalpa*: Tegucigalpa; *Yoro*: Progreso; *location undetermined*: Carmelina; Ruatan I.

NICARAGUA: *Chontales*; *Jinotega*: Jinotega; *Madriz*: Somoto; *Managua*: Managua; 8 mi N. Managua; San Antonio.

COSTA RICA: *Alajuela*: Grecia; *Guanacaste*: Las Cañas; Guanacaste; Piedra Negra; Santa Elena; *Heredía*: Santa Clara; *Puntarenas*: Las Loras nr. Puntarenas; Orotina; San Lucas I., Gulf of Nicoya; San Mateo; *San José*: Santa Ana; San Jose.

PANAMA: *Canal*: Alhajuelo; *Chiriquí*: David; Potrerillos; Volcán de Chiriquí; *Panamá*: La Chorrera; Chepo; Taboga I.; *location undetermined*: La Joya.

Copris laeviceps Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 498 [type: San Andrés Tuxtla, Ver.; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.-Amer., Coleopt. II, 2, p. 54 (distr.); Matthews, 1959, Ciencia XIX (6-7): 135 (key and distr.).

DESCRIPTION OF MALE. *Head*.—Unarmed (with but a low conical process on the clypeus. Clypeus bidentate, clypeal teeth prominent, angular, the margin between them broadly angulate with a slightly deeper median V-shaped notch not cutting through margin. Posterior angles of genae obtuse. Upper surface of head very finely punctate, appearing impunctate, except for a dense transverse band of coarse umbilical and granular punctures extending between eyes. Posterior oblique carina absent. Occipital margin with transverse setigerous groove complete; marginal occipital carina paralleling setigerous groove very sharp and interrupted in middle. Demarcation between gula and submentum arcuate or subangulate. *Thorax*.—Pronotum unarmed. Anterolateral angles subquadrate. Lateral margin evenly curved, without angulations, indistinctly and irregularly serrate just behind anterolateral angles. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus impressed, complete, coarsely punctate. Puncturation of pronotum as follows: very finely punctate, appearing impunctate, except for the following areas, which are coarsely punctate, the punctures umbilical and granular: along entire submargin, on anterolateral lobes, in lateral fossae, in a narrow chain along entire median longitudinal sulcus, and forming two large patches just above lateral fossae on either side; these patches are isolated from all other coarse punctures except those of lateral fossae. Anterior prosternal margin with a low median salience; sternellum not very concave with a suggestion of a median longitudinal carina anteriorly, coarsely, closely punctate, the punctures granular and umbilical. Median lobe of metasternum with some coarse granular punctures anteriorly along sides; median longitudinal groove somewhat effaced anteriorly. *Elytra*.—8th stria arising close to base but not from it, disintegrating halfway down elytron, then resuming intact after hind angle; 9th stria arising from 10th anterior to the halfway point; 10th complete. Striae coarsely punctate, the punctures round, umbilical, separated by a distance equal to a little more than their diameter. Interstriae slightly convex, very finely punctate, appearing smooth. When seen from behind, elytral surface is bent, forming an in-

distinct, obtuse ridge running from hind angle to end of median suture; no striae cross this ridge. *Abdomen*.—Pygidium densely and coarsely punctate, the punctures granular; pygidial margin incomplete, becoming effaced ventrally. *Anterior legs*.—Ventral surface of femur coarsely punctate, the punctures setigerous, on posterior longitudinal two thirds, very finely punctate on anterior third. Forespur slightly expanded distally, rounded and curved down at apex. *Middle legs*.—Coxa with a few coarse punctures on outer face anteriorly near median carina. Trochanter without setae. Ventral surface of femur very finely punctate with a few coarse punctures distally. Tibia below with 1-2 distal seta tufts, above with 1-2 supplementary setae. *Posterior legs*.—Trochanter without setae. Ventral surface of femur coarsely punctate over most of distal half. Tibia below with one distal tuft, above with 1-3 supplementary setae. *Total length*.—11.5-12.5 mm.

DESCRIPTION OF FEMALE. Differs from the male only in having a parallel-sided or tapering forespur (instead of a distally expanded one). In worn specimens this difference is obliterated. *Total length*.—11-13 mm.

DISTRIBUTION. Fig. 12. Known from isolated localities from Jalapa, Ver., to the Reventazón River in Costa Rica. Appears to be an east coast lowland form and may occur throughout the "Mosquitia" coastal plain of Central America, a very poorly collected region. The localities given by Bates are all probably correctly attributed to this species.

BIOLOGY. Nevermann records the following data on his specimens from the Reventazón River and Plain of Limón, Costa Rica: under horse dung, human dung, in the undergrowth at night in the primeval forest ("nachts im Urwald am Gebüsch"), in iguana carcass, at light. Active throughout the year.

REMARKS. This species is very closely related to *incertus* Say and *lugubris* Boh., with which it shares the features characterizing the *minutus* group, plus several others such as the serrate lateral pronotal margin, broadened male forespur, and carinate prosternal-proepisternal suture characterizing the *incertus* complex. In addition, it shows distinctly closer affinities with *lugubris*, with which it shares the type of male genital parameres and sharp transverse occipital marginal carina. However, all the specimens I have seen may be easily told from both *incertus* and *lugubris* by the lack of setae on the posterior margin of the median and posterior trochanters; it differs also in the pronotal puncturation, showing an oval patch of coarse punctures on the sides of the pronotal disc, and in the carinate nature of the posterior elytral angles. All specimens

are small in size and totally devoid of cephalic and pronotal armament.

MATERIAL EXAMINED. 39 males, 26 females.

MEXICO. *Chiapas*: Tuxtla (O. W. Barret), 1 ♂ (USNM); *Veracruz*: Jalapa (Hoega), 2 ♂♂ (BM); Presidio, E of Zongolica, 1200 m., Jul. 1952 (G. Halffter), 1 ♂ (GH); *national record only*: (Bock), 1 ♂, 1 ♀ (USNM).

GUATEMALA: *Alta Vera Paz*: Cacao Trece Aguas, 26 Apr. (Barber and Schwarz), 2 ♀♀ (USNM); Cubilguitz [1050 ft., on road from Cobán to Petén, 10-20 Mar. 1880] (Champion), 1 ♀ (BM); Telemán [100 m, 13-18 May 1880] (Champion), 1 ♂ (BM); *Petén*: ?Pacomón, 2-8 Jun. 1923 (Harry Malleis), 1 ♂ (CAS); Piedras Negras, 1939 (H. M. Smith), 8 ♂♂, 8 ♀♀ (PAS); *national record only*: 1 ♂ (CAS).

BELIZE: Belize (F. C. Bowditch), 5 ♂♂, 3 ♀♀ (MCZ); M-tee Dist., 21 Mar. 1906 (F. C. Bowditch), 4 ♂♂ (MCZ); Punta Gorda, 10-20 Sept. 1906 (F. C. Bowditch), 1 ♀ (MCZ).

HONDURAS: *Atlántida*: Tela, Guaimas distr. [100 m.], 1, 10 May 1923 (T. H. Hubbell), 4 ♂♂, 3 ♀♀ (UMich, USNM).

COSTA RICA: *Limón*: Hamburgfarm, Reventazón, Plain of Limón, 8 May 1925, 29 Aug. 1926, 1 Aug. 1928, 1 Oct. 1932, 25 Jul. 1935, 21 May, 26 Jun. 1936 (F. Nevermann), 10 ♂♂, 8 ♀♀ (USNM); Guápiles, Sta. Clara, 250-300 m., May 1934 (F. Nevermann), 1 ♂ (USNM).

Complex 2. The *minutus* complex

Lateral pronotal margin not finely serrate anteriorly. Prosternal-proepisternal suture not carinate. Both sexes armed in the male manner.

Two closely related species of the Eastern United States: *gopheri* Hubbard and *minutus* (Drury).

Copris gopheri Hubbard

Copris gopheri Hubbard, 1894, Insect Life VI(4): 310 [type: Crescent City, Fla.: United States National Museum]; 1896, Proc. Ent. Soc. Washington III: 299-302 (distr. and biol.); Hamilton, 1896, Ent. News VII: 286 (biol.); Schaeffer, 1906, Trans. American Ent. Soc XXXII: 255 (key).

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus with two low marginal expansions and a deeper median V-shaped emargination not cutting through margin. Posterior angles of genae quadrate. Upper surface of head very finely and sparsely punctate, appearing smooth, except occasionally for a band of granular punctures between eyes just behind horn. Posterior oblique carina absent. Occipital margin with transverse setigerous groove present only at sides; no marginal occipital carina. Demarcation between gula and submentum a flattened arc. *Thorax*.—Pronotum unarmed. Anterolateral angles subquadrate, lateral margin evenly arcuate. Lateral carina absent, represented by a tumosity below lateral fossae. Anterior margin not forming any median point. Median longitudinal sulcus visible on middle of disc, fine, impunctate. Puncturation of pronotum as follows: sparsely and very finely punctate over most of its surface with coarser granular and partly umbilical punctures on anterolateral lobes, usually along margins except median part of hind margin, which is mostly impunctate, in lateral fossae, and to a lesser extent on a patch situated on either side of mid-line dorsal to lateral fossa. Anterior prosternal margin with a very small, acute median tooth which is sometimes absent; sternellum only very slightly concave, with a trace of a longitudinal median carina anteriorly, coarsely umbilico-punctate. Median lobe of metasternum umbilico-punctate along edges anteriorly, median longitudinal groove more impressed posteriorly. *Elytra*.—8th stria with base and posterior half effaced, present only as an isolated impressed line; 9th stria arising from 10th somewhat before middle of elytral length; 10th stria disintegrating momentarily at hind angle. Striae moderately punctate, the punctures round and distinct basally, becoming effaced over most of strial length. Interstriae convex, sparsely and very finely punctate, appearing smooth. *Abdomen*.—Pygidium distinctly granular-punctate, the punctures finer ventrally, margin incomplete, totally effaced ventrally. *Anterior legs*.—Ventral surface of femur coarsely setigerous-punctate, the punctures reniform, except for an area along anterior edge, which is impunctate. Tibial forespur somewhat falciform, curving outwardly (fig. 34). *Middle legs*.—Coxa usually with two rows of granular punctures on outer face near median carina. Ventral surface of femur with a few coarse, reniform, setigerous punctures distally, elsewhere very finely punctate. Tibia below with 2-3 seta tufts distally, above without supplementary setae. *Posterior legs*.—Ventral surface of femur with a very few setigerous punctures distally or none, elsewhere very finely punctate. Tibia below with 2-4 setae distally, above without supplementary setae. *Total length*.—8-10 mm.

Male armament. Head with a low conical horn which is swollen at the base behind. Pronotum unarmed but with a broad, very indistinct, median transverse gibbosity and low tumosities on either side representing the usual pronotal prominences. Minor specimens possess but a low transverse carina on the head and no trace of any prominences on the pronotum.

DESCRIPTION OF FEMALE. Very similar to male. May sometimes be told by the deeper, more rounded clypeal emargination. *Total length.*—9–10 mm.

Female armament. Identical to that of male.

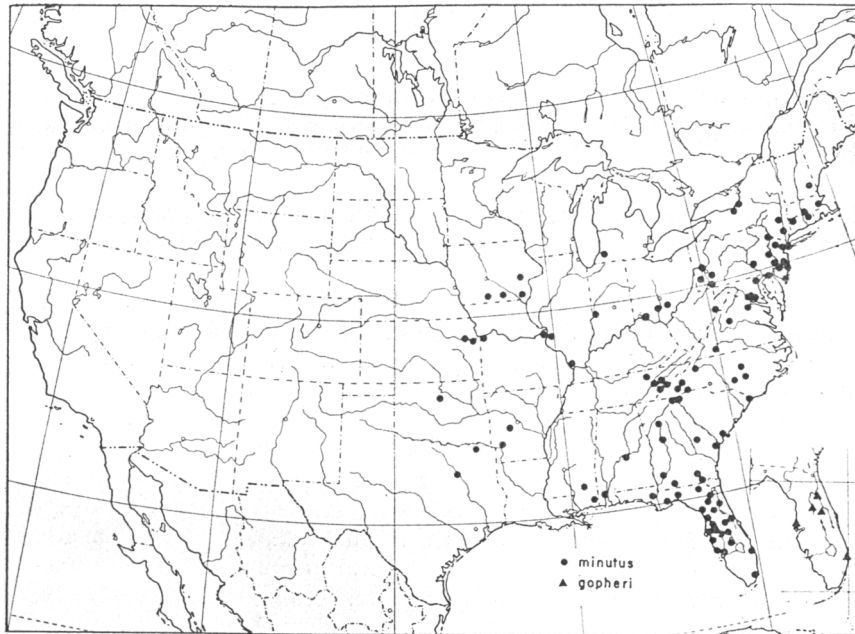


Fig. 14. Distribution of the *minutus* complex. Base map reproduced by permission of the University of Chicago.

DISTRIBUTION. Fig. 14. I have seen specimens only from the southern part of the range of the Florida Gopher Tortoise in peninsular Florida, but Hubbard (1896) reports finding the species at De Funiak Springs in the extreme western part of the state. It is possible that it occurs throughout the range of the tortoise, but it has never been reported outside of Florida.

BIOLOGY. Inhabits the burrows of the Florida Gopher Tortoise as a coprophage. Nothing new has been added to the biological notes made by Hubbard (1894). It has occasionally been taken at light (Hamilton, 1896).

REMARKS. Hubbard did not designate a type specimen for this species. The United States National Museum possesses one specimen of the original type series in the type collection (No. 1299). This specimen, bearing the label "Crescent City, Fla., H. G. Hubbard Coll.," had been entered as a type by Hubbard himself in 1896. It is here designated as lectotype of *Copris gopheri* Hubbard. There are, in addition, numerous other specimens from the type series in the National Museum (including some entered as "types" from the Hubbard and Schwarz collection in 1900) and elsewhere. These all bear the Crescent City label and, although not marked as such, may be considered paratypes.

This species is closely related to *minutus* (Drury) from which it differs in being less punctate and in having an outwardly curved forespur. It can immediately be told from *minutus* by examining the under surface of the prothorax just inside the longitudinal proepimeral carina. This area is impunctate in *gopheri* (and all other *Copris*) and fully punctate in *minutus* (a unique character). In addition, *minutus* shows a distinct anterior segment of the 9th elytral stria, this being absent in *gopheri*.

MATERIAL EXAMINED. 16 males, 12 females (including lectotype).

UNITED STATES: *Florida:* Lake Co.: Leesburg, 2 Jul. 1938 (C. C. Goff), 1 ♀ (OLC); Palm Beach Co.: Lake Worth, 4 ♂♂, 4 ♀♀ (CM); Pinellas Co.: Tarpon Springs, 18 Apr. 1943 (Borys Malkin), 1 ♀ (OLC); Putnam Co.: Crescent City, 15 Jun. 1894 (H. G. Hubbard), 5 ♂♂, 4 ♀♀ (USNM); (Hubbard and Schwarz), 6 ♂♂, 2 ♀♀ (USNM, CAS); 15 Jul. (Fuchs), 1 ♂ (CAS).

Copris minutus (Drury)

Scarabaeus minutus Drury, 1770, Illus. Exot. Ins. I, pp. 78-79, pl. XXXV, fig. 6 [type: New York; British Museum (N. H.)].

Copris minutus, Horn, 1873, Trans. American Ent. Soc. IV: 42-51 (key and descr.); Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 255 (key).

Scarabaeus silenus Fabricius, 1775, Syst. Ent. p. 21, No. 83 [type: America; British Museum (N. H.)].

Scarabaeus ammon Fabricius, 1781, Sp. Ins. I, p. 24, No. 105 [type: America; British Museum (N. H.)]; 1792, Ent. Syst. I, 1, p. 44, No. 147; Olivier, 1789, Ent. I, 3, p. 124, pl. 12, fig. 111; 1790, Encycl. méth. V, p. 161.

Copris ammon, Fabricius, 1801, Syst. Eleuth. I, p. 35, No. 25; Leconte, 1866, List of the Coleoptera of North America, p. 36.

Scarabaeus lar Fabricius, 1787, Mantissa Ins. I, p. 13, No. 124 [type: East India; lost. Co-types in Hunterian Collection, Glasgow]; Staig, 1931, The Fabrician Types of Insects in the Hunterian Collection at Glasgow University, pp. 50-52, pl. 15 (deser. of co-type).

Copris reflexus Panzer, 1794, Faunae Ins. Amer., p. 7 [type: ?].

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus bidentate, clypeal teeth very broad, separated by a deep V-shaped median notch which cuts through margin. Posterior angles of genae quadrate. Upper surface of head sparsely and very finely punctate with genae, occasionally the sides of the clypeus, and a band between the eyes contrastingly, coarsely umbilico-punctate, the punctures granular. Posterior oblique carina absent. Occipital margin with setigerous groove present only at sides, where setae are very long; no marginal occipital carina. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed or not. Anterolateral angles subquadrate, lateral margin rather evenly curved. Lateral carina absent, represented by a longitudinal swelling just below lateral fossae. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus shallow, broad, complete, with coarse granular punctures. Puncturation of pronotum as follows: rather densely, coarsely punctate over entire surface, the punctures granular, finer on anterior declivities away from margin and on either side of dorsal sulcus. Anterior prosternal margin with a minute, acute median tooth; sternellum concave, with coarse granular punctures, sometimes with a trace of a median longitudinal carina anteriorly. Proepimeron evenly punctate over entire surface. Median lobe of metasternum with coarse granular punctures except along median line; median longitudinal groove distinct only posteriorly. *Elytra*.—8th stria incomplete, disintegrating beyond halfway point, but intact at the very base; 9th stria with a distinct, fully punctate segment close to base of elytron, then effaced for a short distance,

arising again at about halfway point as usual, thereafter intact, occasionally the entire stria uninterrupted and fully punctate; 10th stria complete. Striae closely, coarsely punctate, the punctures round and separated by a distance approximately equal to their diameter. Interstriae convex and sparsely, very finely punctate, appearing smooth. *Abdomen*.—Pygidium densely, coarsely punctate, the punctures granular; pygidial margin incomplete, becoming effaced ventrally. *Anterior legs*.—Ventral surface of femur completely punctate, the punctures setigerous, reniform or oval. Tibia below often with a great reduction in the number of short ridges outside of median longitudinal carina. Forespur linear with a blunt apex curved downward and very slightly outward apically (fig. 36). *Middle legs*.—Coxa with a patch of dense, coarse punctures on outer face near longitudinal carina. Ventral surface of femur rather densely, coarsely setigerous-punctate over most or all of surface. Tibia below with 2-4 median distal seta tufts, above without supplementary setae. *Posterior legs*.—Femur and tibia as described for middle legs. *Total length*.—8-12.5 mm.

Male armament. Minor males bear a salient transverse carina on the head. With further development this grows into an acute horn which may be very long in some individuals and curved backward slightly near the apex. The base of the horn on either side posteriorly is climbed for about a third of its length by a prominent carina which appears to be a continuation of the fronto-clypeal suture; these carinae give the horn a swollen appearance at the posterior base (fig. 65). The sides of the horn are coarsely rugose basally. The pronotum is completely unarmed in poorly developed individuals; in better developed ones, the median prominences are seen to be approximated and very broadly truncated, their upper edges forming two median transverse carinae as in *lugubris* and *incertus*. The lateral prominences are at most low and conical, never achieving the laminate stage.

DESCRIPTION OF FEMALE. Very similar to male but usually distinguishable from it in armament and pronotal puncturation, the punctures of the anterior disc abruptly intensifying just behind the median transverse carinae. *Total length*.—9-12 mm.

Female armament. Head horn like that of less developed males, differing in being a little more transverse, very slightly truncate, and apically excavate on the posterior face. Median pronotal prominences very much like male's, but the transverse carinae are more curved in well developed specimens and approximated.

DISTRIBUTION. Fig. 14. The eastern half of the United States in an area corresponding to the Lower and Upper Austral zones (except for the West Gulf and Mississippi Alluvial Plain sections),

climbing a little into the Transition Zone in the mountains of North Carolina and Tennessee.

BIOLOGY. Some aspects of nidification have been discussed. Frequently collected under cow dung, also at light and coming to malt, butyric acid, and fungus baits (only one record of the latter).

REMARKS. This species may immediately be told from all other American *Copris* by the uniformly punctate proepimeron. In all other species, the proepimeron is divided longitudinally by an indistinct carina (the posterior longitudinal proepimeral carina) (fig. 26 lpc), which sharply differentiates an outside, densely punctate area from an inside, almost impunctate one. Although traces of the carina are usually present in *minutus*, this sharp difference in puncturation is not seen and the entire proepimeron is rather uniformly, coarsely punctate. Similarly unique is the presence of a fully punctate anterior segment of the 9th elytral stria near the base of the elytron. This species and the closely related *gopheri* Hubbard are further distinguished by the similarity in armament between the males and females. The females, when developed, possess an acute horn of the male type, and not a truncate and apically excavate one as in all other American *Copris* showing sexual dimorphism.

For an analysis of the geographical variation in sexual dimorphic development in this species see p. 18.

MATERIAL EXAMINED. 352 males, 208 females.

UNITED STATES: *Alabama:* Mobile; Montgomery; *Arkansas:* Garland Co.: Hot Springs; Hempstead Co.: Hope; Pike Co.: Highland; *Connecticut:* Litchfield Co.: Cornwall; Litchfield; Tolland Co.: Storrs; *District of Columbia:* Washington; Woodridge; *Florida:* Alachua Co.: Gainesville; Newman's Lake; Bradford Co.: Starke; Calhoun Co.: Clarksville; Charlotte Co.: Punta Gorda; Citrus Co.; Columbia Co.: High Springs; Suwanee Springs; Dade Co.: Miami; De Soto Co.: Arcadia; Fort Ogden; Hernando Co.: Brooksville; Highlands Co.: Archbold Biol. Sta., Lake Placid; Hillsborough Co.: Lutz; Tampa; Jefferson Co.: Monticello; Levy Co.: Waccasassa R., Gulf Hammock; Manatee Co.: Oneco; Marion Co.: Ocala; Orange Co.: Winter Park; Palm Beach Co.: Lake Worth; Pasco Co.: Dade City; Pinellas Co.: Largo; Tarpon Springs; Polk Co.: Fort Meade; Lakeland; 3 mi SW Lake Marion; Putnam Co.: Crescent City; Interlachen; 8 mi SE Interlachen; Suwannee Co.: 13 mi N O'Brien; Volusia Co.: Enterprise; Wakulla Co.; location undetermined: Natal; Stemper; *Georgia:* Atlanta; Baker Co.: Emory U. Field Sta., Newton; Chatham Co.: Savannah; Emanuel Co.: Swainsboro; Lamar Co.: Barnesville; Rabun Co.: Clayton; Spalding Co.: Experiment; Thomas Co.: Thomasville; Ware Co.:

Waycross; Okefinokee Swamp: Billys I.; location undetermined; The Rock; *Illinois*: Alexander Co.: Olive Branch; St. Clair Co.; *Indiana*: Terre Haute; *Iowa*: Appanoose Co.: Moulton; Decatur Co.: Leon; Henry Co.: Mt. Pleasant; Iowa City; *Kansas*: Doniphan Co.; Douglas Co.: Lawrence; Shawnee Co.: Topeka; *Maryland*: Baltimore; Cecil Co.: Blythedale; Prince George Co.: Branchville; *Massachusetts*: Hampden Co.: Wilbraham; Middlesex Co.: Cambridge; Framingham; Sherborn; *Michigan*: Van Buren Co.: Paw Paw; *Mississippi*: Forrest Co.: Cp. Shelby, nr. Hattiesburg; George Co.: Lucedale; "S. Miss."; *Missouri*: Kansas City; St. Louis; *New Hampshire*: Belknap Co.: Barnstead; *New Jersey*: Atlantic Co.; Burlington Co.: Bordentown; Moorestown; Riverton; Camden Co.: Clementon; Cape May Co.; Essex Co.: Newark; Morris Co.: Boonton; Ocean Co.: Island Beach, Barnegat Bay; Lakehurst; Orange Mts.; Sussex Co.: L. Lackwanna; *New York*: Brooklyn; Greene Co.; Long Island; Orange Co.: New Windsor; West Point; Oswego Co.: Oswego; Wayne Co.; *North Carolina*: Blue Ridge Parkway: Mile 277.7; Buncombe Co.: Black Mt.; Weaverville; Duplin Co.: Faison; Harnett Co.: Dunn; Henderson Co.: Mills River; 16 mi S Asheville; Moore Co.: Southern Pines; Polk Co.: Tryon; Raleigh; Transylvania Co.: Brevard; *Ohio*: Clermont Co.; Hocking Co.; Ross Co.; *Oklahoma*: Payne Co.; *Pennsylvania*: Allegheny Co.; Cumberland Co.: Lemoyne; Dauphin Co.: Deodate; Delaware Co.: Castle Rock; Fayette Co.; Northampton Co.: Easton; Philadelphia Co.: Frankford; Pike Co.; Pittsburgh; Washington Co.; Westmorland Co.: Jeanette; *South Carolina*: Beaufort Co.: Beaufort; Seabrooks I.; Okegee R.; Horry Co.: Little River; Oconee Co.: Clemson College; Fish Hatchery; *Tennessee*: Great Smoky Mts. N. P.: Chilhowee Mts.; Morgan Co.: Burrville; Roane Co.; Sevier Co.: Gatlinburg; *Texas*: Dallas; Dallas Co.; Lamar Co.: Paris; *Virginia*: Arlington Co.: E Falls Church; Blue Ridge Parkway: Mile 162.6; Fairfax Co.: Falls Church; Frederick Co.: Fredericksburg; Nelson Co.; Shenandoah N. P.; *West Virginia*: Cheat Mts.

Group II. The *fricator* group.

Outer face of apical maxillary palpal segment flattened or longitudinally grooved. Lateral pronotal carina present. Lateral pronotal margin sinuate or angulate. Male median pronotal prominences, when present, rounded or acute. Complex punctures nearly always without a granular texture. Sternellum concave, not longitudinally carinate. Pygidial margin usually complete. Male genital parameres bluntly rounded at the apices. 19 species.

Posterior angles of head acute. Anterolateral angles of pronotum broadly rounded or angulate, lateral margin obtusely angulate, not sinuate. Forespur not appreciably bent or curved inward and with apex broadly rounded or obtusely pointed in both sexes. 8th elytral stria disintegrating posteriorly, often also effaced anteriorly. Pygidial margin complete. Large and robust beetles.

Seven species found in the mountains at moderate to very high altitudes in Mexico and Central America: *armatus* Harold, *megasoma* Matthews and Halffter, *klugi* Harold, *moechus* Leconte, *boucardi* Harold, *aspericollis* Gillet, and *subpunctatus* Gillet.

Copris armatus Harold

Copris armatus Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 498 [type: Mexico, D. F. or Toluca, Méx.*; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.-Amer., Coleopt. II, 2, p. 54 (distr.); Gahan, 1894, Ann. Mag. Nat. Hist., ser. 6, XIV: 117 (distr.); Gillet, 1910, Not. Leyden Mus. XXXII: 3 (distr.); Matthews, 1959, Ciencia XIX(6-7): 136 (key and distr.).

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus without teeth or marginal expansions, with a small triangular median notch not cutting inner edge of margin. Upper surface of head closely punctate, the punctures not umbilical, with posterior part of head between eyes and horn and behind them smooth. Posterior oblique carina present but not sharp. Occipital margin with transverse setigerous groove interrupted into three sections, the lateral sections displaced forward and partly overlapping the median one; no marginal occipital carina. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed. Anterolateral angles subquadrate or obtuse, lateral margin slightly angled out at origin of lateral carina. Lateral carina prominent, not issuing from margin anteriorly. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus complete, broadly impressed, and coarsely umbilico-punctate. Puncturation of pronotum as follows: finely to coarsely punctate over entire area, the punctures running together on inner surfaces of lateral prominences apically, the punctures simple except on the following areas, which are coarsely umbilico-punctate: posterior and lateral submargins, lateral fossae, along dorsal sulcus in an anteriorly widening

* Harold gives the range ("patrie") of this species as: "de Mexico et de Toluca", without designating one of these as the type locality.

area, on anterior face in varying proportions, and in depressions between median and lateral prominences where in developed specimens the punctures become sparse, very large, and annular or cicatricial. Anterior prosternal margin with a median tooth which is nearly always truncate and usually quadrate (fig. 52); sternellum sparsely punctate. Median lobe of metasternum impunctate but somewhat wrinkled laterally; median longitudinal sulcus of metasternum with impressed portion ending somewhat short of anterior depression. *Elytra*.—8th stria incomplete, disintegrating at posterior angle; 9th stria arising about halfway down elytral length, occasionally barely visible more anteriorly as a faint, impunctate impressed line; 10th stria complete. Striae closely punctate, the punctures round and separated by a distance approximately equal to their diameter. Interstriae almost flat, very faintly punctate, appearing smooth. *Abdomen*.—Pygidium moderately, evenly umbilico-punctate, the punctures small; pygidial margin complete. *Anterior legs*.—Ventral surface of femur coarsely setiferous-punctate on posterior (upper) longitudinal half, more finely punctate on anterior half. Forespur only slightly curved inward apically, the apex broadly rounded. *Middle legs*.—Coxa with a few coarse setigerous punctures along outer edge, impunctate elsewhere. Proximal half of ventral surface of femur very finely punctate, distal half coarsely setigerous-punctate. Tibia with 2-3, usually two, distal seta tufts medially on ventral side. *Posterior legs*.—Ventral femoral surface punctate, the punctures becoming gradually coarser distally. Ventral distal seta tufts on tibia 1-3. *Total length*.—18.5-23 mm.

Male armament. In better developed individuals the head horn is long and evenly curved back, the outer pronotal gibbosities are laminate and the median ones prominent and approximated. In extreme developments, the very long head horn is bent back at about the middle and tapers to the apex (fig. 69), the median pronotal prominences are sharply conical, approximated, their apices divergent and directed horizontally in profile. The lateral pronotal prominences are directed slightly outward.

DESCRIPTION OF FEMALE. Similar to male, differing only in armament and in the following features: clypeus with two very low rounded marginal expansions flanking median notch, clypeal margin broader and more reflexed than that of male. Head with short impressed lines (transverse punctures) behind horn and eyes. Median dorsal sulcus of pronotum present only on base, fine, sparsely punctate. Puncturation of pronotum as follows: evenly, finely punctate on disc and base, the punctures becoming coarser and more transverse anteriorly, their anterior edges becoming more raised into ridges, until on extreme anterior end of pronotum only

the ridges remain, giving anterior face an asperate appearance. The punctures are umbilical only along posterior and lateral sub-margins, in lateral fossae, and a few along dorsal sulcus. *Total length*.— 19–24 mm.

Female armament. Normal for genus.

DISTRIBUTION. Fig. 15. The Central Volcanic Range of Mexico at altitudes of 1830–3000 m. (6000–9800 ft.) The Central American localities given by Bates refer to other species.

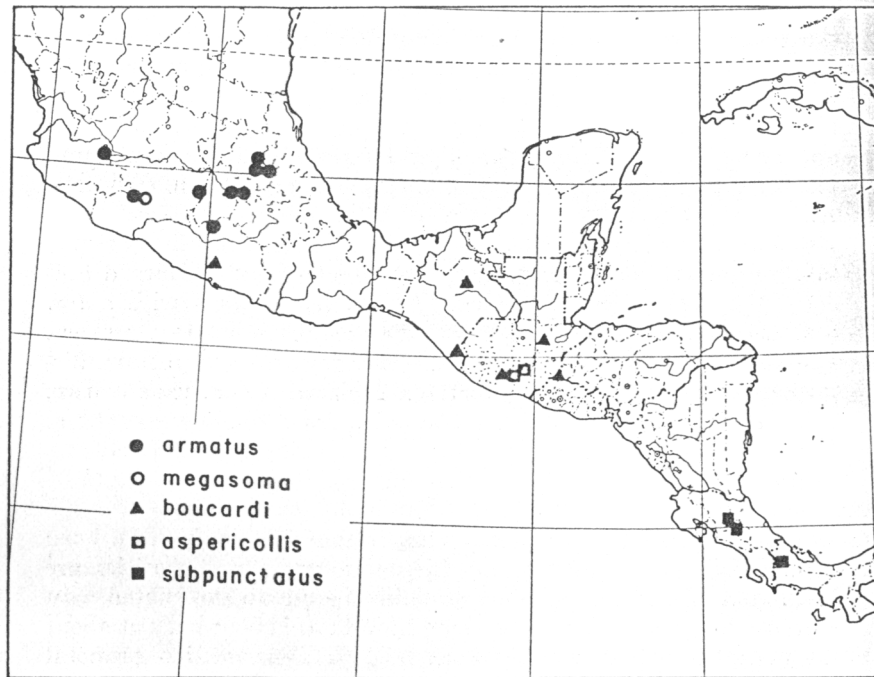


Fig. 15. Distribution of the *armatus* complex, I. Base map reproduced by permission of the University of Chicago.

BIOLOGY. Feeds on cow dung; otherwise nothing is known of its biology. Appears to be active throughout the rainy season of June–October and apparently has not been collected at light.

REMARKS. Because of the punctate (not granulate) anterior pronotal surface in the male, this species could be confused only with *klugi* Harold in this complex. Major males differ very radically from this species in the nature of the median pronotal prominences, which are separated with the apices divergent in

armatus and closely approximated and convergent in *klugi*. In addition, *armatus* is somewhat larger than *klugi* and usually bears a truncate median lobe on the anterior margin of the prosternum. The clypeal margin of the males is also totally different, being evenly rounded with a small median notch in *armatus*, remotely bidentate and broadly emarginate in *klugi*. The females of *armatus* are completely rugose on the anterior pronotal surface and the clypeal margin is practically devoid of expansions flanking the notch.

This species and the fossil *Copris pristinus* Pierce are closely related (see discussion on p. 35).

MATERIAL EXAMINED. 45 males, 30 females.

MEXICO: *Districto Federal*: México, 10 Aug. 1942 (C. Bolívar), 1 ♂ (GH); Villa de Guadalupe, México, 11 Jul. 1949 (G. Halffter), 1 ♂ (GH); *Guerrero*: Teloloapan, 15 Aug. 1957 (D. Douglas), 1 ♀ (GH); *Hidalgo*: Bosque del Chico (N of Pachuca), 29 Jul. 1953 (G. Halffter), 8 ♂♂, 10 ♀♀ (GH); Guerrero Mills (W. M. Mann), 1 ♂, 1 ♀ (MCZ); Real del Monte, Pachuca (Richardson), 1 ♀ (GH); San Miguel (W. M. Mann), 1 ♂ (USNM); 8 km. W. Tulancingo, 4 Aug. 1957 (W. W. Gibson), 1 ♂ (IR); *Jalisco*: 8 mi. S. Guadalajara, late Sep. 1954 (F. X. Williams), 1 ♂ (CAS); *México*: México-Morelia Rd. at border of Michoacán, 13 Sep. 1953 (V. Aguilar), 9 ♂♂, 2 ♀♀ (GH); Salazar [3000 m], Mar. 1952 (found dead), Aug. 1952, 10 Aug. 1953, 25 Jun. 1956 (G. Halffter), 4 ♂♂, 7 ♀♀ (GH); 9 Oct. 1953 (P. Avila, G. García), 1 ♂ (GH); Toluca [2640 m] (Sallé), 1 ♂, 1 ♀ (BM, PAS); *Michoacán*: Bosenchave Nat'l. Pk., 2400 m. 10 Oct. 1953 (Bolívar), 2 ♂♂ (GH); Corupo, 20 Jun. 1947 (T. H. Hubbell), 1 ♀ (USNM); Tancítaro, 6000 ft. 10 Jul. 1940 (Hoogstraal and Knight), 1 ♂ (CAS); 6600 ft., 19 Jul. 1940 (Hoogstraal and Knight), 1 ♀ (CAS); 6000 ft., 24 Jun. 1941 (Hoogstraal and Haag), 2 ♂♂ (CAS); 6500 ft., 28 Jun. 1941 (Hoogstraal and Haag), 3 ♂♂, 1 ♀ (CAS); 6500 ft., 18 Jul. 1941 (H. Hoogstraal), 2 ♂♂ (CAS); Zitácuaro, 15 Jun. 1957 (G. and V. Halffter), 1 ♂ (GH); *national record only*: (Lundholtz), 3 ♂♂, 6 ♀♀ (AMNH); (Sallé), 1 ♂, 1 ♀ (BM); 1 ♂, 3 ♀♀ (CAS).

Copris megasoma Matthews and Halffter

Copris megasoma Matthews and Halffter, 1959, *Ciencia XVIII*(9-10): 194-196 [type: Tancítaro, Mich.; California Academy of Sciences]; Matthews, 1959, *Ciencia XIX*(6-7): 136 (key and distr.).

DESCRIPTION OF MALE (holotype only). *Head*.—Armed. Clypeus with neither teeth nor emargination (median area of clypeal margin in holotype is damaged, but enough of margin remains to reveal no trace of any median notch or teeth). Upper surface of head closely punctate, the punctures simple, with impunctate areas at base of head and about eyes. Posterior oblique carina present. Occipital margin with setigerous groove in three partially overlapping sections; no marginal occipital carina. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed. Anterolateral angles rounded, lateral margin fairly straight. Lateral carina sharp, issuing from anterior angle in holotype (point of issuance of lateral carina usually depends on thoracic development). Anterior margin forming a distinct upwardly directed median angle with inner edge. Median longitudinal sulcus obsolescent, with a few simple punctures. Puncturation of pronotum as follows: base and disc glassy smooth, quite impunctate except for the umbilico-punctate submargin; entire area forward of a transverse line joining hind edges of lateral fossae densely punctate, the punctures umbilical only in lateral fossae and in depressions between median and lateral prominences; there is an impunctate area along mid-line on anterior surface of pronotum. Anterior prosternal margin devoid of any median tooth; sternellum rather flat; moderately punctate. Median lobe of metasternum impunctate; median longitudinal groove complete. *Elytra*.—8th stria incomplete, disintegrating about halfway down elytron; 9th stria originating about halfway down elytron, but also present as a short, faint impunctate line near base of elytron; 10th stria complete. Striae closely, finely, and shallowly punctate, the punctures round or slightly transverse, separated by a distance equal to a little more than their diameter, strial lengths between punctures very fine and shallow. Interstriae almost flat, quite impunctate. *Abdomen*.—Pygidium rather sparsely and very finely punctate, completely margined. *Anterior legs*.—Ventral surface of femur with setigerous punctures on posterior longitudinal half, impunctate on anterior half. Forespur fairly linear, curved slightly downward and inward at apex, ending in a blunt, rounded apex. *Middle legs*.—Coxa impunctate except for a few small setigerous punctures along outer edge apically. Ventral surface of femur impunctate but with a few indistinct punctiform impressions apically. Tibia with two distal seta tufts below. *Posterior legs*.—Ventral surface of femur impunctate. Tibia with 1-2 distal seta tufts below. *Total length*.—28 mm.

Male armament. The head of the holotype bears a short, straight horn abruptly truncated at the apex (perhaps by wear, but the

specimen on the whole is not particularly worn (fig. 70). The pronotum bears the usual four prominences, the two median ones situated far apart, slightly divergent and truncated when seen from above, obliquely flattened when seen from the front, the lower surfaces slightly concave. The two lateral prominences are laminate, not very developed, their upper edges sloping downward in lateral view.

DESCRIPTION OF FEMALE (allotype only). Similar to the male, but differing in armament and in the following features: anterolateral angles of pronotum more rounded, the lateral carina issuing considerably behind the angle. Puncturation of pronotum quite different, consisting of a dense granulation on the anterior face and lateral surfaces before the fossae, becoming asperate on anterior portion of disc, these asperations giving place to transverse punctures posteriorly, which fade out at about the transverse midline of the pronotum, the base of which is therefore completely impunctate and glassy smooth except for a row of umbilical punctures along the posterior submargin. The forespur is more worn, being evenly tapering from the base, only very slightly curved inward apically, the apex being more acute. Pygidium more faintly punctate. The entire insect is considerably broader in relation to its length than the male; this is particularly noticeable with regard to the pronotum. *Total length*.—29.5 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 15. Known only from the type locality at Tancítaro, Michoacán, 1800–1900 m. (5900–6300 ft.).

BIOLOGY. Unknown.

REMARKS. This appears to be nearly the largest species of *Copris* in the world, being slightly exceeded in size only by the African *C. draco* Arrow, as far as I am aware. In appearance the specimens are reminiscent of large *Pinotus* and are equally robust. The only other species with which this one could be confused is *armatus* Harold. From *armatus* it differs in apparently not having any median notch in the clypeal margin, in the ventral femoral surfaces, which are quite impunctate, in the anterior margin of the prosternum, which does not bear any median lobe or tooth, in the completely impunctate pronotal disc, and, of course, in size, the largest *armatus* measuring but 24 mm. in total length. Its specific distinctness is also shown by the difference in the male median pronotal prominences, which are flattened at the apices in *megasoma*, conical and round in cross section in *armatus* (figs. 69, 70). It is closely related to the fossil *C. pristinus* Pierce.

MATERIAL EXAMINED. Holotype and allotype.
 MEXICO. *Michoacán*: Tancítaro, 1900 m, Jul. 1940 (Hoogstraal and Knight), 1 ♂ (CAS); 1800 m, 20 Jul. 1941 (Hoogstraal), 1 ♀ (CAS).

Copris klugi klugi Harold

Copris klugi Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 498-499 [type: Oaxaca, Oax.; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.-Amer., Coleopt. II, 2, p. 54 (distr.); Matthews, 1959, Ciencia XIX(6-7): 136 (key and distr.).

Copris hintoni Saylor, 1933, Canadian Ent. LXV (10): 238-239 [type: Real de Arriba, State of Mexico, 6300 ft.; California Academy of Sciences]; Matthews and Halffter, 1959, Ciencia XVIII(9-10): 193 (synon.).

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus with two remote, very small teeth, sometimes barely perceptible, and a very shallow median triangular notch not cutting through margin. Upper surface of head sparsely punctate along margin, the punctures not umbilical, rest of head very finely punctate, appearing smooth. Posterior oblique carina distinct. Occipital margin with transverse setigerous groove complete; no marginal occipital carina. Demarcation between gula and submentum slightly angulate. *Thorax*.—Pronotum armed. Anterolateral angles obtuse. Lateral margin curved inward slightly behind origin of lateral carina. Lateral carina sharp. Anterior margin not forming any median point or angulation. Median longitudinal sulcus complete, impressed, coarsely umbilico-punctate. Puncturation of pronotum as follows: entirely punctate, with no rugosities; finely punctate on base, the punctures becoming cicatricial then umbilical anteriorly in the depressions, more impressed but simple on outside of lateral prominences; punctures coarse and umbilical along posterior and lateral submargins, in lateral fossae, along dorsal sulcus in an anteriorly widening band, in depressions between median and lateral prominences, and on all anterior declivities, where punctures are moderately sparse, separated by more than their diameters except in very minor specimens, and not accompanied by any rugosity or asperation; sometimes these punctures on anterior surface are not umbilical. Anterior prosternal margin without any median tooth; sternellum sparsely punctate. Median lobe of metasternum finely to coarsely umbilico-punctate along edges; median impressed line complete. *Elytra*.—8th stria incomplete, interrupted at hind angle;

9th stria arising halfway down elytral length; 10th complete. Striae closely punctate, the punctures transverse, separated by about their width. Intervals slightly convex, very finely punctate, appearing smooth. *Abdomen*.—Pygidium entirely margined, moderately, finely umbilico-punctate. *Anterior legs*.—Ventral surface of femur coarsely setigerously punctate except for a very finely punctate anterior area. Forespur parallel sided, curving sharply downward and inward apically, apex broadly rounded, occasionally acute. *Middle legs*.—Coxa impunctate or with a few fine punctures along median longitudinal carina. Ventral surface of femur finely punctate with some coarser setigerous punctures distally. Tibia below with 1-2 distal seta tufts. *Posterior legs*.—Ventral surface of femur finely punctate with at least a few reniform, usually setigerous, punctures distally. Tibia below with 2-3 distal seta tufts. *Total length*.—15-19 mm.

Male armament. In major individuals, the head horn is elongated and evenly curved, gradually tapering or linear, the median prominences are acute, closely approximated without merging, their outer edges evenly converging forward, and the lateral prominences are laminate as usual and are directed forward and slightly outward (fig. 71).

DESCRIPTION OF FEMALE. Similar to male but differing in armament and in the following features: clypeal teeth more prominent and rounded, the emargination between them narrower. Head surface more densely punctate. Occipital margin with transverse setigerous groove often interrupted. Pronotum with a deeply impressed, umbilico-punctate median longitudinal sulcus at base, rest of disc (except along the margin) finely punctate, becoming either coarsely umbilico-punctate or asperate and transversely pitted, or both, on anterior declivity; anterior declivity always with at least some umbilical punctures, especially at sides; posterior and lateral submargins and lateral fossae coarsely umbilico-punctate. Median and posterior tibiae below with 2-4 median seta tufts distally. *Total length*.—14-20 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 16. Occurring throughout the Eje Volcánico Transversal and Sierra Madre del Sur at altitudes of 1500-2000 m. (5000-6500 ft.). The type locality is Oaxaca, Oax. (collected by Boucard) and I have seen specimens collected by Sallé from the state of Oaxaca. Since then it has not been collected so far south. Bates records it from Guatemala, but his determination needs confirmation.

BIOLOGY. Collected under cow dung; otherwise the biology is unknown. Active from May to August.

REMARKS. The numerous paratypes I have examined which bear the name *hintoni* Saylor are perfectly typical *klugi* in every respect. It appears that Saylor described his species through a misapplication of the name *klugi* to the species known as *boucardi* Harold, judging by his discussion. These two species may be confused because the males are armed in a very similar manner, but *boucardi* is always densely granulate on the anterior pronotal surface in the male, whereas *klugi* is punctate, a distinction which Harold overlooked in his original descriptions, preferring to use the fact that *klugi* is punctate on the median dorsal sulcus of the pronotum while the other species is not, a character which will also serve to distinguish them. Furthermore, they do not occur together. *C. klugi* might also be confused with *mexicanus* Matthews and Halffter and *sallei* Harold; however, the latter two species have sinuate anterior pronotal angles.

MATERIAL EXAMINED. 55 males, 60 females.

MEXICO: *Aguascalientes*: Aguascalientes, Aug. 1957 (G. Halffter), 1 ♀ (GH); *Guerrero*: Taxco, Jun. 1937 (Embury), 4 ♂♂ (CAS); *México*: Malinalco, 1780 m., Jul. 1946 (G. Halffter), 1 ♂ (GH); Real de Arriba, Temascaltepec, 6300 ft., 1931, 1932 (H. E. Hinton), 21 ♂♂, 19 ♀♀ (CAS); Tejupilco, Temascaltepec, 1932 (H. E. Hinton), 1 ♀ (CAS); Temascaltepec, Feb. 1931 (G. B. Hinton), 5 ♂♂, 9 ♀♀ (CAS); Tenancingo, 22 May 1956 (G. and V. Halffter), 3 ♂♂, 1 ♀ (GH); 10 km. S Villa Morelos, 26 August 1956 (G. and V. Halffter), 1 ♀ (GH); *Michoacán*: Tuxpan, 15 Jun. 1957 (G. and V. Halffter), 1 ♂ (GH); Zitácuaro, 15 Jun. 1957 (G. and V. Halffter), 4 ♂♂, 17 ♀♀ (GH); *Morelos*: Cuernavaca, 3 Aug. 1938 (L. J. L.), 1 ♂, 1 ♀ (OLC); Jul. 1957 (W. W. Gibson), 2 ♂♂ (IR); 27 Aug. 1957 (G. Halffter), 3 ♂♂, 2 ♀♀ (GH); 3 mi. NW Cuernavaca, 17 Jun. 1959 (H. E. Evans), 6 ♂♂, 5 ♀♀ (CU); Tepoztlán, 10 Jun. 1951 (G. Halffter), 1 ♀ (GH); *Oaxaca*: Capulálpam [2000 m.] (Sallé), 1 ♂ (BM); Juquila [2000 m.] (Sallé), 1 ♀ (BM); *Puebla*: 1 mi. N Atlixco, 29 Jun. 1955 (U. Ks. Mex. Exp.), 1 ♀ (UKs); *Veracruz*: Jalapa (Hoegel), 1 ♀ (USNM).

Copris klugi sierrensis n. subsp.

Holotype: 3 mi. NE Santa María de los Angeles, Jalisco, Mexico, 17 July 1954 (R. H. Brewer), ♂; California Academy of Sciences.

DESCRIPTION. This form is distinguishable primarily by its proportionately smaller horn in the male. When the horn height is plotted against femoral length for all specimens of the species (fig. 6) it is seen that this form falls along a significantly different

line from that followed by the more southern subspecies. This form differs further in that there is a faint sclerotized longitudinal band on the dorsal surface of the male parameres. The females are indistinguishable from *k. klugi*.

DISTRIBUTION. Fig. 16. The Sierra Madre Occidental from Jalisco to Chihuahua at altitudes of 1380–2600 m. (4500–8500 ft.). In Durango, where the closely related *moechus* Leconte occurs, *k. sierrensis* appears to undergo an altitude displacement by that species, *moechus* being found here at altitudes of up to 2300 m. (7500 ft.), whereas *k. sierrensis* is found only at 2500 m. or higher in this region.

BIOLOGY. Unknown.

REMARKS. Means for distinguishing this form from the closely related and sympatric *moechus* Leconte are discussed under the latter species. The females of *klugi* invariably show at least a few umbilical punctures amid the rugosities on the anterior pronotal face; this character is not shared by other females in the complex.

MATERIAL EXAMINED. 23 Males, 17 females.

MEXICO: *Chihuahua*: 20 mi. SW Camargo, 4500 ft. 13 Jul. 1947 (Michener), 1 ♂ (AMNH); Namiquipa (W. F. Foshag), 1 ♀ (USNM); *Durango*: 6 mi. NE El Salto, Durango Dist., 8500 ft., 10 Aug. 1947 (Gertsch), 1 ♂ (AMNH); Las Adjuntas, 8500 ft., 8 Jun. 1953 (R. K. Selander), 1 ♂ (IR); Otinapa, 8200 ft., 11 Aug. 1947 (Gertsch), 1 ♂ (AMNH); *Jalisco*: 8 mi. S. Guadalajara, 28 Sep. 1954 (F. X. Williams), 2 ♂♂ (IR); 3 mi. NE Santa María de los Angeles, 6200 ft., 17 Jul. 1954 (R. H. Brewer), 6 ♂♂, 3 ♀♀ (CAS); *Zacatecas*: ?Laguna Balderrama, 8200 ft., 7 Jul. 1954 (R. H. Brewer), 9 ♂♂ (CAS); Sain Alto, 7000 ft., 14 Aug. 1947 (Cazier), 1 ♂ (AMNH); 10 mi. NW Sombrerete, 7700 ft., 1 Jul. 1954 (R. H. Brewer), 1 ♂, 13 ♀♀ (CAS).

Copris moechus Leconte

Copris moecha Leconte, 1854, Proc. Acad. Nat. Sci. Philadelphia VII: 222 [type: Camp 14*]; Museum of Comparative Zoology]; Leconte, 1858, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, IV: 9–42 (distr.); Horn, 1873, Trans. American Ent. Soc. IV: 42–51 (key and descr.); Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 255 (key).

* I have not been able to determine the location of "Camp 14". This refers to the United States and Mexican Boundary Commission explorations of 1850–1853 during which one member of the expeditions, Dr. Thos. H. Webb, made "large collections . . . in the region between the Rio Grande and the Colorado River of California, chiefly in the valley of the Gila" (Leconte, 1858). Leconte in the

Copris clavicornis Matthews and Halffter, 1959, Ciencia XVIII(9-10): 191-194 [type: 100 km W of Sta. Bárbara, Chih.; American Museum of Natural History]; Matthews, 1959, Ciencia XIX(6-7): 136 (key and distr.). **New synonymy.**

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus with two low angular teeth and a U- or V-shaped notch between them, not cutting through margin. Upper surface of head densely, evenly punctate, the punctures simple, with a basal impunctate area between eyes and horn, and behind both. Posterior oblique carina reduced. Occipital margin with transverse setigerous groove interrupted into three sections, the latter ones displaced forward and partly overlapping the median. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed. Anterolateral angles obtuse, lateral margin curved inward slightly behind origin of lateral carina. Lateral carina sharp, issuing from margin. Anterior margin not forming any median point or angle. Dorsal median longitudinal sulcus complete and impressed, sparsely umbilico-punctate. Puncturation of pronotum very variable, as follows: basal part of disc shallowly punctate, the punctures usually simple, or impunctate; rest of disc densely punctate, the punctures usually simple; posterior and lateral submargins, lateral fossae, and depressions between median and lateral prominences coarsely umbilico-punctate; the anterior surfaces may be entirely asperate (as in the holotype of *clavicornis*) or more usually both asperate and punctate, the punctures simple or umbilical, the rugosities and punctures always very dense (one specimen seen was densely umbilico-punctate over the entire pronotum, without asperation). Anterior prosternal margin with a broad, low, rounded median lobe (no median tooth); sternellum moderately punctate. Median lobe of metasternum impunctate but with some faint punctiform impressions laterally, or umbilico-punctate anteriorly; median longi-

latter work places the type locality of *C. moechus* in Arizona, while Horn (1873) places it erroneously in Texas. However, a reading of the personal narrative of the leader of the Commission (Bartlett, 1854) reveals that two additional expeditions were carried out: one from the headquarters at the "Copper Mines" (Santa Rita del Cobre, Chih., now Santa Rita, N.M.) to Fronteras and Arispe, Sonora, the other from El Paso south to Chihuahua, Chih. and thence southeast to Saltillo, Coah., and Monterrey, N.L. Dr. Webb took part in both of these and it was almost certainly during the latter expedition, which passed right through the presently known range of *moechus*, that the type specimen was collected. This places the type locality in Chihuahua, probably near the capital, and this species cannot be considered as occurring within even the present boundaries of the United States.

tudinal impressed line complete. *Elytra*.—8th stria incomplete, disintegrating at posterior angle; 9th stria arising about halfway down elytron; 10th stria complete. Striae closely punctate, the punctures transverse, separated by a distance equal to about their width. Interstriae slightly convex, very finely punctate, appearing smooth. *Abdomen*.—Pygidium completely margined, densely umbilico-punctate. *Anterior legs*.—Ventral surface of femur densely and coarsely setigerous-punctate on posterior longitudinal half, finely punctate on anterior half. Forespur relatively straight and parallel-sided, bluntly rounded and sometimes slightly dilated apically. *Middle legs*.—Coxa finely punctate along median longitudinal carina, occasionally with a very few large setigerous punctures along outer edge. Ventral surface of femur finely punctate with a few coarser setigerous punctures distally. Tibia below with 1-2 distal median seta tufts. *Posterior legs*.—Ventral surface of femur finely punctate, more coarsely so distally, with or without stigerous punctures. Tibia below with 2-3 distal median seta tufts. *Total length*.—15.5-20 mm.

Male armament. In major males the head horn is elongated and slightly bent, dilated transversely at the apex, and the pronotal prominences are produced, the median ones closely approximated, acute, not at all divergent but not merging, and directed slightly upward, the lateral ones laminate and directed forward parallel to the long axis or slightly divergent (fig. 81).

DESCRIPTION OF FEMALE. Similar to male but differing in armament and in the following features: clypeal teeth rounded, more prominent, flanking a broader, U-shaped notch. Pronotum punctate on upper part of disc and sides below lateral carina, umbilico-punctate along posterior submargin and in lateral fossae, densely granulate or asperate elsewhere, especially on anterior declivity, which never shows any punctures or depressions. Median longitudinal sulcus impunctate and impressed only on superior part of disc. Both median and posterior tibiae with 2-3 distal seta tufts below. *Total length*.—13-21 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 16. The mountains of Southern Chihuahua and Northern Durango at altitudes of 1520-2420 m. (5000-8000 ft.).

BIOLOGY. Unknown.

REMARKS. This species is extraordinarily variable in the puncturation of the anterior pronotal face in the male, which ranges all the way from being completely rugose (without punctures) to completely punctate. Of the more than 90 male specimens examined, however, only one was completely punctate (without asperation). Possibility for confusion exists in attempting to separate the punctate males of this species from *arizonensis* Schaeffer and

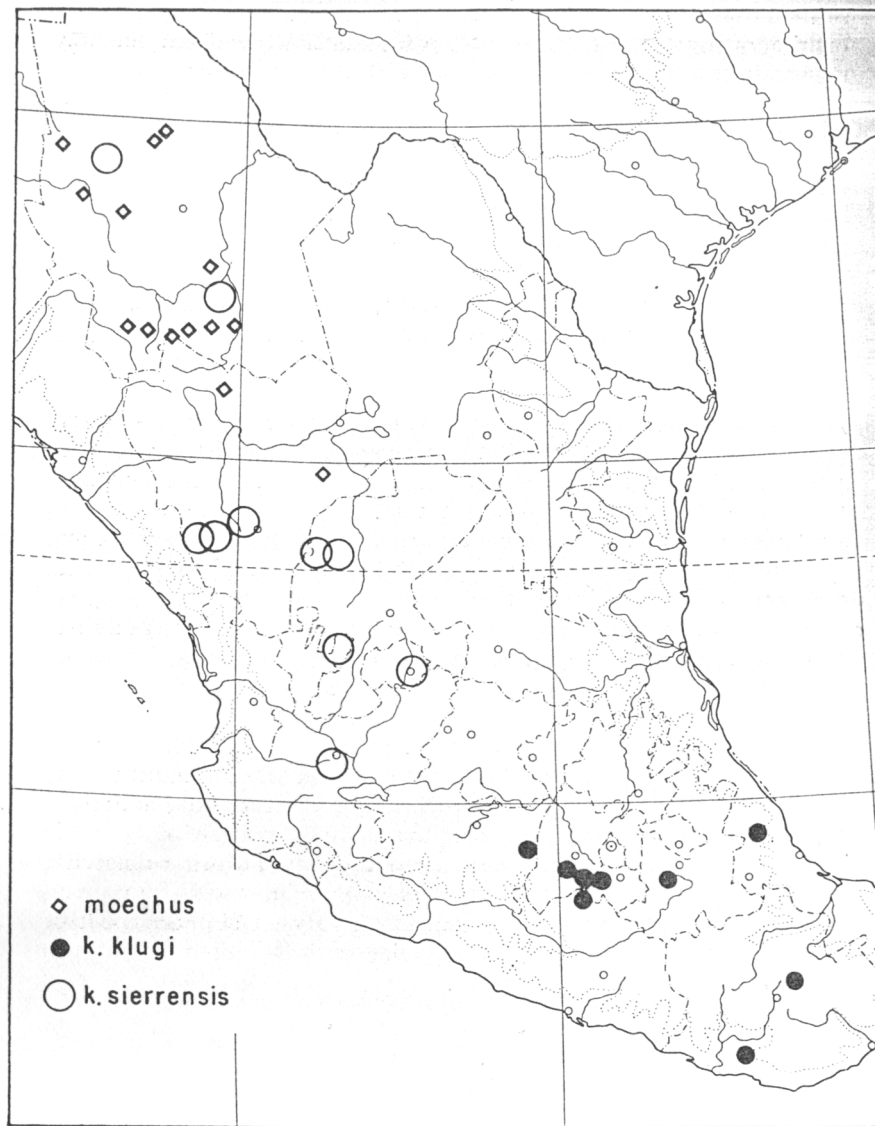


Fig. 16. Distribution of the *armatus* complex, II. Base map reproduced by permission of the University of Chicago.

klugi Harold, both of which occur in the same area. *C. arizonensis* may immediately be told by its very shallow, arcuate median clypeal emargination, acute forespur, and fully complete 8th elytral stria. With regard to the latter species, difficulty may be encountered, since *klugi* and *moechus* are very closely related. However, *klugi* is never rugose or asperate on the anterior pronotal surface, but usually relatively sparsely punctate (sometimes almost impunctate). *C. moechus*, when (very rarely) punctate exclusively here, is very densely so. There also appears to be a geographical or altitude separation between the two species; I have not seen both from the same locality. In Durango, the American Museum Expedition collected *moechus* exclusively at altitudes of up to 8000 ft. (2430 m.) and *klugi* exclusively at 8200 ft. (2500 m.) and higher.

Upon recently examining the type of this name I was very surprised to find that it belonged to this Mexican species, which had just been redescribed under the name *clavicornis* Matthews and Halffter. The common Arizona species which has gone under the name *moechus* for a very long time is here described as new under the name *lecontei* n. sp. There can be little doubt that the specimen in the Leconte Collection labelled as the type of this species actually is such, since it bears the number "14" corresponding with the type locality given as "Camp 14".

MATERIAL EXAMINED. 93 males (including holotype) and 126 females.

MEXICO: *Chihuahua*: Agua Caliente, Sta. Bárbara Dist.; Buena Vista; Catarinas; Cuevas, Matamoros Dist.; Gaborachic; 8 mi. S Gallego; 12 mi. W Gran Morelos; 10 mi. N Jiménez; Madera; Madera Chic; 8 mi. W Matachic; Naica; Parral; 15 mi. E Parral; 2 mi. W Pedernales; Primavera; Salaices; San José Babicora; Santa Bárbara; Km. 36 Sta. Bárbara-Ojito; 63 mi. W Sta. Bárbara; Valle de Olivos; *Durango*: Encino; Las Puentes; San Isidro, Cuencamé Dist.

Copris boucardi Harold

Copris boucardi Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 497-498 [type: Juquila, Oax.; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.-Amer., Coleop. II, 2, p. 54, 1889, Suppl., p. 387 (distr.); Matthews, 1959, Ciencia XIX(6-7): 136 (key and distr.).

DESCRIPTION OF MALE *Head*.—Armed. Clypeus with two barely perceptible teeth, the margin between them very shallowly emarginate with a slightly deeper median notch which is sometimes absent. Posterior angles of genae very acute. Upper surface of head closely punctate, the punctures simple, except for impunctate areas around eyes and behind horn. Posterior oblique carina developed, sharp. Occipital margin with transverse setigerous groove interrupted into three parts, the lateral sections displaced forward and partly overlapping median one. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed. Anterolateral angles subquadrate, margin behind them almost straight. Lateral carina sharp, not issuing from margin anteriorly. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus distinct, complete, umbilico-punctate at least anteriorly. Puncturation of pronotum as follows: very finely punctate, appearing smooth and shiny, over entire base; lateral surfaces shallowly punctate or ridged; anterior declivity and inside surface of lateral prominences granulate or asperate; posterior submargin, dorsal sulcus anteriorly and also sometimes for its entire length, lateral fossae, and cavities between median and lateral prominences (even in minor males) umbilico-punctate. Anterior prosternal margin variable, either without any median tooth, with a rounded one, or bidentate; sternellum moderately punctate. Median lobe of metasternum with a few punctiform impressions laterally and anteriorly; median longitudinal impressed line usually complete. *Elytra*.—8th stria incomplete, disintegrating about halfway down elytron; 9th stria arising about halfway down; 10th complete. Striae finely but distinctly punctate, the punctures round and separated by a distance equal to two or more times their diameter. Interstriae sparsely and very finely punctate, appearing smooth, and slightly convex. *Abdomen*.—Pygidium completely margined, moderately umbilico-punctate, the punctures small. *Anterior legs*.—Ventral surface of femur coarsely setigerous-punctate on posterior (upper) longitudinal half, impunctate on anterior half. Forespur straight in dorsal view, narrowing apically, the apex broadly rounded. *Middle legs*.—Coxa impunctate. Femur below distinctly setigerous punctate only at distal end, impunctate elsewhere. Tibia below with 1-2 distal seta tufts. *Posterior legs*.—Ventral surface of femur entirely finely punctate, without setigerous punctures. Tibia with 0-3 seta tufts distally below. *Total length*.—19-23.5 mm.

Male armament. Minor and medium males have median pronotal prominences which are approximated but not extremely so. Not until well developed males are examined is the characteristic nature

of the median pronotal prominences seen. In these individuals, the median prominences are more or less pyramidal, very closely approximated, and directed sharply upwards (fig. 73). The head horn is gently curved, not bent, in some instances almost straight, and in other instances massive for most of its length when seen from the side, then abruptly narrowing apically. The lateral pronotal prominences are directed somewhat outward in dorsal view.

DESCRIPTION OF FEMALE. Similar to male, but differing in armament and in the following features: clypeal teeth more prominent, rounded and approximated, with a shallow notch between them. Dorsal longitudinal sulcus of pronotum impressed only basally or entirely very faint. Puncturation of pronotum as follows: impunctate on disc, shallowly punctate on rest of base, anterior half of pronotum densely granulate; umbilical punctures are present only along posterior submargin and in lateral fossae. *Total length*.—19–21 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 15. Found on the volcanoes of northern Central America and Chiapas at altitudes of 1000–1200 m. (3300–4000 ft.). The type locality is Juquila in southern Oaxaca and I have seen a female ascribable to this species from Omilteme, Guerrero (also cited by Bates), so it is probable that it occurs in Mexico south of the depression of the Río Balsas as well. The British Museum has two male specimens labelled “Venezuela”, but this record is certainly erroneous.

BIOLOGY. Unknown.

REMARKS. This species is very closely related to *aspericollis* Gillet occurring in the same area, minor males and females of the two species being difficult to distinguish (see key). These two species provide a good example of how two sympatric, closely related species may differ radically in male secondary sexual characters. The apices of the median pronotal prominences of *boucardi* are very closely approximated in developed males, those of *aspericollis* being quite widely divergent (figs. 73, 74). Its separation from the superficially similar *klugi* Harold is discussed in the remarks under the latter species.

MATERIAL EXAMINED. 13 males, 16 females.

MEXICO: *Chiapas*: Ocosingo, 1200 m., Jun.–Sep. 1917 (M. del Toro), 1 ♂ (GH); Volcán de Tacaná (Coffee belt), 30 Sep. 1956 (V. Aguilar), 1 ♂, 2 ♀♀ (GH); 7500 ft., 4 Apr. 1939 (F. Brodkorb), 1 ♀ (USNM); *Guerrero*: Omilteme [W of Chilpancingo], 8000 ft., Jul. (H. H. Smith), 1 ♀ (BM).

GUATEMALA: *Alta Vera Paz*: Senahú [1000 m.] (Paul Haase), 2 ♀♀ (USNM); *Chimaltenango*: Capetillo [Valley between volcanoes Agua and Fuego, 17 Apr.-12 May, 1879] (Champion), 1 ♀ (BM); *national record only*: (Sallé) 1 ♂ (BM); 3 ♂♂ (AMNH, CAS).

EL SALVADOR: *Santa Ana*: Monte Cristo, 7-9 May, 1958 (O. L. Cartwright), 5 ♂♂, 9 ♀♀ (USNM).

Copris aspericollis Gillet

Copris aspericollis Gillet, 1910, Not. Leyden Mus. XXXII: 3 [type: Central America; Musée Royal d'Histoire Naturelle, Brussels]; Matthews, 1959, Ciencia XIX(6-7): 136 (key and distr.).

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus with two very low teeth, the margin between them very shallowly emarginate with a deeper median notch not cutting through the margin. Upper surface of head strongly and densely punctate, the punctures shallow and simple, disappearing at extreme base of head, posterior oblique carina distinct. Occipital margin with transverse setigerous groove complete but somewhat bent at middle of each side. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed. Anterolateral angles subquadrate in developed specimens, rounded in undeveloped ones, lateral margin slightly inwardly curved behind origin of lateral carina. Lateral carina sharp, almost issuing from margin anteriorly. Anterior margin of pronotum not forming any point or angle medially. Median longitudinal sulcus very faint, almost wanting. Puncturation of pronotum as follows: upper part of disc almost impunctate, the longitudinal sulcus impunctate, rest of upper surface and lateral surfaces punctate, the punctures simple; anterior declivities densely and coarsely granulate or asperate; posterior submargin and lateral fossae umbilico-punctate. Anterior prosternal margin without any median lobe or with a rounded low one; sternellum densely punctate. Median lobe of metasternum with numerous punctiform impressions laterally and anteriorly; median longitudinal impressed line complete. *Elytra*.—8th stria incomplete, disintegrating posteriorly; 9th stria arising about a third of the way down the elytral length; 10th complete. Striae on dorsal part of elytra distinctly punctate, the punctures slightly transverse and separated by a distance equal to once or twice their width; striae 7, 8, and 9 less punctate but the punctures can still be made out. Interstriae very slightly convex, impunctate. *Abdomen*.—Pygidium moder-

ately umbilico-punctate, the punctures very small; pygidial margin usually complete, sometimes effaced at apex. *Anterior legs*.—Ventral surface of femur coarsely setigerous-punctate on posterior (upper) longitudinal half, more finely punctate on anterior half. Forespur almost straight in dorsal view, tapering slightly to a rounded apex, curved down at apical third. *Middle legs*.—Coxa impunctate. Femur below finely punctate, with a few, usually setigerous, coarse punctures distally. Tibia below with 2–3 distal median seta tufts. *Posterior legs*.—Femur like that of middle legs. Tibia with 1–2, usually one, seta tuft distally on ventral surface. *Total length*.—21–21.5 mm.

Male armament. The head horn is not very tapering but comes to a rather abrupt end, and is noticeably bent in the middle (fig. 74). The median thoracic prominences are slightly divergent and conical, their lower surfaces not flattened, and directed horizontally in lateral view. The lateral prominences are laminate, rather acute, and directed forward, their dorsal edges parallel in dorsal view.

DESCRIPTION OF FEMALE. Similar to male, but differing in armament and in the following features: clypeal teeth more prominent, rounded, and approximate, with a V-shaped notch between them. Pronotum more extensively granulate, the granules extending from face over sides and anterior surface of disc, which takes on an asperate appearance. Base of disc finely punctate; umbilical punctures are confined to posterior submargin and lateral fossae. Pygidium more finely punctate and always completely margined. *Total length*.—21–23.5 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Known only from the area around Guatemala City at altitudes of 340–1700 m. (1100–5600 ft.).

BIOLOGY. Feeds on cow dung. Some aspects of nidification are discussed on p. 31.

REMARKS. This species is poorly represented in collections, probably reflecting the generally uncollected nature of Central America rather than any rarity of the species. I collected it in a cow pasture on the road southeast from Guatemala City, indicating that it probably is abundant in central Guatemala, but I did not encounter it again elsewhere in Central America. It is most closely related to *boucardi* Harold (see remarks under that species) and to *subpunctatus* Gillet, which it strongly resembles in habitus, being however much more strongly punctate than the latter species. It also differs from the latter in the shape of the male median pronotal prominences, which are conical in *aspericollis* and flattened at the apices in *subpunctatus*.

MATERIAL EXAMINED. Seven males, seven females.

GUATEMALA: *Escuintla*: Escuintla [338 m., Feb. or Apr. 1881] (Champion), 1 ♂, 1 ♀ (BM); *Guatemala*: 18 km. SE Guatemala City, 610 m., 22 Jul., 1958 (Neff and Matthews), 1 ♂, 3 ♀♀ (EGM); S. José Pinula [1500-2000 m.] May, 1924 (W. M. Mann), 1 ♂ (USNM); *national record only*: 1 ♂, 1 ♀ (CAS); 3 ♂♂, 2 ♀♀ (MCZ).

Copris subpunctatus Gillet, new combination

Copris aspericollis var. *subpunctatus* Gillet, 1910, Not. Leyden Mus. XXXII: 3 [type: Costa Rica; Musée Royal d'Histoire Naturelle, Brussels].

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus with two very low teeth, the margin between them very shallowly angular with a deeper central notch not cutting through the margin. Upper surface of head strongly and densely punctate, the punctures shallow and simple, except for an impunctate area at base of head and about the eyes. Posterior oblique carina distinct. Occipital margin with transverse setigerous groove complete but somewhat bent at middle of each side. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed. Anterolateral angles acute in developed specimens, subquadrate or rounded in less developed ones, lateral margin slightly inwardly curved behind the angle. Lateral carina sharp, not issuing from margin in developed specimens, almost issuing from it in less developed ones. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus very faint, obsolescent. Punctuation of pronotum as follows: upper part of disc almost impunctate, longitudinal sulcus impunctate; rest of upper surface of pronotum and lateral surfaces punctate, the punctures simple or, in developed specimens, umbilical on anterior part of disc; anterior declivities densely and coarsely granulate and asperate; posterior submargin and lateral fossae umbilico-punctate; in the most developed individuals, the cavities between the median and lateral prominences are grossly annular-punctate or cicatricial. Anterior prosternal margin with a broadly truncate or rounded median lobe; sternellum concave, densely punctate. Median lobe of metasternum impunctate or more usually with punctiform indentations along the edges anteriorly; median longitudinal groove complete. *Elytra*.—8th stria incomplete, disintegrating at posterior angle; 9th arising about a third of the way down elytron; 10th complete. Striae practically impunctate, the punctures repre-

sented by slight widenings of the fine strial line; stria 8 impunctate. Interstriae very slightly convex, impunctate. *Abdomen*.—Pygidium moderately umbilico-punctate, the punctures very small; pygidial margin usually complete, sometimes effaced at apex. *Anterior legs*.—Ventral surface of femur with coarse setigerous punctures on posterior longitudinal half, more finely punctate on anterior half. Forespur almost straight in dorsal view, tapering slightly to a rounded apex, curved downward for apical third. *Middle legs*.—Coxa impunctate. Ventral surface of femur finely punctate. Tibia below with 2-3 distal seta tufts. *Posterior legs*.—Femur as described for middle legs. Tibia below with 1-2, usually one, seta tuft distally. *Total length*.—17-24.5 mm.

Male armament. In extremely developed specimens, the head horn is massive and sharply bent in the middle, the disc is humped behind the median pronotal prominences, and these are divergent in dorsal view and directed slightly upward in lateral view (fig. 72), their lower surfaces being flattened or even slightly excavate. The lateral pronotal prominences are distinctly directed outward in dorsal view.

DESCRIPTION OF FEMALE. Similar to male, differing in armament and in the following features: clypeal teeth more prominent, rounded, and approximate, with a V-shaped notch between them; pronotum more extensively granulate, the granules extending from face over sides and anterior surface of disc, which takes on an asperate appearance; base of disc finely punctate; umbilical punctures are confined to posterior submargin and lateral fossae. Pygidium more finely punctate and completely margined. *Total length*.—22-25 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 15. Known only from the environs of San José and Irazú Volcano, Costa Rica, and Chiriquí Volcano, Panamá, at altitudes of 1000-2000 m. (3300-6600 ft.).

BIOLOGY. Unknown. All specimens appear to have been collected at light, from October to June.

REMARKS. This is certainly one of the most striking and beautiful species of the genus, the male achieving an extreme in horn development and the reduced puncturation of the integument imparting a glossy sheen to the body surface. It is here elevated to species rank primarily because it differs from *aspericollis* Gillet in the shape of the male median pronotal prominences (see p. 133). Both sexes are most easily told from *aspericollis* by the obsolescent elytral strial punctures (I have seen no intermediate specimens), but in all other non-dimorphic characters it is apparently identical

with the Guatemalan species.

MATERIAL EXAMINED. 19 males, nine females.

COSTA RICA: *Alajuela*: Desengaño, 2000 m. (P. Biolley), 1 ♂ (CM); *Cartago*: Guayabillos, SW slope Irazú, 2200 m., Mar. 1933 (F. Nevermann), 2 ♂♂ (USNM); Irazú Volcano, 6-7000 ft. (H. Rogers), 1 ♀ (USNM); south slope, 2800-3000 m., Sep. 1931 (F. Nevermann), 1 ♂ (USNM); 1625 m., 15 May 1951 (O. L. Cartwright), 2 ♂♂ (USNM); Pacayas, SE slopes of Volcán de Irazú, 6000-6250 ft., 6 Oct. 1923 (Rehn and Lankester), 2 ♀♀ (PAS); *Heredía*: Río Sucio (H. Rogers), 1 ♂, 2 ♀♀ (AMNH, MCZ); *Limón*: Hamburgfarm, 30 Mar. (C. P. Dodge), 1 ♀ (MCZ); *San José*, 1000-1200 m., May 1921, 27 Apr. 1922, 1 Dec. 1923, 15, 18 May 1925, May, Dec. 1931, 18 Apr. 1932, 17 May 1933, 10 Jan., 15 Dec. 1934 (F. Nevermann), 11 ♂♂, 4 ♀♀ (USNM); 1160 m., Jun. 1943 (Biolley), 1 ♂, 2 ♀♀ (CM).

PANAMA: *Chiriquí*: Chiriquí, 2 ♂♂, 1 ♀ (CM).

Complex 2. The *arizonensis* complex.

Posterior angles of head acute. Anterolateral angles of pronotum obtusely angulate, the lateral margin not sinuate. Forespur with the apex acute and curved inward, strongly so in the male. 8th elytral stria complete. Pygidial margin complete.

One species found in the mountains of Chihuahua and bordering United States territory: *arizonensis* Schaeffer.

Copris arizonensis Schaeffer

Copris arizonensis Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 254-255 [type: Huachuca Mts., Ariz.; United States National Museum]; Matthews, 1959, Ciencia XIX(6-7): 135 (key and distr.).

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus with a broad, very shallow, arcuate emargination without any median notch. Upper surface of head evenly punctate on outer, flattened portions and on horn, impunctate elsewhere; the punctures are shallow and simple except often for some of those on genae, which are umbilical. Posterior oblique carina evident only directly behind eye. Occipital margin with transverse setigerous groove broken into three parts, the lateral ones displaced slightly forward. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed. Anterolateral angles obtuse, the lateral margin

slightly angled out at origin of lateral carina. Lateral carina prominent, issuing from margin anteriorly. Anterior margin of pronotum not forming any median point or angle. Dorsal median longitudinal sulcus incomplete, faint, sometimes wanting. Entire pronotal surface regularly and densely umbilico-punctate, the punctures varying in size, being smallest on convex areas and largest in depressions; highly developed individuals tend to become impunctate on disc. Anterior prosternal margin with a very small median process which is sometimes bidentate; sternellum sparsely and grossly umbilico-punctate. Median lobe of metasternum umbilico-punctate, sometimes only along edges; median longitudinal impressed line usually complete. *Elytra*.—8th stria complete; 9th arising about a third of the way down elytron; 10th complete. Striae closely punctate, the punctures slightly transverse, separated by a distance approximately equal to their width. Interstriae almost flat, very faintly punctate, appearing smooth. *Abdomen*.—Pygidium rather densely and coarsely umbilico-punctate, completely margined. *Anterior legs*.—Ventral surface of femur grossly umbilico-punctate over most of its area, more finely punctate along anterior margin. Forespur curved inward at apex and tapering to a sharp point. *Middle legs*.—Coxa with scattered umbilical punctures on outer face. Ventral surface of femur punctate, the punctures setigerous and larger distally. Tibia with 1-2, usually two, distal seta tufts ventrally. *Posterior legs*.—Femur like that of middle legs. Tibia with 2-3 distal seta tufts ventrally. *Total length*.—14-20.5 mm.

Male armament. Minor individuals have the median pronotal prominences approximated but not merged. With further development they grow forward into a single bifurcate median process (fig. 68). The most developed individuals bear a long, evenly curved head horn which is slightly transversely clavate at the apex, and the median pronotal prominences are seen in side view to be very acute and directed slightly upwards, in dorsal view to be closely approximated with their outer edges parallel or very slightly directed outward. The lateral prominences are directed forward.

DESCRIPTION OF FEMALE. Similar to male, but differing in armament and in the following features: the low clypeal teeth are more closely approximated and the emargination between them is broadly angulate, with no median notch or a very feeble one. Surface of pronotum densely punctate over entire area, the punctures usually entirely umbilical, but some specimens have simple punctures on disc and sides, in which case the anterior area of disc is somewhat ridged. Forespur somewhat less bent apically

and less acute than that of male. *Total length*.—15.5–22 mm.

Female armament. The head horn consists of a prominent transverse process which is apically excavate, its sides sharply



Fig. 17. Distribution of the *remotus* and *arizonensis* complexes. Base map reproduced by permission of the University of Chicago.

divergent apically in front or rear view and recurved backwards in developed specimens. The least developed specimen seen bore a horn with its sides parallel; none were seen with a horn narrowing apically.

DISTRIBUTION. Fig. 17. Known from the Huachuca and Chiricahua mountains of Arizona, the Continental Divide in southern New Mexico, the general region of the Davis and Chisos mountains of Texas, and two highland localities in Chihuahua, at altitudes of 1350–1900 m. (4500–6300 ft.). Perhaps occurring in all intervening highlands, which have not been collected very much.

BIOLOGY. Nothing at all is known of the biology of this species; all specimens for which the collecting method was specified were collected at light. It appears to be active from May to August.

REMARKS. Schaeffer did not designate a holotype for this species. The type collection of the United States National Museum contains two specimens—a male (No. 42,570) and a female. These specimens were entered in 1929 from the Brooklyn Museum and recorded in the record book as cotypes; each bears the label "Huachuca Mts.". The male, a rather worn specimen, is here designated as lectotype of *Copris arizonensis* Schaeffer.

This species stands alone among the American forms not so much because of unusual characters as because of a unique combination of characters found in other complexes. It shares with the *armatus* complex the large size and simple anterolateral angles, with the *remotus*, *fricator*, and *rebouchei* complexes the shape of the forespur and the complete 8th elytral stria, and with the *remotus* complex the shape of the male head. The shape of the female head horn is, however, quite unique.

MATERIAL EXAMINED. 31 males (including lectotype), 22 females.

UNITED STATES: *Arizona*: Cochise Co.: Chiricahua Mts.; Chiricahua Mts., Cave Creek; Southwest Res. Sta. 5 mi. W. Portal; Chiricahua Mts., Painted Cyn Ranch; Huachuca Mts.; Huachuca Mts., Carr Canyon; Huachuca Mts., Garden Canyon; Huachuca Mts., Ramsey Canyon; Palmerlee; *Pima Co.*: Tucson; *Santa Cruz Co.*: Mt. Washington, Nogales; *New Mexico*: Grant Co.: Tyrone, 8 Aug. 1939 (K. Stager), 1 ♀ (AMNH); *Texas*: Big Bend Nat'l Pk.: Basin Area, 5400 ft., 18 May 1959 (Howden and Becker), 1 ♀ (HH); Brewster Co.: Alpine, 15–30 May, 15–30 Jun., 28 Jul., 1–15 Aug., 1926 (O. C. Poling, R. C. Casselbury), 5 ♂♂, 1 ♀ (AMNH); 25 Jul. 1936 (J. G. Gehring), 1 ♂ (MCZ); S. G. Ranch, 26 Jun., 1 ♀ (MCZ); Jeff Davis Co.: Davis Mountains, 28 Jun. 1946 (Van Dyke), 1 ♂, 2 ♀♀ (CAS).

MEXICO: *Chihuahua*: Parral, 16 Jul. 1947 (Spieth), 2 ♂♂ (AMNH); 15 mi. E Parral, 5500 ft., 15 Jul. 1947 (Cazier), 2 ♂♂, 1 ♀ (AMNH); Primavera, 5500–6000 ft., 30 Jun. 1947 (Cazier), 1 ♂ (AMNH); Sta. Bárbara, 6300 ft., 17 Jul. 1947 (Cazier), 1 ♂ (AMNH).

Complex 3. The *remotus* complex.

Posterior angles of head subquadrate or usually acute. Anterolateral angles of pronotum acute, the margin behind them sinuate. Median longitudinal sulcus of pronotum coarsely punctate. Forespur with the apex acute in both sexes. Median coxae with gross umbilical punctures on the outer face. Pygidial margin

complete or not.

Four species found at low to moderate altitudes in Central and Eastern Mexico (and bordering United States territory) and Central America: *remotus* Leconte, *mexicanus* Matthews and Half-ter, *sallei* Harold, and *costaricensis* Gahan.

Copris remotus remotus Leconte

Copris remotus Leconte, 1866, Proc. Acad. Nat. Sci. Philadelphia XVIII: 381 [type: Texas, near the Rio Grande; Museum of Comparative Zoology]; Horn, 1873, Trans. American Ent. Soc. IV: 42-51 (key and descr.); Harold, 1886, Berliner Ent. Zeitschr. XXX: 148 (descr.); Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 255 (key); Lindquist, 1935, Circular U.S.D.A. No. 351, pp. 2-4 (biol.); Matthews, 1959, Ciencia XIX (6-7): 135 (key and distr.).

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus with two remote, very small teeth, the margin between them curved inward in a broad, very shallow arc; no median notch. Posterior angles of genae acute. Upper surface of head entirely punctate, the punctures denser and simple along margin, sparser and umbilical on posterior part of genae and base. Posterior oblique carina reduced. Occipital margin with transverse setigerous groove broken into three parts, the median one devoid of setae. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed. Anterolateral angles acute, immediately followed by an indentation or erosion of margin, indistinct in some specimens; lateral margin angled out at origin of lateral carina. Lateral carina distinct, issuing from margin. Anterior margin usually not forming any median point, but sometimes forming a downwardly directed one and occasionally an upwardly directed one, formed by inner edge of margin. Median longitudinal sulcus distinct, broadly impressed, more coarsely punctured than rest of disc. Puncturation of pronotum as follows: elevated areas of base of pronotum impunctate or very finely punctate, the following areas abruptly, contrastingly, coarsely umbilico-punctate: posterior and lateral submargins, lateral fossae, dorsal longitudinal sulcus in an anteriorly broadening band, and all anterior declivities, including excavations between median and lateral prominences; median anterior face is often impunctate in an area of varying size about median line. Anterior prosternal margin without any median tooth; sternellum regularly, coarsely umbilico-punctate. Median lobe of metasternum coarsely umbilico-punctate anteriorly and

laterally; median longitudinal groove present and complete. *Elytra*.—8th stria complete; 9th arising at anterior third of elytral length; 10th complete. Striae very coarsely, closely punctate, the punctures somewhat transverse and separated by a distance equal to once or twice their width. Interstriae convex, very finely punctate, appearing smooth. *Abdomen*.—Pygidium with margin complete, densely umbilico-punctate. *Anterior legs*.—Ventral surface of femur coarsely punctate on posterior longitudinal half, finely punctate on anterior, with some larger punctures along anterior margin. Forespur linear, somewhat broadened apically, the extreme apex bent inward to a dull point. *Middle legs*.—Coxa with scattered large umbilical punctures on outer face and a few smaller ones on inner face. Ventral surface of femur very finely punctate basally, with coarse setigerous punctures distally. Tibia below with 2-4 median seta tufts. *Posterior legs*.—Femur as described for middle legs. Tibia usually with up to six seta tufts arranged in an irregular row up the ventral surface. *Total length*.—12-15.5 mm.

Male armament. In major males, the head horn is long, evenly arcuate and tapers to a moderately sharp apex, the median pronotal prominences are two remote, slightly diverging, forwardly directed, blunt cones, the apices of which are sometimes a little obliquely compressed and separated from each other by a distance equal to their separation from the lateral prominences, which are laminate, directed forward and a little outward (fig. 78).

DESCRIPTION OF FEMALE. Similar to male, but differing in armament and in the following features: clypeal teeth more prominent and margin between them broadly angulate, not arcuate (there is no median notch, as in the male); nearly all females show a small downwardly directed point at middle of anterior pronotal margin; puncturation of pronotum similar to that of male, with abruptly contrasting smooth and coarsely punctate areas, but the crowded punctures on anterior part of disc and anterior declivity tend to be simple, rather than umbilical; dorsal longitudinal sulcus of pronotum is impressed basally and umbilico-punctate. *Total length*.—14-16 mm.

Female armament. The head horn is transverse but thick. The median pronotal transverse carinae are well separated by a punctate depression, the inner ends of the carinae being sometimes curved up to form two points.

DISTRIBUTION. Fig. 17. Southern Texas, Nuevo León, and northern Tamaulipas in an area centering about the lower Rio Grande (Río Bravo) Valley at altitudes of sea level to 600 m.

(2000 ft.), with one (perhaps inexact) record from Saltillo, Coahuila, at 1589 m. (5200 ft.) and one specimen from Oklahoma. In addition, I have seen two specimens from "Aquilares", Arizona, a place I cannot find on any map. The presence of this species in Arizona is very doubtful.

BIOLOGY. Lindquist gives an excellent account of the nidification of this species, which is summarized on pp. 29-30. It comes to light and is found under cow dung.

REMARKS. The contrasting smooth and coarsely punctate areas on the pronotum serve to distinguish this species from all others which occur in the United States. For some reason it is confused with *lecontei* n. sp. in collections although the species are quite dissimilar and do not, apparently, occur together. Aside from showing the above mentioned characteristic, it is more coarsely punctate than *lecontei*, the males have a very shallow clypeal emargination, relatively blunt forespurs, a more sharply curved horn, and the median pronotal prominences are divergent. It is closely related to *costaricensis* Gahan, with which it shares the type of puncturation, but from which it may easily be distinguished by the complete pygidial margin.

MATERIAL EXAMINED. 25 males (including holotype), 17 females.

UNITED STATES: *Oklahoma:* Comanche Co.: Wichita N.F., 10 Sep. 1930 (T. H. Hubbell) 1 ♂ (USNM); *Texas:* Bexar Co.: San Antonio, 21 Dec. 1942 (E. S. Ross), 1 ♀ (CAS); Cameron Co.: Port Isabel, 23-27 Jun. 1956 (H. E. Evans and E. G. Matthews), 1 ♀ (EGM); Comal Co.: (C. Schaeffer), 1 ♂ (USNM); Dimmit Co.: Tex, Exp. Sta. Light trap, 4, 17 Mar., 12 Aug. 1933, 14 Mar., 24 Apr. 1934 (S. E. Jones), 4 ♂♂, 1 ♀ (OLC); Duval Co.: Realtos, Jul. 1939 (K. Stager), 2 ♀♀ (AMNH); Kleberg Co.: Kingsville (C. T. Reed), 2 ♂♂, 3 ♀♀ (CU); Lee Co.: Fedor, June, 1 ♂ (CM); Maverick Co.: Eagle Pass, May 1914, 1 ♂ (CM); Nueces Co.: Corpus Christi, 28 Jun. 1942 (E. S. Ross), 1 ♂ (CAS); Uvalde Co.: Sabinal, 9 Jun. 1910 (F. C. Pratt), 3 ♀♀ (USNM); Uvalde, 11 Apr., 24 Jun., 1 Aug. 1931 (A. W. Lindquist), 3 ♂♂, 1 ♀ (USNM); state record only: 8 ♂♂, 1 ♀ (USNM, CM).

MEXICO: *Coahuila:* Saltillo, 6 Dec. 1954 (J. Moncada), 1 ♀ (GH); *Nuevo León:* Monterrey, 6 Oct. 1946, 2 ♂♂ (GH); 5 Mar. 1955 (Alfonso Terraza), 1 ♀ (GH); 24 Mar. 1957 (B. Moscoso), 1 ♂, 1 ♀ (GH); *Rancho Presa Nueva*, Jun. 1934 (H. A. Howies), 1 ♀ (USNM); *Tamaulipas:* 8 mi E of Padilla, 19 Dec. 1941 (Cantrell-Friauf), 1 ♂ (USNM).

Copris remotus dicyrtus Matthews and Halffter
new combination

Copris dicyrtus Matthews and Halffter, 1959, Ciencia XVIII (9-10): 198-200 [type: Ciudad Victoria, Tamps.; United States National Museum]; Matthews 1959, Ciencia XIX(6-7): 135 (key and distr.).

DESCRIPTION. This subspecies is a southern form of the typical *remotus*. It differs from *r. remotus* only in the nature of the lateral pronotal prominences of the male, which are completely absent in the holotype (while the median prominences are well developed) and curiously reduced to tubercles in the other male, accentuating a tendency seen in the typical form. The other differences cited in the original description of *dicyrtus* have not stood up when additional specimens were found; consequently this form is here reduced to subspecies level.

MATERIAL EXAMINED. Holotype and allotype, one additional male and two females.

MEXICO. *Tamaulipas*: Ciudad Victoria, 1, 3 Jun. 1950 (G. Halffter), 1 ♂, 1 ♀ (USNM); 47 km. S Ciudad Victoria, Rt. 1, km. 659, 900 ft., 5 Jul. 1948 (W. Nutting), 1 ♂, 2 ♀♀ (USNM).

Copris mexicanus Matthews and Halffter

Copris mexicanus Matthews and Halffter, 1959, Ciencia XVIII(9-10): 194-196 [type: Tancitaro, Mich.; California Academy of Sciences]; Matthews, 1959, Ciencia XIX(6-7): 135 (key and distr.).

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus bidentate, the teeth remote and very small, with a very shallow, obtuse median notch. Posterior angles of genae acute. Upper surface of head closely punctate except for base and area between eyes, which are smooth; some of punctures on genae are umbilical, the rest simple. Posterior oblique carina prominent but rounded. Occipital margin with transverse setigerous groove broken into three partially overlapping sections. Demarcation between gula and submentum arcuate with a suggestion of median angulation. *Thorax*.—Pronotum armed. Anterolateral angles subquadrate with point of angle made salient by an inward curve of lateral margin immediately behind it, the margin curving out again at origin of lateral carina. Lateral carina sharp. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus present only on disc proper, impressed, umbilico-punctate, the field of punctures

broadening anteriorly. Puncturation of pronotum as follows: base and disc glassy smooth, impunctate except for dorsal sulcus and submargin, which are umbilico-punctate; entire submargin, lateral fossae, depressions between prominences, and median anterior face rather sparsely umbilico-punctate; no simple punctures on pronotum except for a few on outer surface of lateral prominences. Anterior prosternal margin without any median tooth; sternellum sparsely punctate. Median lobe of metasternum with umbilical punctures anteriorly and laterally; median longitudinal groove complete. *Elytra*.—8th stria complete; 9th arising at about anterior third of elytral length; 10th complete. Striae closely and distinctly punctate, the punctures transverse, separated by a distance about equal to their width. Interstriae slightly convex, impunctate. *Abdomen*.—Pygidium moderately umbilico-punctate, completely margined. *Anterior legs*.—Ventral surface of femur with coarse setigerous punctures on posterior longitudinal two thirds, very finely punctate on anterior third. Forespur linear to apical third, where it is curved downward and inward and tapers to a fairly acute point. *Middle legs*.—Coxa with a few large umbilical punctures on middle of outer face. Ventral surface of femur with many coarse setigerous punctures distally, some regularly distributed, fine punctures over rest of surface. Tibia below with 2-3 distal seta tufts. *Posterior legs*.—Femur as described for middle legs. Tibia below with 2-4 distal seta tufts arranged in a row along length of tibia. *Total length*.—16-16.5 mm.

Male armament. In the four specimens examined, the head horn is rather straight with the sides evenly tapering. The median pronotal prominences are acute and closely approximated, their outer edges evenly converging forward, their apices not turned upward in lateral view. The lateral pronotal prominences are laminate, not well developed, their dorsal edges sloping downward anteriorly in lateral view, parallel in dorsal view (fig. 67).

FEMALE. Unknown.

DISTRIBUTION. Fig. 17. Known only from three localities in Michoacán on the northern slope of the depression of the Río Balsas.

BIOLOGY. Unknown.

REMARKS. This species is closely related to *costaricensis* Gahan and *sallei* Harold. From the former it may be told by its complete pygidial margin and by the lack of an acute median tooth on the anterior pronotal margin. It differs further in that the median pronotal sulcus is less coarsely punctate than in *costaricensis* and the male median pronotal prominences apparently do not merge. It is difficult to estimate the degree of relationship of this species (known only from the males) to *sallei* Harold (of which I have

seen only females). There is little doubt that they are distinct species, not only because of the difference in geographical distribution, but also because the *sallei* specimens I have seen differ from *mexicanus* in possessing blunt (not curved and acute) forespurs, a median tooth on the anterior pronotal margin, and an incomplete 8th elytral stria. None of these differences is associated with secondary sexual characters in this complex.

MATERIAL EXAMINED. Holotype, male paratype, and two additional males.

MEXICO: *Michoacán*: Tancítaro, 1800 m., 24 Jun. 1941 (Hoogstraal and Haag), 1 ♂ (CAS); Huétamo, 2100 m., 8 Jul. 1947 (T. H. Hubbell), 1 ♂ (UMich); Jct. Hwy. 4 and Huétamo rd. 15 mi. E of Morelia, 2100 m., 8 Jul. 1947 (T. H. Hubbell), 2 ♂♂ (USNM).

Copris sallei Harold

Copris sallei Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 496-497 [type: Córdoba, Ver.; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.—Amer., Coleopt. II, 2, p. 54 (distr.); Matthews, 1959, Ciencia XIX(6-7): 135 (key and distr.).

DESCRIPTION OF MALE. Given by Baron von Harold as follows: Oblongus, clypeo obtuse bidentato, thoracis angulis anticis acutiusculis postice sinuatis, elytris fortiter punctato-striatis, punctis inter se approximatis. Mas: Cornu erecto fortiter et fere subangulatum recurvo; thorace quadridentato, dentibus mediis approximatis, sulci fortiter punctato et profundo usque ad basin prolongato divisus, foveolis lateralibus et excavationibus grosse umbilico-punctatis. . . . Long. 13-17 mill.

An illustration of a developed male specimen which, in my opinion, has been correctly determined to be this species is given by Bates (1887, plate 3, fig. 12, 12a). This figure shows the clypeal margin to be remotely bidentate, with the teeth minute and pointed, and the margin between them very shallowly, angularly emarginate; the hind angles of the head are acute; the fospur is straight, and the median pronotal prominences are approximated but not merging.

DESCRIPTION OF FEMALE. *Head*.—Armed. Clypeus with two prominent, subangular, approximated teeth separated by a shallow, rounded median notch not cutting through margin. Posterior angles of genae subacute. Upper surface of head outwardly densely punctate, the punctures umbilical on genae and on an area of clypeus on either side of horn, with a few or many umbilical punc-

tures between eyes; rest of head impunctate. Posterior oblique carina sharp. Occipital margin with transverse setigerous groove broken into three parts. Demarcation between gula and submentum slightly angulate. *Thorax*.—Pronotum armed. Anterolateral angles acute, immediately followed by a sharp inward curve of margin. Lateral carina prominent, issuing from margin. Anterior margin of pronotum forming a small, downwardly directed median point. Median longitudinal sulcus deeply impressed, coarsely umbilico-punctate. Puncturation of pronotum as follows: Middle of disc and base impunctate; anterior face dorsally impunctate; posterior submargin and lateral fossae grossly annular-punctate; lateral and anterior submargins and anterior portion of sides of pronotum largely umbilico-punctate; anterior portion of disc densely punctate, the punctures round, cicatricial, or linear, simple or umbilical. Anterior prosternal margin devoid of a median tooth; sternellum grossly umbilico-punctate. Median lobe of metasternum with large umbilical punctures along sides; median longitudinal groove evenly impressed. *Elytra*.—8th stria incomplete, disintegrating or becoming effaced posteriorly; 9th stria arising at the anterior third of elytral length; 10th complete. Striae coarsely punctate, the punctures circular, subumbilical, and separated by a distance equal to once or twice their diameter. Interstriae slightly convex, impunctate. *Abdomen*.—Pygidium completely margined, moderately umbilico-punctate. *Anterior legs*.—Ventral surface of femur coarsely setigerous-punctate on posterior longitudinal half, impunctate on anterior. Forespur rather straight in dorsal view, somewhat expanded distally, ending in a bluntly rounded apex. *Middle legs*.—Coxa with some umbilical punctures on outer face. Ventral surface of femur impunctate basally, with some coarse setigerous punctures distally. Tibia below with 2-3 distal seta tufts. *Posterior legs*.—Femur and tibia as described for middle legs. *Total length*.—14.5-16 mm.

Female armament. Head horn low, gibbous, only slightly transverse, arcuately carinate apically. Median pronotal prominences in the form of two slightly curved, sharp transverse carinae separated at the midline by a small punctate depression which is a continuation of the median longitudinal sulcus. Lateral pronotal prominences obsolescent.

DISTRIBUTION. Fig. 17. Known from only two localities: Córdoba ("Cordova"), Veracruz, and the state of Chiapas. Through the courtesy of the British Museum I was able to examine the specimens seen by Bates and recorded as belonging to this species in the *Biologia Centrali Americana*. As suspected, all but

the specimens from Córdoba are *C. costaricensis* Gahan. This species has not been collected at Córdoba since Sallé visited the area almost a hundred years ago and it must be considered extraordinarily rare.

BIOLOGY. Unknown.

REMARKS. I have seen only two females which can be ascribed to this species. All other specimens I have seen bearing the *sallei* label have been referable to *costaricensis* Gahan, *lecontei* n. sp., or *mexicanus* Matthews and Halffter. The two specimens seen differ considerably in the degree of puncturation, the "Cordova" specimen being more heavily punctate. This specimen may be part of the original series collected by Sallé and used by Harold for his description, though it does not bear a paratype label. The others are presumably in the Paris Museum with the type. Both specimens I have seen are from the British Museum collection.

This species is evidently very close to *costaricensis* Gahan, differing only in apparently possessing blunt forespurs, an incomplete 8th elytral stria, and a complete pygidial margin. From *mexicanus* Matthews and Halffter it differs only in showing a small median tooth on the anterior pronotal margin (like *costaricensis*), blunt forespurs, and an incomplete 8th elytral stria. Until more specimens are collected the status of these three species must remain confused.

MATERIAL EXAMINED. Two females.

MEXICO: *Chiapas*: State record only, 1905 (Fry), 1 ♀ (BM); *Veracruz*: Córdoba (Sallé), 1 ♀ (BM).

Copris costaricensis costaricensis Gahan

Copris costaricensis Gahan, 1894, Ann. Mag. Nat. Hist., ser. 6, XIV: 116-117 [type: San Francisco de Guadalupe, Costa Rica, 1200 m.; British Museum (N. H.)]; Matthews, 1959, Ciencia XIX(6-7): 135 (key and distr.).

Copris furcillatus Felsche, 1910, Deutsche Ent. Zeitschr.: 345 [type: Chiriquí, Panamá; Dresden Museum]; Gillet, 1911, Ann. Soc. Ent. Belgique 55: 319 (synon.).

DESCRIPTION OF MALE. *Head*.—Armed or not. Clypeus with two very low teeth and a shallow triangular notch between them almost cutting through margin. Posterior angles of genae subquadrate. Upper surface of head coarsely punctate, the punctures umbilical between eyes, on either side of horn, and on genae, simple elsewhere. Posterior oblique carina sharp. Occipital margin with transverse setigerous groove broken into three parts. Demarcation

between gula and submentum arcuate or slightly angulate. *Thorax*.—Pronotum armed or not. Anterolateral angles acute immediately followed by a sharp indentation or curve of the margin less evident in some specimens. Lateral carina sharp, issuing from margin. Anterior margin forming a small, downwardly directed median point, occasionally an upwardly (inwardly) directed one as well. Median longitudinal sulcus deeply impressed, coarsely umbilico-punctate. Puncturation of pronotum as follows: coarsely umbilico-punctate in all depressions and along margins; raised areas of pronotal base, prominences, and most of anterior declivities contrastingly impunctate; no simple punctures. Anterior prosternal margin without any median tooth; sternellum coarsely punctate. Median lobe of metasternum umbilico-punctate anteriorly and laterally; median longitudinal impressed line complete. *Elytra*.—8th stria complete; 9th arising at anterior third of elytron; 10th complete. Striae very coarsely punctate, the punctures circular, umbilical, and separated by a distance equal to about their diameter or up to three times their diameter, depending on the location. Interstriae convex, impunctate. *Abdomen*.—Pygidium with the margin incomplete, its inner border totally effaced ventrally, moderately umbilico-punctate. *Anterior legs*.—Ventral surface of femur coarsely setigerous-punctate on posterior longitudinal half; impunctate on anterior. Forespur curved downward or slightly inward at apex, tapering to a sharp point. *Middle legs*.—Coxa with some umbilical punctures on outer face. Ventral surface of femur impunctate basally, becoming coarsely setigerous punctate distally. Tibia below with two distal seta tufts. *Posterior legs*.—Femur as described for middle legs. Tibia below with 2-3 distal seta tufts. *Total length*.—12-16 mm.

Male armament. In minor and medium individuals the head horn is straight and the median pronotal prominences are closely approximated and parallel, but not merging. Major males bear a long, slightly bent head horn tapering to the apex, the median pronotal prominences are merged together into a single bifurcate process, the ends of which diverge in dorsal view and bend downwards in lateral view, and the lateral pronotal prominences are laminate, directed forward when seen from above, rounded apically when seen from the side (fig. 80).

DESCRIPTION OF FEMALE. Identical to male in every respect except in armament. *Total length*.—13-15.5 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 17. The highlands of Costa Rica and Panama at altitudes of 1000-1500 m. (3300-4900 ft.).

BIOLOGY. Nevermann has attached the following data to his specimens from San José, C.R.: on carcass of *Didelphis richmondi*, in garbage pit (Abfallgrube), at light (3 ♂♂, 2 ♀♀). Another collector has recorded it from cow dung. It appears to be active throughout the year in Costa Rica.

REMARKS This species is easily told by its incomplete pygidial margin, the inner border of which is effaced ventrally. It is also the only known species with a sinuate lateral pronotal margin to be found in Central America. The major males are unique in the complex in that the median pronotal prominences are merged into a single bifurcate process. It is closely related to the enigmatical *sallei* Harold, the two specimens of the latter species that I have seen differing from *costaricensis* only in that the inner border of the pygidial margin is quite complete all the way around, the fore-spurs are blunt, and the 8th elytral stria is partly or totally effaced posteriorly. Both species show an acute median tooth on the anterior pronotal margin.

MATERIAL EXAMINED. 13 males, eight females.

COSTA RICA: *Cartago:* Las Mercedes, Jul. 1921, 1 ♀ (USNM); *San José:* San José, 1000—1200 m., Oct. 1925, Oct. 1928, Jun. 1931, 20 Oct. 1932, 17 Apr. 1933, 17 May 1933, 4 Oct. 1934, 22 Oct. 1935, 7 Oct. 1932 (F. Nevermann), 6 ♂♂, 3 ♀♀ (USNM); 10 Jun. 1943, 1 ♀ (AMNH); 9 Mar. 1924, 1 ♂ (USNM); 15 May, 1924, 1 ♂ (USNM); *location undetermined:* Azahar de Carboga (Underwood), 1 ♂, 1 ♀ (CM); *national record only:* 1897 (Pittier), 2 ♂♂ (USNM).

PANAMA: *Chiriquí:* Potrerillos, 1 ♀ (CAS); Volcán de Chiriquí, 2500—4000 ft. [6—8 Jun. 1882] (Champion), 1 ♂ (BM).

Copris costaricensis dolichocerus n. subsp.

Holotype: Volcán de Tacaná, Chiapas, Mexico, 1 Oct. 1956 (V. Aguilar), ♂; United States National Museum.

DESCRIPTION. Differs from the typical subspecies only in the greater proportional length of the male cephalic horn. When the height of the male horn is plotted against the length of the hind femur on a graph (fig. 7), the specimens of this species are seen to fall into two lots and to follow different curves, corresponding to their geographical origin.

DISTRIBUTION. Fig. 17. Chiapas and Guatemala at 1500—2000 m. I have ascribed the two known Guatemalan females to this subspecies purely on the basis of geographical distribution, as the females are not separable from the Costa Rican subspecies.

BIOLOGY. Unknown.

REMARKS. This form is recognized on the basis of the same character distinguishing the subspecies of *klugi* and *lecontei*. Different horn-length allometric relationships in this genus suggest a fundamental (perhaps genetic) difference which is sometimes (but not in this case) reflected in other morphological characters.

MATERIAL EXAMINED. Three males, seven females.

MEXICO: *Chiapas*: El Verjel, 6 Oct. 1939 (C. Bolívar), 3 ♀♀ (GH); Volcán de Tacaná (Coffee Belt), 1 Oct. 1956 (V. Aguilar), 3 ♂♂, 2 ♀♀ (USNM, GH).

GUATEMALA: *Quezaltenango*: San Isidro, 1500 m. [10-23 Sep. 1880] (Champion), 1 ♀ (BM); *Quiché*: Santa Cruz del Quiché, 13 Aug. 1947 (C. and P. Vaurie), 1 ♀ (AMNH).

Complex 4. The *rebouchei* complex.

Posterior angles of head quadrate. Anterolateral angles of pronotum acute, the margin behind them sharply sinuate. Median longitudinal sulcus of pronotum impunctate or very finely punctate. Forespur with the apex acute and curved inward in both sexes. Median coxae devoid of coarse punctures. 8th elytral stria complete. Pygidial margin complete or not. Complex punctures usually minutely granulate.

Three species found at low to moderate altitudes in Central and Western Mexico and bordering United States territory: *lecontei* n. sp., *rebouchei* Harold, and *halfpteri* Matthews.

Copris lecontei lecontei new species

Holotype: Huachuca Mts., Arizona, ♂; United States National Museum.

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus bidentate, the teeth not at all prominent, very obtuse, their inner edges meeting at a very broad angle forming the median emargination; no median notch. Upper surface of head densely punctate except for area between eyes, which is sparsely and very finely punctate or impunctate; all punctures simple. Posterior oblique carina sharp. Occipital margin with transverse setigerous groove broken into three sections which do not overlap. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed. Anterolateral angles with a salient point followed by a sharp inward curve of the margin, which is then angled out again at origin of lateral

carina. Lateral carina sharp and prominent. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus deeply impressed, with a few punctures or impunctate. Puncturation of pronotum as follows: densely punctate over all dorsal and lateral surfaces, the punctures smaller and less dense, or sometimes absent, on disc, becoming more sparsely punctate on anterior declivities; punctures simple except for those of the following areas, which are coarse and umbilical: along entire submargin, a few along median longitudinal sulcus and median line of anterior face, in lateral fossae, and hollows between prominences. Anterior prosternal margin with a low, truncate median tooth; sternellum moderately umbilico-punctate. Median lobe of metasternum with shallow umbilical punctures along sides and anteriorly; median longitudinal groove complete to anterior pit. *Elytra*.—8th stria complete; 9th arising about one third of way down elytron; often a more anterior segment of 9th stria is present, not quite issuing from base or joining posterior section and not punctate; 10th stria complete. Striae coarsely crenato-punctate, the punctures very little deeper than the striae, round, separated by a distance equal to their diameters or less. Interstriae very slightly convex, sparsely, finely punctate, appearing smooth, or quite impunctate. *Abdomen*.—Pygidium rather densely, coarsely umbilico-punctate, the margin complete or rarely incomplete, the inner edge of margin being effacted ventrally (fig. 59). *Anterior legs*.—Ventral surface of femur with coarse setigerous punctures on posterior longitudinal half, impunctate on anterior half. Forespur straight and parallel-sided to apical third, where it takes a sharp bend inwards and tapers to a sharp point. *Middle legs*.—Coxa impunctate. Ventral surface of femur very sparsely and finely punctate or impunctate except distally, where the punctures are coarse and setigerous. Tibia below with three distal seta tufts. *Posterior legs*.—Like middle legs, but tibia below with a row of 4-5 seta tufts. *Total length*.—10-15.5 mm.

Male armament. Medium specimens bear a horn which is practically straight, the rearward curvature being barely perceptible (fig. 75). The horn of major specimens is gently arcuate and slightly expanded transversely at the apex. The pronotum bears four prominences as usual, the two median ones compressed, slightly upwardly directed, and approximated, but always with a punctate depression between them.

DESCRIPTION OF FEMALE. Similar to male, but differing in armament and in the following features: usually some umbilical punctures between eyes on upper surface of head; puncturation on

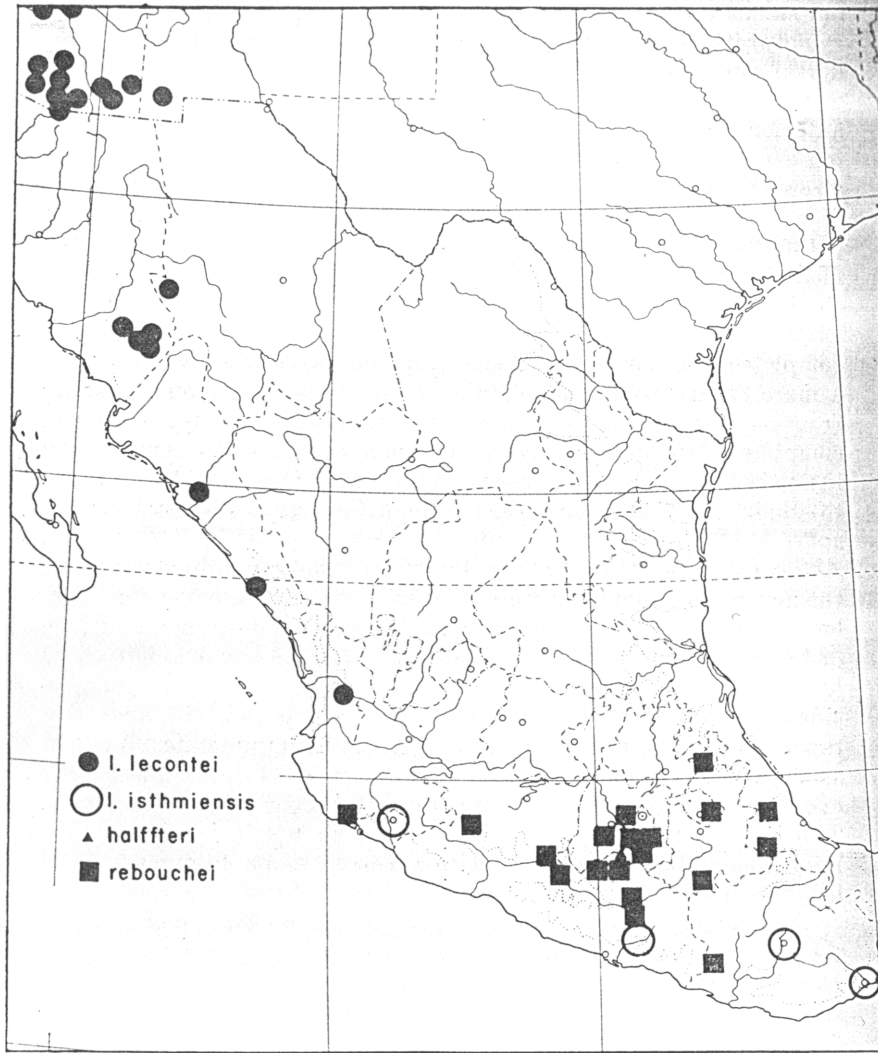


Fig. 18. Distribution of the *rebouchei* complex. Base map reproduced by permission of the University of Chicago.

anterior part of disc much denser and merging, the punctures umbilical only along submargins and in lateral fossae. *Total length*.—11–15 mm.

Female armament. Typical for the genus.

DISTRIBUTION. Fig. 18. Known from practically all the mountain ranges of southeast Arizona at altitudes of 2500 to 6000 ft. (760–1800 m.) but found most frequently at about 4000 ft. (1200 m.). There is one record each from the Animas Mts. of New Mexico and the Río Mayo in Chihuahua and there are several records from the Sierra de Alamos in southern Sonora at altitudes of but a few hundred metres. Thence there are isolated records down the west coast of Mexico to Nayarit at altitudes of sea level to 1500 m. (4900 ft.).

BIOLOGY. Unknown. In Arizona it is apparently most abundant in late summer.

REMARKS. The relationship of this species to *rebouchei* Harold is extremely close. This cannot be seen in the Arizona specimens, which are very different from *rebouchei*, being much more heavily punctate on the pronotum and the males bearing median pronotal prominences of a different type (figs. 75, 76). However, as we examine *lecontei* further south in Sinaloa and Nayarit we find it becomes increasingly less punctate and the median pronotal prominences become more laminate and remote, approaching both *rebouchei* and *l. isthmiensis* in form. *C. rebouchei* possesses an acute tooth on the prosternal margin (fig. 54), whereas in *lecontei* there is at most a rounded expansion or truncate process here, and in *rebouchei* the pygidial margin is always quite effaced medially, whereas in *lecontei* it is nearly always either engraved for its entire length or continued medially by a close-set row of punctures (fig. 59).

This species has been long familiar under the name *moechus* Leconte. A recent examination of the type of *moechus* revealed it to belong to a Mexican species hitherto bearing the name *clavicornis* Matthews and Halffter. As there were no synonyms available for this common species, it is here described as new and dedicated to the distinguished American systematist, J. L. Leconte.

MATERIAL EXAMINED. 244 males, 249 females.

UNITED STATES: *Arizona*: Cochise Co.: Carr Cyn, Huachuca Mts.; Lower Carr Cyn, Huachuca Mts.; Chiricahua Mts.; Huachuca Mts.; Mule Mts., Gilman Ranch, 8 mi. N Bisbee; Palmerly; 3 mi. E Portal; Ramsay Cn., Huachuca Mts.; San Bernardino Ranch; Texas Pass, Dragoon Mts.; Webb; SE end Whetstone Mts., Sands Ranch; Gila Co.: Globe; Base Pinal Mts.; Rice; Pima Co.: Baboquivari Mts.; Baboquivari Mts., Kitts Peak Rincón; Baboquivari

Mts., El Mirador Reh., 4 mi. NW Sasabe; Baboquivari Canyon, W side Baboquivari Mts.; Brown's Canyon, E side Baboquivari Mts.; Elkhorn Ranch, E slope N end Baboquivari Mts.; Sycamore Canyon, N of Baboquivari Canyon, W side Baboquivari Mts.; Continental; Santa Catalina Mts.; Santa Rita Mts.; Santa Rita Mts. Old Parker Ranch; Sierritas, Black Dike Prospect; Tucson; Tucson, St. Xavier Mission; Santa Cruz Co.: Elgin; Nogales; Patagonia; Ruby; 21 mi. SE Ruby; Sonoita R., Patagonia; 25 mi. E Sonoita; Tumacacori Nat'l. Mon.; Yanks Spring, 4 mi. SE Ruby, Pajaritos Mts.; Washington Mts., nr. Nogales; Yavapai Co.: Prescott; *New Mexico*: Hidalgo Co.: Animas Mts., Double Adobe Ranch.

MEXICO: *Chihuahua*: Río Mayo, Aug. (Gentry), 1 ♂ (CAS); *Nayarit*: Tepic, 28 Jul. 1953 (C. and P. Vaurie), 2 ♂♂, 2 ♀♀ (AMNH); 27 Jul. 1954 (M. Cazier, W. Gertsch, Bradts), 1 ♀ (AMNH); *Sinaloa*: Culiacán, 250 ft., 21 Jul. 1959 (H. E. Evans), 2 ♂♂, 2 ♀♀ (CU); Mazatlán, 15-17 Sep. 1918, 1 ♂, 1 ♀ (USNM), 9 mi. N Mazatlán, 100 ft., 12-16 Jun. 1953 (R. K. Selander), 1 ♀; El Venadío [4.5 mi. N Mazatlán]*, 16 Jun. 1918 (J. A. Kuseche), 41 ♂♂, 35 ♀♀ (USNM, CAS); *Sonora*: Agua Marina nr. Alamos, 20 Jul. 1955 (R. and O. Flint), 1 ♂ (EGM); Alamos, 29 Jul. 1940 (R. P. Allen), 1 ♂, 3 ♀♀ (CAS); 10 mi. W Alamos, 21 Jul. 1954 (M. Cazier, W. Gertsch, Bradts), 1 ♂ (AMNH); Minas Nuevas, 7 Aug. 1952 (C. and P. Vaurie), 15 ♂♂, 9 ♀♀ (AMNH); Río Mayo, Aug., 3 ♀♀ (CAS); Sta. Rosa Ranch, N of Navojoa, 2 Aug. 1952 (C. and P. Vaurie), 1 ♂, 2 ♀♀ (AMNH).

Copris lecontei isthmiensis n. subsp.

Holotype: Tehuantepec, Oaxaca, Mexico, 12 July 1955 (P. and C. Vaurie), ♂; American Museum of Natural History.

DESCRIPTION. The Oaxaca and Colima males of *lecontei* are sharply separated from the rest of the species by the greater proportional length of the cephalic horn. When the height of the cephalic horn is plotted against the length of the hind femur on a graph (fig. 8), it is seen that the specimens from these two states fall along a very different curve from that followed by the rest of the species. In appearance this subspecies is very close to *rebouchei* Harold, being distinguished only by the complete pygidial margin and absence of an acute prosternal process. *C. l. isthmiensis* is very

* This locality is given as "Venodio" on the specimens. For its correct spelling and location I am indebted to E. J. Cantrell (unpublished information).

sparsely punctate on the pronotum in the male and the median pronotal prominences are remote and laminate as in *rebouchei*. Except in horn allometry, this form seems to merge imperceptibly with the northern subspecies.

DISTRIBUTION. Colima, Guerrero, and Oaxaca at sea level to 1520 m. (5000 ft.). I have ascribed the single female from Jalisco to this subspecies arbitrarily, since the females are not distinguishable from the northern form.

BIOLOGY. Unknown.

REMARKS. A poorly represented form, distinguishable from *rebouchei* Harold primarily by its completely margined pygidium. It could, with almost equal justification, be ascribed to *rebouchei*, since their horn allometry curves coincide (fig. 9). For the present, however, I prefer to attach greater weight to the morphological, rather than to the allometric, evidence.

MATERIAL EXAMINED. Eight males, five females.

MEXICO: *Colima*: Colima, 18 Jun. 1943 (H. D. Smith), 1 ♀ (USNM); Volcán de Colima (L. Conradt), 3 ♂♂, 2 ♀♀ (USNM); state record only (L. Conradt), 2 ♂♂ (USNM); *Guerrero*: 10 mi. S Chilpancingo, 25 Jun. 1932 (Hobart Smith), 1 ♂ (PAS); *Jalisco*: Atenquique, 30 Jun. 1949 (W. D. Clarke), 1 ♀ (CAS); *Oaxaca*: Oaxaca, Jul. (Embury), 1 ♂ (CAS); 30 Jun. 1955 (P. and C. Vaurie), 1 ♀ (AMNH); Tehuantepec, 12 Jul. 1955 (P. and C. Vaurie), 1 ♂ (AMNH).

Copris rebouchei Harold

Copris rebouchei Harold, 1869, Ann. Soc. Ent. France, ser. 4, IX: 497 [type: Puebla, Pue.; Museum d'Histoire Naturelle, Paris]; Bates, 1887, Biol. Cent.—Amer., Coleopt. II, 2, p. 54, 1889, Suppl., p. 387 (distr.); Matthews 1959, Ciencia XIX (6-7): 135 (key and distr.).

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus bidentate, the teeth moderately prominent in unworn specimens, broad, rounded, separated by a U-shaped median notch which does not cut through margin. Upper surface of head moderately punctate outwardly with basal and central portions impunctate; all punctures simple. Posterior oblique carina very sharp. Occipital margin with transverse setigerous groove interrupted into three non-overlapping portions; demarcation between gula and submentum a rounded, broad V. *Thorax*.—Pronotum armed. Anterolateral angles with the point made salient by a deep inward curve

of margin immediately behind it, the margin then angled out at origin of lateral carina. Lateral carina very sharp. Anterior margin of pronotum not forming any median point or angle, or sometimes forming a very slight one. Median longitudinal sulcus shallow, fine, and impunctate. Pronotum impunctate except for the following areas, which are sparsely and coarsely umbilico-punctate: posterior and lateral submargins, including anterolateral lobes, lateral fossae, and hollows between median and lateral prominences; in addition, there are usually some scattered smaller umbilical punctures along anterior margin and mid-line of anterior face, including the hollow between median prominences; some shallow punctiform impressions on outside faces of lateral prominences. Anterior prosternal margin with a minute, acute median tooth (fig. 54); sternellum sparsely punctate. Median lobe of metasternum impunctate except for a few umbilical punctures along edges; median longitudinal groove fine but complete. *Elytra*.—8th stria complete, sometimes tending to disintegrate at the very base; 9th stria arising one-third the way down elytron; 10th complete. Striae coarsely crenato-punctate, the punctures round, scarcely deeper than the striae, separated by a distance equal to their diameter or less. Interstriae convex and impunctate. *Abdomen*.—Pygidium moderately umbilico-punctate, the margin incomplete, its inner border effaced ventrally. *Anterior legs*.—Ventral surface of femur with coarse setigerous punctures on posterior longitudinal half, impunctate on anterior half. Forespur parallel-sided for basal two thirds, then sharply bent inwards, almost at a right angle, tapering to a sharp point. *Middle legs*.—Coxa impunctate. Ventral surface of femur impunctate on basal half, with sparse setigerous punctures on apical half. Tibia below with two distal seta tufts. *Posterior legs*.—Femur as described for middle legs. Tibia below with a row of 3–4 median seta tufts. *Total length*.—12–15 mm.

Male armament. The head horn gradually tapers to an acute apex and is very slightly curved or practically straight. The pronotal prominences are all laminate, the median ones only slightly closer to each other than each is to the lateral prominence, and directed forward parallel to each other with a deep concavity between each (fig. 76). In lateral view the median prominences are rounded at the apex, the lateral ones acute as usual.

DESCRIPTION OF FEMALE. Similar to male, but differing in armament and in the following features: clypeal teeth more prominent and round, median notch often more rounded than that of male; pronotum impunctate at base of disc, becoming densely punctuate over most of dorsal and lateral surfaces, the punctures

transverse and accompanied by ridges; anterior face impunctate; the punctures are umbilical only along margins and in lateral fossae. *Total length*.—11.5–15 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 18. The Central Volcanic Range and the depression of the Río Balsas. In the western part of its range the species descends to sea level, occurring in the same areas as the closely related *lecontei*, n. sp., but over most of its range it occurs at altitudes of 430–1520 m. (1400–5000 ft.), with a single record at 3000 m. (9800 ft.).

BIOLOGY. Found under cow dung; otherwise its biology is unknown. Active throughout the rainy season.

REMARKS. This smooth and shiny species can always be told by its incomplete pygidial margin, the inner border of which is completely effaced for the median third or more of its length (fig. 58), and by the minute, acute median tooth on the anterior posternal margin. Its relationship to *lecontei* is discussed under the latter species.

MATERIAL EXAMINED. 63 males, 58 females.

MEXICO: *Guerrero*: Ajuchitlán; Altamirano (NE of Coyuca de Catalán); Apipilulco; Balsas; Cacahuamilpa; 25 km. N Chilpancingo; Iguala; 8 mi. N Iguala; 5 mi. S Iguala; Mexcala; Teloloapan; *Jalisco*: 3 mi. E Jaluco (43 mi. SW La Resolana); *México*: Salazar; Tejupilco, Temexcaltépec; *Michoacán*: El Sabino, Uruapan; Huétamo; *Morelos*: 7 km. S Alpuyeca; Cuautla; Cuernavaca; 10 mi. S Cuernavaca; 25 km. S Cuernavaca; Jojutla; ?Oxtepec; ?Progreso; Puente de Ixtla; Tepoztlán; ?Tequesquitengo; Valle de Morelos; Vista Hermosa, 15 km. S Cuernavaca; *Oaxaca*: Tepetlapa; *Puebla*: Km. 259 on Oaxaca Rd. (nr. Acatlán); Pahoatlán (nr. Huachinango); *Tlaxcala*: 21 mi. W Apizaco; *Veracruz*: Coatepec; Presidio.

Copris halfteri Matthews

Copris halfteri Matthews, 1959, *Ciencia* XIX(6–7): 133–134 [type: Cacahuamilpa, Gue.; United States National Museum].

DESCRIPTION OF MALE. *Head*.—Armed. Clypeus bidentate, the teeth prominent, rounded, approximated, separated by a U-shaped median notch not cutting through margin. Upper surface of head shallowly punctate only along edges, rest of surface being impunctate; punctures simple except for a few umbilical ones at hind edges of genae. Posterior oblique carina very prominent.

short, curved backwards at inner end, abruptly cut off. Occipital margin with setigerous groove divided into three partially overlapping sections. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed. Anterolateral angles with the point made prominent by a sharp inward curve of margin immediately behind it, the margin then sharply angled out at origin of lateral carina. Lateral carina very sharp. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus of pronotum moderately impressed, fine, complete, and impunctate. Puncturation of pronotum as follows: entire base forward of submargin extremely faintly punctate, appearing impunctate, becoming more visibly punctate forward of a transverse line joining hind limits of lateral fossae, the punctures being shallow and somewhat cicatricial, becoming round and subumbilical only on anterolateral lobes, and abruptly disappearing on anterior declivity, which is therefore impunctate except for a few shallow punctures about the mid-line and along anterior margin; the punctures are umbilical along posterior and lateral submargins and in lateral fossae. Anterior prosternal margin with a median process of unique shape, being very salient, parallel-sided, and bilobate at apex, which is also slightly reflexed; sternellum concave, not longitudinally carinate, sparsely umbilico-punctate. Median lobe of metasternum impunctate, but wrinkled and with some faint punctiform impressions at edges; median longitudinal impressed line complete. *Elytra*.—8th stria incomplete, disintegrating beyond halfway point; 9th stria arising close to 10th a little forward of halfway point; 10th complete. Striae crenato-punctate, the punctures little wider and no deeper than the striae, separated by a little more than their diameter. Interstriae slightly convex, sparsely, regularly, and very finely punctate, appearing smooth. *Abdomen*.—Pygidium moderately and rather shallowly punctate, the punctures small and umbilical; pygidial margin complete. *Anterior legs*.—Ventral surface of femur coarsely setigerous-punctate on posterior longitudinal half, impunctate on anterior. Forespur straight and parallel-sided to near apex, where it makes a sudden, right-angled (or even a little acute-angled) inward bend, tapering to a sharp point (fig. 42). *Middle legs*.—Coxa impunctate. Ventral surface of femur very finely punctate on basal half, coarsely setigerous-punctate on distal half. Tibia below with three distal median seta tufts. *Posterior legs*.—Femur and tibia as described for middle legs. *Total length*.—14.5–15 mm.

Male armament. Male armed like a female. Head horn typical of the female in the genus, well developed, transverse, low, parallel-sided, truncate and excavate at the apex. Pronotum with the

median prominences low, transverse, and cariniform, like those of a female, but quite narrow and separated by a deep, rounded median depression. The lateral prominences are low conical bumps (fig. 77).

DESCRIPTION OF FEMALE. Very similar to male, differing only in armament. *Total length*.—15 mm.

Female armament. Head horn like that of the male, but lower and more excavate at the apex. Median pronotal prominences in the form of much sharper transverse carinae which are longer and strongly curved, their inner ends turned up and forming prominent points separated by a depression which is smaller than that of the male; the notal surface is depressed behind these carinae. Lateral prominences as in male.

DISTRIBUTION. Fig. 18. Known only from the type locality at Cacahuamilpa, Guerrero.

BIOLOGY. Found in cow dung, otherwise unknown.

REMARKS. This species is truly remarkable and quite unique with regard to its male armament, which is of the female type. The prominent bilobate process of the median prosternal margin (fig. 55) is also unique. It may further be told from *rebouchei* Harold, which it otherwise closely resembles, by the complete pygidial margin (fig. 60). It was collected in association with some typical specimens of *rebouchei*.

It appears that a similar phenomenon may be observed in some Old World species of *Copris* (Balthasar, personal communication), where occasionally male individuals of known species may appear with female armament. In such cases these have been interpreted as being individual gynandromorphs rather than separate species. It is impossible that this could be the case here because, for one thing, the females also show the distinguishing characters of the bifurcate prosternal process and complete pygidial margin. It may well be, however, that the species arose from such individuals which were initially merely gynandromorphs.

MATERIAL EXAMINED. Holotype, allotype, and male paratype.

MEXICO: Guerrero: Cacahuamilpa, 25 Aug. 1956 (G. and V. Halffter), 2 ♂♂, 1 ♀ (USNM, GH).

Complex 5. The *fricator* complex.

Posterior angles of head subquadrate or acute. Anterolateral angles of pronotum acute, the margin immediately behind them sinuate or emarginate. Entire pronotal surface coarsely and very densely punctate. Forespur with the apex acute in both sexes.

Eighth elytral stria complete. Pygidial margin nearly always complete.

Three species found at low to moderate altitudes in the Eastern United States and extreme southern Ontario: *inemarginatus* Blatchley, *ficator* (Fabricius), *howdeni* Matthews and Halffter.

Copris inemarginatus Blatchley

Copris inemarginatus Blatchley, 1918, Canadian Ent. L: 54-55 [type: Dunedin, Fla.; Purdue University, Lafayette, Indiana]; Wickham, 1919, American Journ. Sci., ser. 4, XLVII (281): 355-357 (fossil); Young, 1959, Coleop. Bul. XIII: 103-106 (fossil and distr.).

DESCRIPTION OF MALE. *Head*.—Armed with a very low horn. Clypeus without teeth or median notch, with a very slight median sinuation. Posterior angles of genae acute. Upper surface of head entirely punctate, all raised surfaces and basal portion of genae umbilico-punctate, outer portions with the punctures simple and merged together, forming irregular ridges; horn and area immediately around it impunctate. Posterior oblique carina absent. Occipital margin with setigerous groove interrupted into three parts. Demarcation between gula and submentum irregular, with a slight median rearward extension of the setose submental area. *Thorax*.—Pronotum unarmed. Anterolateral angles obtuse with the point drawn out into a point or tubercle. Lateral margin slightly angulate at origin of lateral carina. Lateral carina not prominent, rounded, not issuing from margin. Anterior margin not forming any median point or angle. Median longitudinal sulcus visible on dorsal part of disc, fine, shallow, and impunctate. Puncturation of pronotum as follows: densely punctate over entire surface, the punctures shallow and often indistinct, simple on dorsal part of disc, cicatricial or umbilical elsewhere, separated by a distance equal to a little more than their diameter, and annular along the hind and lateral submargins. Anterior prosternal margin with two very minute teeth close together at the middle; sternellum coarsely umbilico-punctate. Median lobe of metasternum cicatricio-punctate along sides; medium longitudinal groove strongly impressed on posterior two-thirds of metasternum only, effaced anteriorly. *Elytra*.—8th stria complete; 9th arising about halfway down elytral length; 10th complete. Striae crenato-punctate, the punctures elongated, shallow, flanked by undulations of the interstitial margins which give the punctures a transverse appearance.

Interstriae strongly convex, very finely punctate, appearing smooth. *Abdomen*.—Pygidium completely margined, densely umbilico-punctate. *Anterior legs*.—Ventral surface of femur coarsely setigerous-punctate over most of area, more finely punctate along anterior margin basally. Forespur bent in apically and tapering abruptly to an acute apex. *Middle legs*.—Coxa with numerous

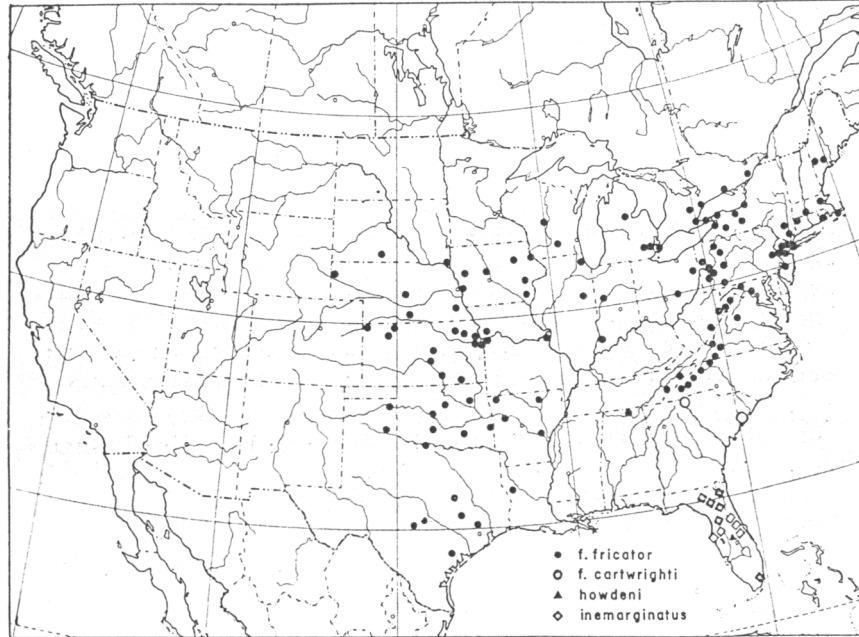


Fig. 19. Distribution of the *fricator* complex. Base map reproduced by permission of the University of Chicago.

umbilical punctures along median carina and a row of coarser setigerous ones along outer edge. Ventral surface of femur impunctate except for a few coarse setigerous punctures distally. Tibia below with 4–6 seta tufts arranged in a longitudinal row along most of tibial length. *Posterior legs*.—Femur as described for middle legs. Tibia with 6–8 seta tufts in a longitudinal row over most of length of tibia. *Total length*.—11–14 mm.

DESCRIPTION OF FEMALE. Not differing in any external respect from the male. *Total length*.—12–15 mm.

DISTRIBUTION. Fig. 19. Northern and Central Florida and Miami.

BIOLOGY. Found under cow dung. It is most active during the winter and spring from November to April. Blatchley records finding it under a dead turtle and at a porch light in January. Young (1959) describes it as highly characteristic of the scrub habitat in Florida.

REMARKS. I believe this species to be an early offshoot from the stem leading to *fricator*, with which latter species it shares the characters here used to differentiate the *fricator* complex, but from which it differs primarily in retaining the very finely punctate elytral interstriae of the presumed ancestor in the *rebouchei* or *remotus* complexes. It is also easily distinguished by the clypeal margin, which lacks any teeth or emargination—a unique feature of this species. It differs further from *fricator* and *howdeni* in that the outer head punctures above are merged to form irregular grooves, in not showing the fine shagreening of interpunctural surfaces characteristic of those two species, and in not bearing a salient median tooth on the anterior prosternal margin; the under surface is also somewhat less densely punctate.

MATERIAL EXAMINED. 68 males, 56 females.

UNITED STATES: Florida: Alachua Co.: Gainesville; High Springs; Dade Co.: Miami; Duval Co.: Jacksonville; Hillsborough Co.: Lutz; Tampa; Marion Co.: 4 mi. NW Dunellon; Orange Co.: Orlando; Osceola Co.: Kissimmee; Pinellas Co.: Dunedin; Putnam Co.: Interlachen; 8 mi. S. Interlachen; Seminole Co.: Sanford; Suwannee Co.: 13 mi. N. O'Brien; Volusia Co.: Enterprise; location undetermined: Stemper; Weeki Wachee.

Copris fricator fricator (Fabricius)

Scarabaeus fricator Fabricius, 1787, Mant. Ins., p. 15, No. 140 [type: East India; Hunterian Collection, Glasgow]; 1792, Ent. Syst. I, 1, p. 54, No. 176; Olivier, 1789, Ent. I, 3, p. 122, pl. 16, fig. 149; 1790, Encycl. méth. V, p. 161.

Copris fricator, Fabricius, 1801, Syst. Eleuth. I, p. 45, No. 67; Gillet, 1911, Ann. Soc. Ent. Belgique LV: 314; Staig, 1931, The Fabrician Types of Insects in the Hunterian Collection at Glasgow University, pp. 48-50, pl. 14 (descr. of type); Arrow, 1931, Fauna of British India, Colept., Lamell. III, p. 107 (synon.).

Scarabaeus tullius Olivier, 1789, Ent. I, 3, pl. 11, fig. 98, pl. 19, fig. 88b [type: East Indies; Hope Mus., Oxford]; 1790, Encycl. méth. V, p. 159.

Copris tullius, Fabricius, 1801, Syst. Eleuth. I, p. 44, No. 65; Lansberge, 1886, Tijdschr. v. Ent. XXXIX: 16 (synon.); Gillet, 1911, Ann. Soc. Ent. Belgique LV: 290 (discuss. of synon.); Lindquist, 1933, Jour. Kansas Ent. Soc. VI(4): 1-9 (biol.).

Copris anaglypticus Say, 1823, Jour. Acad. Nat. Sci. Philadelphia III: 204 [type: United States; destroyed]; 1859, Complete Writings, ed. Leconte, II, p. 131; Horn, 1873, Trans. American Ent. Soc. IV: 42-51 (key and descr.); Schaeffer, 1906, Trans. American Ent. Soc. XXXII: 256 (key); Arrow, 1931, Fauna of British India, Coleopt., Lamell. III, p. 107 (synon.).

DESCRIPTION OF MALE. *Head*.—Armed or not. Clypeus bidentate, the teeth rounded, broad, and very low, often completely worn down, with a median V-shaped notch between them which cuts through the margin. Posterior angles of genae subquadrate. Upper surface of head entirely closely punctate, the punctures simple except at least some of those on genae, between eyes, and, in minor specimens, on upper part of clypeus. Surface between punctures often very finely shagreened. Posterior oblique carina absent. Occipital margin with transverse setigerous groove broken into several parts. Demarcation between gula and submentum arcuate. *Thorax*.—Pronotum armed or not. Anterolateral angles with the point made prominent by a sharp inward curve of margin immediately behind it, the margin then angled out at origin of lateral carina. Lateral carina well developed, sharp. Anterior margin of pronotum not forming any median point or angle. Median longitudinal sulcus obsolescent, visible as a shallow impunctate line over most of length of disc, or totally effaced. Pronotum entirely densely umbilico-punctate (many punctures not umbilical in well developed specimens), the punctures separated by a distance more or less equal to their diameter, smaller on anterior declivity, larger and annular along posterior submargin. Surface between punctures often very finely shagreened. To the naked eye the texture imparts a silky sheen to the pronotum. Prosternal-proepisternal suture not carinate; anterior prosternal margin with a salient median process which is usually quadrate, sometimes acute or rounded; sternellum with very large, shallow punctures. Median lobe of metasternum densely and shallowly umbilico-punctate, the punctures finer on middle; median longitudinal groove impressed on posterior two thirds, the anterior third very shallow. *Elytra*.—8th stria complete; 9th arising about halfway down elytral length, very close to 10th; 10th complete. Striae very shallow, broad, crenulated, with the punctures obsolescent or absent. Interstriae slightly convex,

profusely and distinctly umbilico-punctate, the punctures small setigerous, and separated by a distance equal to many times the diameter. Surface between punctures finely shagreened, especially along sides of elytra. Small specimens tend to a reduction in size and number of interstitial punctures and to a more profuse shagreening. *Abdomen*.—Pygidium densely umbilico-punctate, the margin complete. *Anterior legs*.—Femur below entirely, densely umbilico-punctate. Forespur tapering to an acute point, curved inward and slightly downward for its apical third. *Middle legs*.—Coxa with a few small punctures along median longitudinal carina, rest of surface finely shagreened and often wrinkled. Ventral surface of femur entirely, coarsely punctate, the punctures reniform and setigerous. Tibia below with a row of up to eight median seta tufts over most of its length. *Posterior legs*.—Femur and tibia as described for middle legs. *Total length*.—10.5–18.5 mm.

Male armament. Very variable in development (but not in form), small specimens bearing no horns or gibbosities whatever, medium sized ones bearing a straight, evenly tapering and transversely flattened horn on the head, and two moderately approximated median pronotal prominences which are a little transversely carinate. The lateral prominences are represented by the usual conical bumps. Large specimens bear a long, rather straight, and usually distinctly clavate horn, the apex being transversely expanded and rounded. The median prominences are prominent rounded gibbosities which are approximated but always with a depression between them, and the lateral prominences are cariniform and not very prominent (fig. 66).

DESCRIPTION OF FEMALE. Very similar to male, differing only in armament (in specimens possessing it) and in the fact that the clypeal teeth are more rounded and prominent, the notch between them more U-shaped. Slightly worn minor females are quite indistinguishable from minor males. *Total length*.—12–18 mm.

Female armament. Normal for the genus.

DISTRIBUTION. Fig. 19. The Eastern United States (penetrating into Canada along the northern shores of lakes Erie and Ontario) in an area corresponding to the Upper Austral (Carolinian) Zone, but descending well into the Lower Austral in the western part of its range. In the eastern part of its range, in the Appalachian Mountains, it climbs well into the Transition Zone. In Western North Carolina the subspecies does not appear to be found at altitudes lower than 2500 ft. (760 m.), nor south of Balsam and Sunburst. This is the northernmost of the American species and the only one definitely occurring in Canada, to my knowledge.

BIOLOGY. Found abundantly under cow dung and occasionally coming to light. Nidification is discussed on pp. 28-29.

REMARKS. Specimens from Kansas, Oklahoma, Arkansas, Texas, Louisiana, and Missouri are characterized by a rather uniform small size and consequent low development of armament (fig. 3); this difference does not appear to be sharply set off from the rest of the populations (see more complete discussion on p. 19), nor is it accompanied by any other feature that I could find, and it appears doubtful that anything would be gained by introducing a subspecific name here.

It is regrettable that this species should undergo yet another name change, but there is no doubt that the specimen now considered to be the type of *Scarabaeus fricator* F. belongs to this species. Mr. R. A. Crowson was kind enough to compare some Pennsylvania specimens of this species with the type in the Hunterian Collection at Glasgow, whereupon he pronounced them identical. The synonymy of *fricator* and *anaglypticus* was actually pointed out by Arrow in 1931, a fact which seems to have been overlooked by everyone on this side of the Atlantic until recently and which would also have been overlooked by me if it had not been pointed out by Father F. S. Pereira and Mr. O. L. Cartwright.

There is still considerable doubt as to whether the specimen in Glasgow does indeed represent the type of *fricator* (Balthasar, personal communication) particularly as Olivier evidently considered the species *tullius* and *fricator* as being quite distinct. The Glasgow specimen was separated from its label for some time (Staig, 1931; Crowson, personal communication) and reunited with some doubt. Nevertheless, it appears to me on reading Olivier that the differences he mentions are sexual and not specific; there is no indication that he was aware that the type of *fricator* he described was actually a female (the Glasgow type is a female, an indication that it probably is the true type). Furthermore, it appears to me that in the interest of nomenclatorial stability the supposed Fabrician types in the Hunterian Collection should be accepted in the absence of any contradictory evidence; otherwise they would serve no purpose and the situation would remain confused for all time.

MATERIAL EXAMINED. 182 males, 182 females.

CANADA: *Ontario:* Ancaster; Fisher Glen; Grimsby; Guelph; Leamington; Marmora; Pt. Pelee; Spencerville; Toronto; Trenton.

UNITED STATES: *Alabama:* Madison Co.: Monte Sano St. Pk.; *Arkansas:* Arkansas Co.: Arkansas R.; Benton Co.: Bentonville; Lawrence Co.: Imboden; Logan Co.: Cove Lake nr. Paris; *Connecticut:* Litchfield Co.: Cornwall; *Illinois:* Champaign Co.: Urbana; Cook Co.: Evanston; Dupage Co.: Lyons; Lake Co.: Lib-

ertyville; McHenry Co.: Algonquin; *Indiana*: Knox Co.: Vincennes; Lafayette; *Iowa*: Buchanan Co.: Independence; Clayton Co.: Guttenberg; Crawford Co.: Denison; Henry Co.: Mt. Pleasant; Johnson Co.: Iowa City; Polk Co.: Herrold; Pottawatomie Co.: Council Bluffs; Story Co.: Ames; *Kansas*: Cheyenne Co.; Douglas Co.: Lawrence; Ellsworth Co.: Ellsworth; Jackson Co.; Johnson Co.; Leavenworth Co.; McPherson Co.; Montgomery Co.; Norton Co.; Pottawatomie Co.: Onaga; Reno Co.: Medora, Sand Hills; Saline Co.; Sedgwick Co.: Wichita; Sheridan Co.; Wyandote Co.; *Louisiana*: Sabine Co.: Many; *Maine*: Kennebec Co.: Monmouth; Oxford Co.: Bethel; *Maryland*: Montgomery Co.: Forest Glen; Washington Co.: Hagerstown; *Massachusetts*: Barnstable Co.: Woods Hole; Hampden Co.: Chicopee, Ludlow, Wilbraham; Middlesex Co.: Concord; *Michigan*: Detroit: Highland Park; Livingston Co.: George Reserve; Midland Co.; Washtenaw Co.; *Missouri*: Clinton Co.: Lathrop; Jefferson Co.: Webster Groves; Kansas City; *Nebraska*: Brown Co.: Koshopah; Custer Co.: Ansley; Lancaster Co.: Bennet; Phelps Co.: Holdredge; Sioux Co.; *New Jersey*: Burlington Co.; Essex Co.: Newark, Orange; Middlesex Co.: New Brunswick; Morris Co.: Boonton; Passaic Co.: Clifton; Somerset Co.; Warren Co.: Phillipsburg; *New York*: Erie Co.: Hamburg; Long Island; New York City: Brooklyn, Queens; Niagara Co.: Olcott; Orange Co.: New Windsor; West Point; Oswego Co.: Oswego; Tompkins Co.: Ithaca; Ulster Co.; Wayne Co.; Westchester Co.: Yonkers; Wyoming Co.: Pike; *North Carolina*: Blue Ridge Parkway: Cumberland Knob Pk.; Miles 291.4, 339.2; Buncombe Co.: Weaverville; Haywood Co.: Sunburst; Jackson Co.: Balsam; *Ohio*: Columbiana Co.: Millport; Licking Co.: Newark; *Oklahoma*: Canadian Co.; Coal Co.: Cairo; Grady Co.: Ouachita Nat'l Forest; Payne Co.: Stillwater; Rogers Co.: Claremore *Pennsylvania*: Allegheny Co.; Beaver Co.: New Brighton; Fayette Co.: Ohiopyle; Forest Co.; Indiana Co.: Indiana; Jefferson Co.; Lawrence Co.: Slippery Rock; Northampton Co.: Easton, Wind Gap; Pittsburgh; Washington Co.; Westmoreland Co.: Jeanette; *Rhode Island*: Washington Co.: Watch Hill; *South Dakota*: Bennett Co.: Martin; Clay Co.: Vermillion; Union Co.: Elk Point; *Tennessee*: Greene Co.: Greeneville; Sevier Co.: Gatlinburg; *Texas*: Blanco Co.: Cypress Mills; Brazos Co.: College Station; Gillespie Co.: Fredericksburg; Hall Co.: 5 mi. W Memphis; Hemphill Co.: Canadian; Kerr Co.: Kerrville; Leon Co.: Peeler; Limestone Co.: Mexia; Montgomery Co.: Conroe; Victoria Co.: Victoria; Wichita Co.: Burkburnett, Red River; *Virginia*: Blue Ridge Parkway: Miles 162, 167, 210; Shenandoah Nat'l Pk., Mile 95; Washington Co.: Blacksburg; *West*

Virginia: Greenbrier Co.: White Sulphur Springs; Hardy Co.: Wardensville; Pendleton Co.: Cheat Mts.; Wisconsin: Madison; Wood Co.: Cranmoor.

Copris fricator cartwrighti Robinson, new combination

Copris cartwrighti Robinson, 1941, Trans. American Ent. Soc. LXVII: 131-132 [type: Cashiers Valley Road, Oconee Co., S. C., 16 Oct. 1934; United States National Museum].

DESCRIPTION. Differs from *fricator fricator* (F.) in that both sexes are always devoid of any cephalic or pronotal armament: the head horn is represented by a low transverse tumosity; the pronotum may be strongly convex in larger individuals but it never shows any distinct prominences or carinae. In addition, the elytral interstriae are somewhat more densely punctate than in *f. fricator* (see discussion below).

DISTRIBUTION. The mountainous portions of extreme northwestern South Carolina at over 2000 ft. altitude. One specimen from the coast at Charleston, S. C.

BIOLOGY. Found under cow dung. From the collected material it appears that this form is most active during the cooler months of the year. I could not find it in May, at a time when *f. fricator* was very active a little further north.

REMARKS. This form was described by Robinson as a distinct species distinguished from *fricator* by the absence of horns or thoracic protuberances. As we have seen, specimens of *fricator* often lack this armament, particularly in southwestern populations. A better character for distinguishing this form is the denser puncturation of the elytral interstriae, but even this does not serve to distinguish many individuals of *cartwrighti*. To be specific, in comparing 15 individuals of *cartwrighti* with an equal number of *fricator* from adjacent North Carolina populations, counting the number of punctures in a single row in 2 mm. of length at the middle of the left fourth interstria, the following ranges were obtained: *cartwrighti*—15-24 punctures, *fricator*—13-19 punctures. The means were 19.26 and 15.93 respectively. Adopting a criterion recommended by Mayr et al. (1953), one sees that these differences are below the conventional level of subspecific distinctness. The form would not merit recognition were it not for its apparent geographical separation from *f. fricator*. In May, 1959, in an attempt to determine the exact limits of the two forms, I collected under cow dung in Western North Carolina and extreme

northwestern South Carolina in the type locality of this form. Unfortunately I was unable to find *cartwrighti*, but *fricator* was abundant in dung at an altitude of 2500 ft. and higher near Asheville, N. C., or about 55 air miles away from the *cartwrighti* locality. In the intervening distance neither form could be found at all at any altitude. The other closest records of *fricator* are at Balsam and Sunburst, N. C., at an approximately equal distance away. This sort of negative evidence is not conclusive, but it does suggest the presence of an hiatus between the ranges of the two forms, and until connecting specimens are proved to be present in the intervening areas it seems best to retain this form as a distinct subspecies, particularly as there is some evidence that *cartwrighti* is a winter form.

MATERIAL EXAMINED. Eight male and seven female paratypes, one additional specimen.

UNITED STATES: *South Carolina:* Charleston Co.: Charleston, May 1944 (R. Peters), 1 (USNM); Oconee Co.: Cashiers Valley Rd., 3, 16 Oct. 1934 (O. L. Cartwright), 5 ♂♂, 6 ♀♀ (OLC, USNM); [Walhalla Federal] Fish Hatchery, 28 Apr. 1939 (O. L. Cartwright), 2 ♂♂, 1 ♀ (OLC, USNM); Jocassee, 13 Jul. 1936 (O. L. Cartwright), 1 ♂ (OLC).

Copris howdeni Matthews and Halffter

Copris howdeni Matthews and Halffter, 1959, Ciencia XVIII (9-10): 200-202 [type: Oneco, Manatee Co., Fla.; United States National Museum].

DESCRIPTION OF MALE. *Head.*—Unarmed. Clypeus bidentate, the teeth approximated, very low, with a very shallow U- or V-shaped notch between them, not cutting through the margin. Posterior angles of genae subquadrate. Upper surface of head entirely, densely, evenly punctate, the punctures umbilical except along margin of clypeus. Posterior oblique carina absent. Occipital margin with transverse setigerous groove broken into several sections. Demarcation between gula and submentum variable, arcuate or broadly angulate, in one specimen forming a median V. *Thorax.*—Pronotum unarmed. Anterior angles with the point slightly expanded into a small rounded tooth. Lateral margin angled out at origin of lateral carina. Lateral carina evident but not sharp, running straight from margin to lateral fossa. Anterior margin of pronotum not forming any median point. Median

longitudinal sulcus visible only on middle of disc, faint. Pronotum entirely, evenly, densely punctate, the punctures umbilical, separated by a distance equal to somewhat less than their diameter. Anterior prosternal margin with a distinct quadrate median tooth; sternellum only slightly convex, grossly umbilico-punctate. Median lobe of metasternum coarsely umbilico-punctate except along midline; median longitudinal groove complete. *Elytra*.—8th stria complete; 9th arising from 10th about halfway down elytron; 10th complete. Striae crenulate, broad, flat, devoid of punctures. Interstriae completely flat, densely and coarsely umbilico-punctate, the punctures separated by a distance equal to somewhat less than their diameter. *Abdomen*.—Pygidium very densely umbilico-punctate, the margin usually complete. *Anterior legs*.—Ventral surface of femur entirely, densely umbilico-punctate, the punctures smaller anteriorly. Forespur gradually narrowing to a point, the apex curved sharply inward and slightly downward. *Middle legs*.—Coxa with numerous umbilical punctures. Ventral surface of femur densely punctate over entire surface. Tibia below with 2–3 seta tufts and usually a row of seta insertions up its length. *Posterior legs*.—Femur and tibia as described for middle legs. *Total length*.—13–14 mm.

DESCRIPTION OF FEMALE. With the clypeal teeth slightly more prominent and the notch between them deeper, otherwise identical to male. *Total length*.—15 mm.

DISTRIBUTION. Fig. 19. Known from two localities in central Florida.

BIOLOGY. Unknown. All specimens were collected at light in the month of March.

REMARKS. This species and *f. cartwrighti* Robinson represent isolated southern populations apparently derived from *f. fricator* (F.). It differs in no respect from *fricator* specimens of similar size except in the coarsely and densely punctate, rugose, and absolutely flat elytral intervals. Its separation from *fricator* as a full species is based primarily on its geographical isolation and appears justified on the basis of the great ecological and climatic differences between its habitat and that of *fricator*.

MATERIAL EXAMINED. Four males (holotype and three male paratypes), one female.

UNITED STATES: *Florida*: Manatee Co.: Oneco, 23, 25 Mar. 1954, 26 Mar. 1955 (D. M. Anderson, W. W. Boyle, G. E. Ball), 4 ♂♂ (CU, USNM, GII, HH); Polk Co.: 3 mi. SW Lake Marion, 14 Mar. 1956 (H. Howden), 1 ♀ (HH).

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PLATES.

- Fig. 20. Granular umbilical puncture on pronotal submarginal of *C. incertus*, much enlarged.
- Fig. 21. Granular setigerous puncture on metasternum of *C. incertus*, much enlarged.
- Fig. 22. Umbilical puncture on pronotal submargin of *C. armatus*, much enlarged.
- Fig. 23. Setigerous puncture on posterior margin of proepimeron of *C. armatus*, much enlarged.
- Fig. 24. Head of female *C. lugubris*, dorsal view.
toc—transverse occipital carina
tog—transverse occipital groove (entire)
- Fig. 25. Head of female *C. rebouchei*, dorsal view.
poc—posterior oblique carina
tog—transverse occipital groove (divided into three parts)
- Fig. 26. Ventral view of *C. fricator*.
lpc—longitudinal proepimeral carina
ml—median lobe of metasternum
pc—pleural carina
pp—prosternal-proepisternal suture
- Fig. 27. Posterior view of inside of prothorax showing position of deeply sunken coxa, diagrammatic.
cx—coxa
stn—sternellum
trm—tergal remotor muscle, in two parts

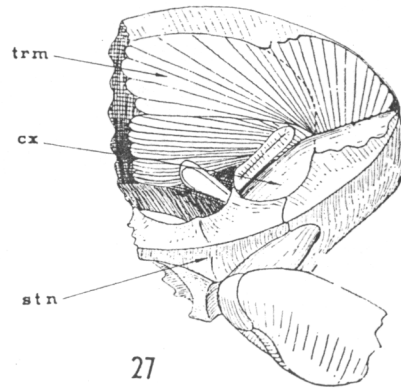
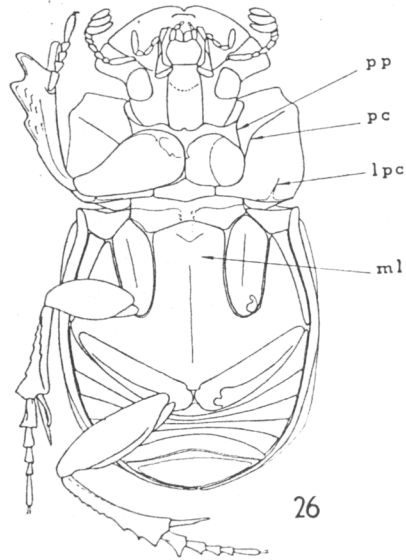
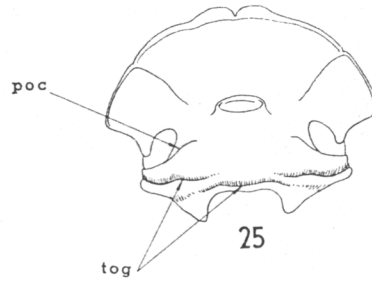
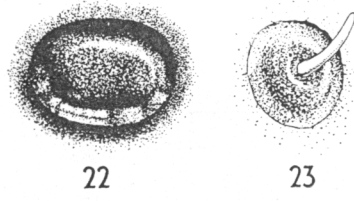
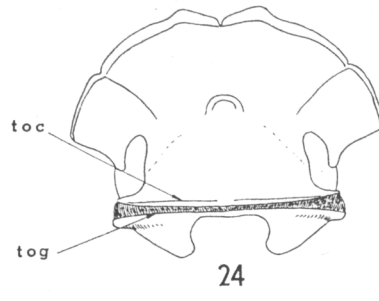
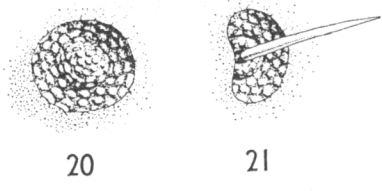
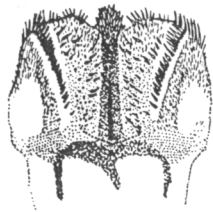


Plate II

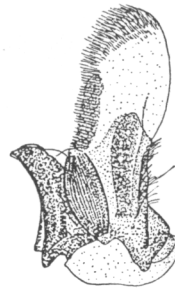
- Fig. 28. Labrum-epipharynx of *C. gopheri*, ventral view.
Fig. 29. Left mandible of *C. gopheri*, dorsal view.
 a. Same, in ventral view.
Fig. 30. Labium and left maxilla of *C. gopheri*, ventral view.
Fig. 31. Left maxilla of *C. gopheri*, dorsal view.
Fig. 32. Hypopharynx and ligula of *C. armatus*, three-quarter dorsal view. Positions of labial palpi represented by dotted outlines.



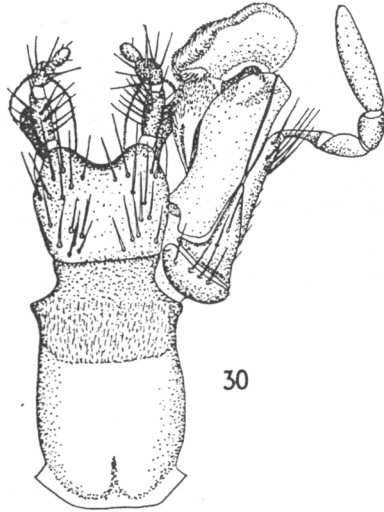
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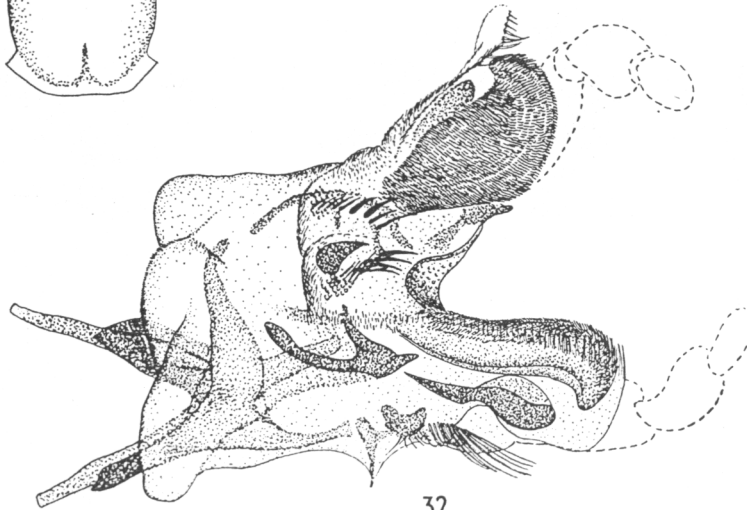
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Figs. 33-48. Right tibial forespur in direct dorsal view.

- Fig. 33. *C. lugubris*
 34. *laeviceps*
 35. *gopheri*
 36. *minutus*
 37. *armatus*
 38. *klugi*
 39. *arizonensis*
 40. *lecontei*
 41. *subpunctatus*
 42. *halffteri*
 43. *remotus*
 44. *mexicanus*
 45. *sallei*
 46. *costaricensis*
 47. *inemarginatus*
 48. *fricator*

Fig. 49. Right hind tibia and tarsus of *C. fricator* in ventral view.
 st—ventral and distal seta tufts

Fig. 50. Right hind tibia and tarsus of *C. lugubris* in dorsal view.
 ss—supplementary setae

Figs. 51-57. Median processes of anterior margin of prosternum,
 much enlarged.

- Fig. 51. *C. minutus*
 52. *armatus*
 53. *lecontei*
 54. *rebouchei*
 55. *halffteri*
 56. *inemarginatus*
 57. *fricator*

Figs. 58-60. Pygidia.

Fig. 58. *C. rebouchei*, pygidial margin incomplete.

59. *lecontei*, pygidial margin interrupted, completed by punctures.

60. *halffteri*, pygidial margin complete.

Fig. 61. Genital capsule of male *incertus* showing apical dorsal hook on paramere.

Fig. 62. Genital capsule of *lugubris* showing absence of apical hook.

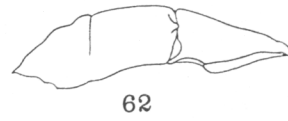
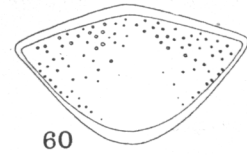
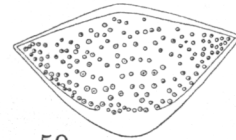
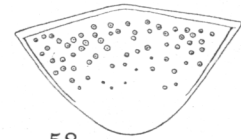
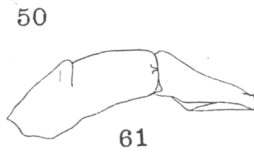
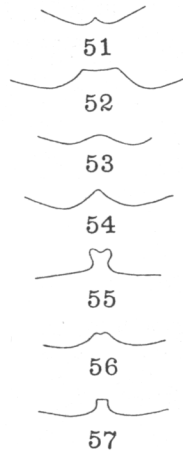
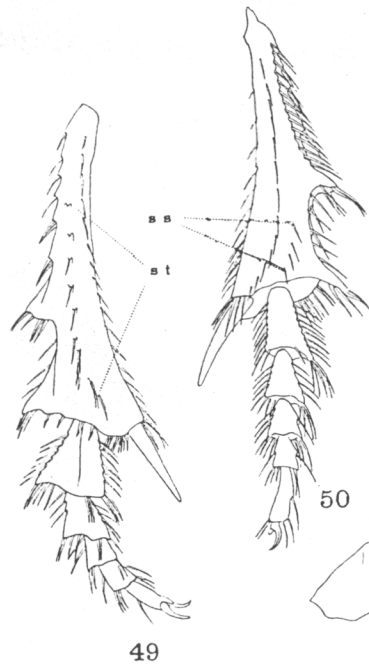
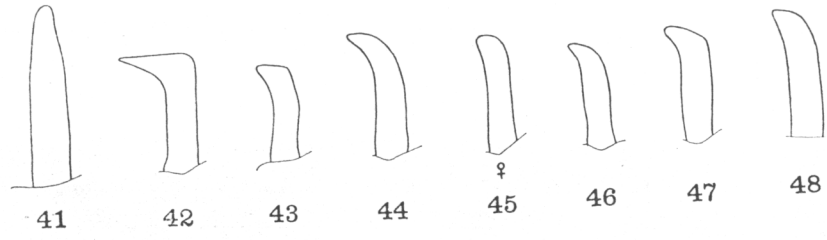
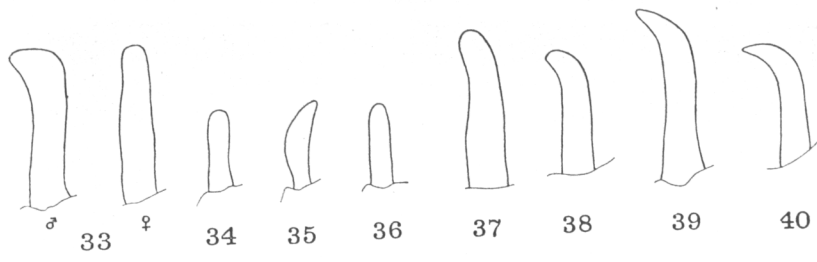
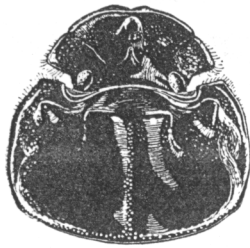


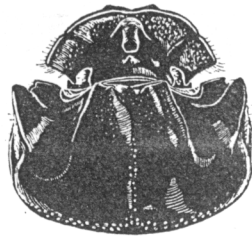
Plate IV

Forebodies of major males in dorsal and lateral views.

- Fig. 63. *C. incertus*, Jalapa, Ver.
- Fig. 64. *C. lugubris*, Managua, Nic.
- Fig. 65. *C. minutus*, Clarksville, Fla.
- Fig. 66. *C. fricator*, Pittsburgh, Pa.
- Fig. 67. *C. mexicanus*, holotype, Tancítaro, Mich.
- Fig. 68. *C. arizonensis*, Alpine, Tex.



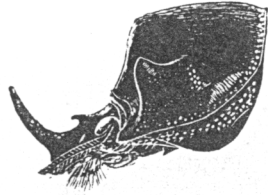
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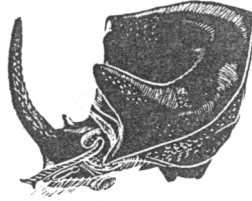
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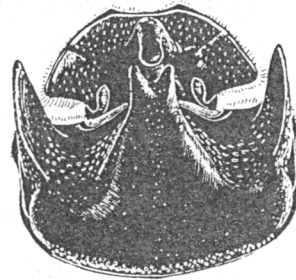
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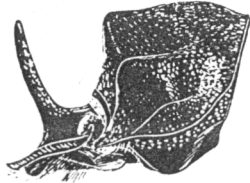
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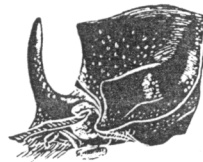
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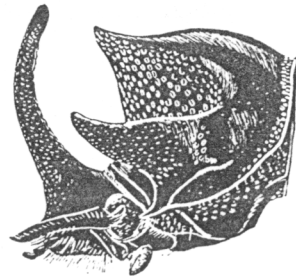
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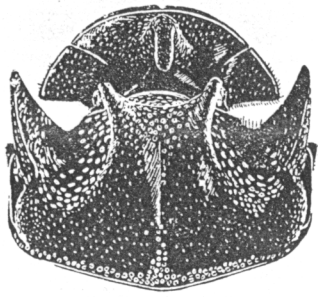
Plate V

Forebodies of major males in dorsal and lateral views.

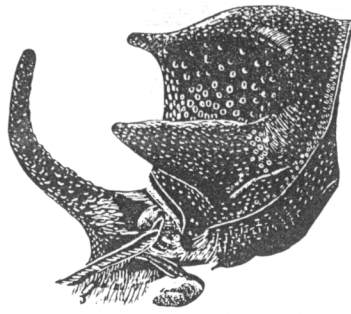
Fig. 69. *C. armatus*, Tancítaro, Mich.

Fig. 70. *C. megasoma*, holotype, Tancítaro, Mich.

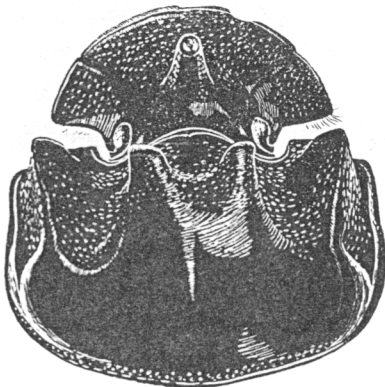
Fig. 71. *C. klugi*, Temascaltepec, Méx.



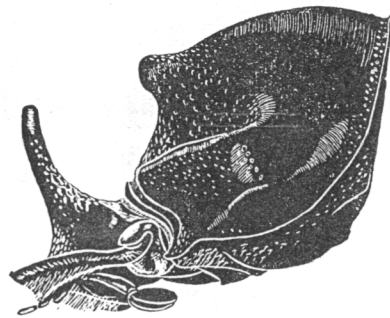
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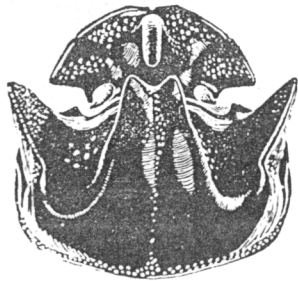
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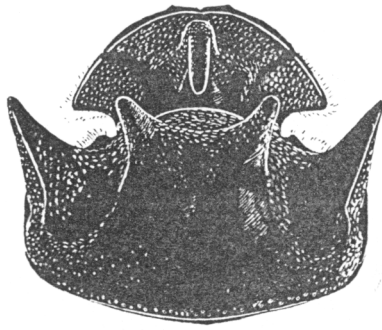
Plate VI

Forebodies of major males in dorsal and lateral views.

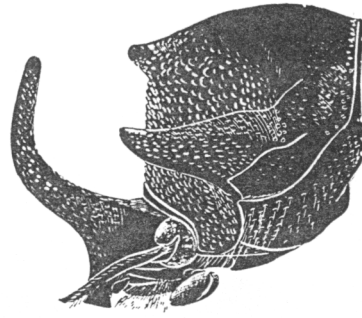
Fig. 72. *C. subpunctatus*, San José, C. R.

Fig. 73. *C. boucardi*, Guatemala.

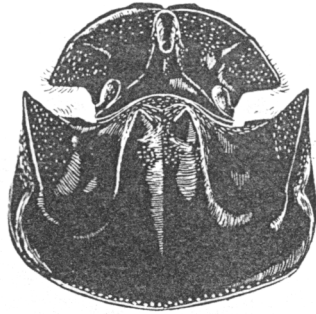
Fig. 74. *C. aspericollis*, Guatemala.



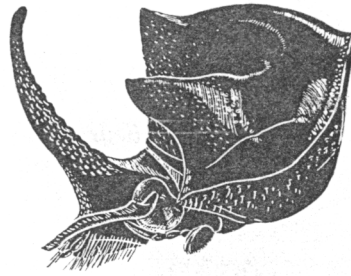
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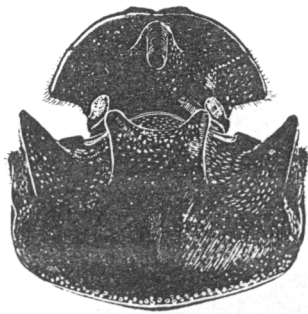
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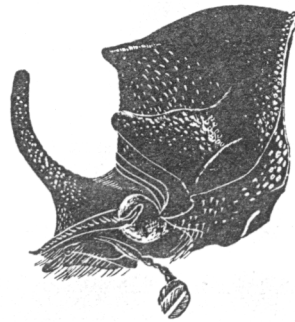
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Plate VII

Forebodies of major males in dorsal and lateral views.

- Fig. 75. *C. lecontei*, Tucson, Ariz.
- Fig. 76. *C. rebouchei*, Tequesquitengo, Mor.
- Fig. 77. *C. halfteri*, holotype, Cacahuamilpa, Gue.
- Fig. 78. *C. r. remotus*, Texas.
- Fig. 79. *C. r. dicyrtus*, holotype, Victoria, Tamps.
- Fig. 80. *C. costaricensis*, Azahar de Carboga, C. R.
- Fig. 81. *C. moechus*, Sta. Bárbara, Chih.



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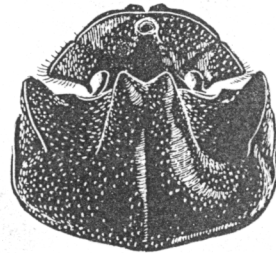
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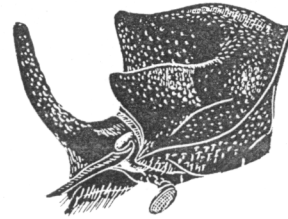
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Plate VIII

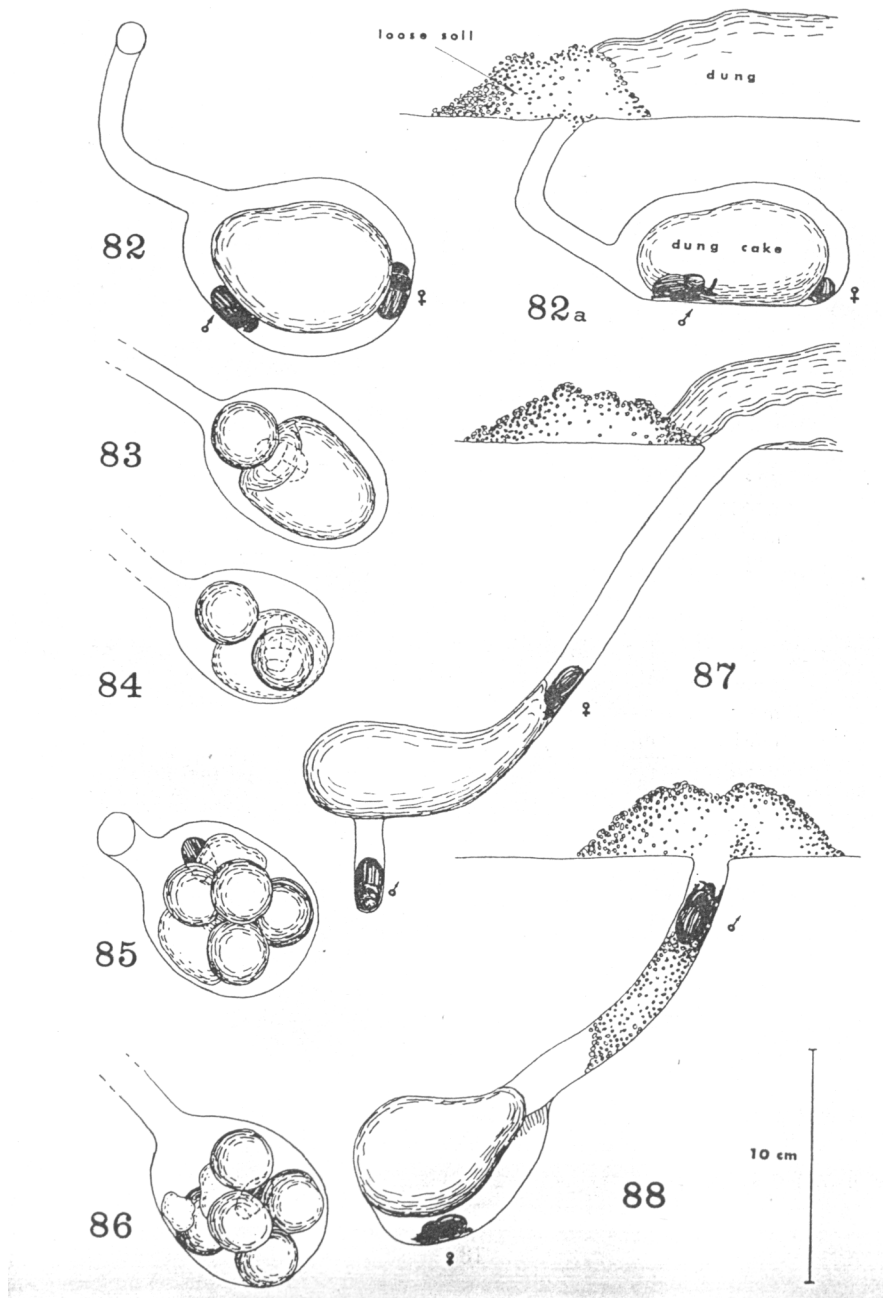
Nest diagrams of two species of *Copris* showing positions of beetles at moment when nests were uncovered. Redrawn from field sketches.

Fig. 82. *C. fricator*, dung cake before cutting of brood ovoids, in top view. North Carolina.

a. Same, in lateral view.

Figs. 83-86. *C. fricator*, different nests in top view showing successive stages in the fashioning of the brood ovoids from one to five completed ovoids. Irregular lumps are part of original dung cake. Beetle present is the female only. North Carolina.

Figs. 87-88. *C. lugubris*, two different nests showing spaces beneath dung cake and tunnel partially blocked with loose soil in lower figure. Nicaragua.



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