

MORPHOLOGICAL COMPARISONS OF COPRINAE, APHODINAE AND GEOTRUPINAE (COLEOPTERA, SCARABAEIDAE)*

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INTRODUCTION

Adult scarabaeid beetles have been the subject of but three studies concerned with their external morphology. The first of these, by Straus-Dürckheim (1828) treats the common European cockchafer, *Melolontha vulgaris*; the second, by Willcox (1896), treats *Phyllophaga* (*Lachnosterna*) *fusca*, one of the common June beetles; and the third, by Hayes (1922), covers *Phyllophaga crassissima*, another common June beetle. Straus-Dürckheim's study is beautifully illustrated, but largely beyond use because the author worked under the handicaps of a very new and undeveloped science. Willcox's study is sketchy and of a semi-popular nature, leaving the work of Hayes as the only modern and usable account.† These studies concern three genera of phytophagous scarabs; the large and peculiar group of scavengers is untouched. It is hoped that the present study will offer a better understanding of the life and habits of the latter group.

Three large subfamilies of these scavengers or dung-eaters are represented in Illinois: the Coprinae, the Aphodinae, and the Geotrupinae. Our common tumble-bug, *Canthon laevis* (Drury) was collected for study as a representative of the first subfamily; *Aphodius fimetarius* (L.), the copper-winged aphodius, represents the second subfamily; and *Bolbocerosoma bruneri* Dawson and McColloch, represents the last, selections being made to combine simplicity of structure with ease of collection. The tumble-bug and the copper wing were taken in good numbers at St. Joseph and Urbana, Illinois, while *Bolbocerosoma* came from Rapidan, Minnesota, as well as from Urbana.

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† Since this writing Roger B. Friend has published "The Asiatic Beetle in Connecticut," as Bulletin 304 of the Connecticut Agricultural Experiment Station.

ACKNOWLEDGMENTS

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TAXONOMIC RELATIONSHIPS

A short summary, taken in part from Leng (1921), is given below to show the taxonomic position of the beetle selected from each subfamily for study. Only closely related genera are listed, and the particular one studied is in italics.

Family Scarabaeidae

Subfamily Coprinae

Tribe Scarabaeini

Genera *Canthon**Deltochilum**Megathopa*

Tribe Coprini

Subfamily Aegialiinae

Subfamily Aphodiinae

Tribe Aphodiini

Genera *Aphodius**Oxymus*

Tribe Eupariini

Tribe Psammobiini

Subfamily Ochodaeinae

Subfamily Hybosorinae

Subfamily Geotrupinae

Tribe Bolbocerini

Genera *Bolboceras**Odontaeus**Bolbocerosoma**Eucanthus*

Tribe Geotrupini

Subfamily Pleocominae

Subfamily Golaphyrinae

Subfamily Acanthocerinae

Canthon heads the list as the simplest in structure. *Aphodius* follows, occupying a position between *Canthon* and *Bolbocerosoma*.

Scarabs can be recognized by the lamellate antennae (Figs.

35, 36, 37) and the fact that the epimera of the mesothorax extend to the coxae (Figs. 53, 54, 55).

The three subfamilies represented in this study have the following structural modifications in common, according to Dawson (1922): "Abdominal spiracles situated in the membrane connecting the sternites and tergites, the last spiracle covered by the elytra; ligulae always distinct from the mentum; the species all living on decomposing organic matter, many of them in excrement and a few in dung."

The Coprinae are further modified so that they may be known by the short and rounded outline, expanded clypeus which hides the mouthparts from dorsal view; hind tibiae usually with a single spur; last tarsal segment usually without the two erect setae between the claws; elytra truncate; pygidium exposed and abdomen with six firmly united sternites.

Aphodinae are small beetles of cylindrical form bearing two spurs on the posterior tibiae; entire elytra covering the pygidium; free sternites and bearing two erect setae on the fifth tarsal segment, between the claws. Mandibles and labrum are rarely visible from above.

Geotrupinae are rounded and convex, of good size, with prominent mandibles and labrum, 11-segmented antennae, and covered pygidium.

HABITS

Digging is an important bit of work of any scarab and is doubly important to the dung-eaters. All of them have broadened front tibiae with scalloped margins (Figs. 50, 51, 52) and so arranged that they can be swung into use front and side where they are most efficient in scraping away the soil. Dung eating is another common habit but its demands are not answered so uniformly; *Canthon* and *Aphodius* have soft and sensitive labrum, maxillae and mandibles (Figs. 25, 28, 31, 33) easily useful in manipulating the soft food. These parts are hidden from dorsal view by the clypeus which is broad and scoop-like (Figs. 7, 9) so that dung and dirt may be "nosed" aside by upward thrusts of the head. *Bolbocerosoma* departs from this, its mandibles, maxillae, and labrum (Figs. 29, 34) being strongly chitinized and exposed by a normal clypeus (Fig. 11).

Canthon spends a large part of its time above ground in the sun, walking, flying, and modelling dung balls. Long and fairly

thin legs give it the freedom that neither *Aphodius* nor *Bolbocerosoma* have or demand in their subterranean life. Its legs are bowed in addition, so that it may grasp its dung ball with pincher-like effect, its hind and middle tarsi being well set with spines to facilitate holding and manipulating it.

Aphodius spends most of its time burrowing in the dung of cows or horses, a soft medium. It uses its sturdy hind and middle legs in horizontal piston-like thrusts to push the body along. These hind and middle legs are made up of a succession of cone-like swellings each crowned with a half-circle of spines that are effective on the backward thrust but slip easily through the dung when pulled forward.

Bolbocerosoma is one of the earth borers, so called because it digs straight and narrow tubes into the earth. Its legs, like those of *Aphodius*, are sturdy, and are also spined, enabling it to clamber up and down in its perpendicular burrow. The body, as nearly a perfect hemisphere as that of any insect, enables the beetle to pivot on its legs anywhere in the burrow and "about face," doing away with the necessity of a chamber in which to turn.

SIZE, SHAPE, AND COLOR

Both the dorsal and ventral surfaces of *Canthon* (Fig. 1) are convex, the ventral structures thereby being thrown into view. Even the propleuron is easily visible. A dorsal outline is broad through the elytra, tapering gently toward either end. *Aphodius* (Fig. 4) is cylindrical in dorsal view, its ends rounding off abruptly. Laterally it shows much less of the ventral structures than *Canthon*, in which the vertical distance from the dorsum to the edge of the elytra does not exceed the vertical distance from the edge of the elytra to the ventral surface. The prothorax is prolonged ventrally so as to cover most of the pleuron from lateral view. In *Bolbocerosoma* (Fig. 5) all of the pleuron is hidden from this view. The abdomen, meso- and metasterna are intermediate in convexity between those of *Canthon* and *Aphodius*.

Genus	Color	Length	Shape
<i>Canthon</i> .	Dull black, slightly bronzed.	11-19 mm.	Sub-ellipsoidal.
<i>Aphodius</i> .	Shining black, and coppery.	6.5-8.5 mm.	Sub-cylindrical.
<i>Bolbocerosoma</i> .	Black and orange.	10-13 mm.	Sub-hemispherical.

EXTERNAL SEXUAL DIFFERENCES

The antennae, which frequently show sexual dimorphism in Sscarabaeidae, show none in these three species. Where cephalic tubercles occur, as in *Aphodius* and *Bolbocerosoma*, they are more prominent in the male than in the female. In *Bolbocerosoma* those which lie on the meson of the female are represented by a horizontal ridge in the male. Males of *Canthon* show a deeper emargination of the ninth sternite than do the females (Fig. 2). *Bolbocerosoma* (Fig. 6) approaches this difference; the ninth sternite of the males is truncate at the tip, while that of the females is not. Males of *Canthon* are peculiar in having the protibial spur broadened at its distal end (Fig. 3).

Genus	Female	Male
<i>Canthon</i> .	Protibial spur slender, pointed. Last sternite with shallow notch.	Protibial spur triangular or bifurcate. Last sternite with deeper notch.
<i>Aphodius</i> .	Cephalic tubercles small. Lacks dorsal prothoracic depression.	Cephalic tubercles larger. Dorsal depression on prothorax.
<i>Bolbocerosoma</i> .	Cephalic tubercles small.	Cephalic tubercles larger.

HEAD

Dorsal Aspect: The most striking difference occurs in *Bolbocerosoma* (Fig. 11) which has both its mandibles and labrum plainly visible and chitinous. The clypeus is not expanded, occurring as a subrectangular piece distad of the front. In *Canthon* (Fig. 7) and *Aphodius* (Fig. 9) both mandibles and maxillae are hidden by the greatly expanded clypeus which is fused with the canthus along its lateral margin. The canthus of *Bolbocerosoma* is not fused with the clypeus and is angular.

Both clypeus and front in *Canthon* are without tubercles although two teeth occur, one on each side of the meson along the cephalic margin of the clypeus. The front in *Aphodius* bears three tubercles in a transverse row; that of *Bolbocerosoma* is similarly armed in the male, but bears a transverse ridge in the female. Both sexes of *Bolbocerosoma* bear a tubercle on the clypeus in addition, but those of *Aphodius* are unarmed.

Ventral Aspect: The ventral view of the head of *Aphodius* (Fig. 10) is striking in being dilated laterally to such an extent as to leave the articulations of the maxillae, and the entire inner margin of the eye exposed to view. These parts in *Canthon* and *Bolbocerosoma* are hidden by the base of the maxilla. In both *Canthon* and *Aphodius* the clypeus appears ventrally, but in *Bolbocerosoma* it does not. The latter shows its mandibles in this view.

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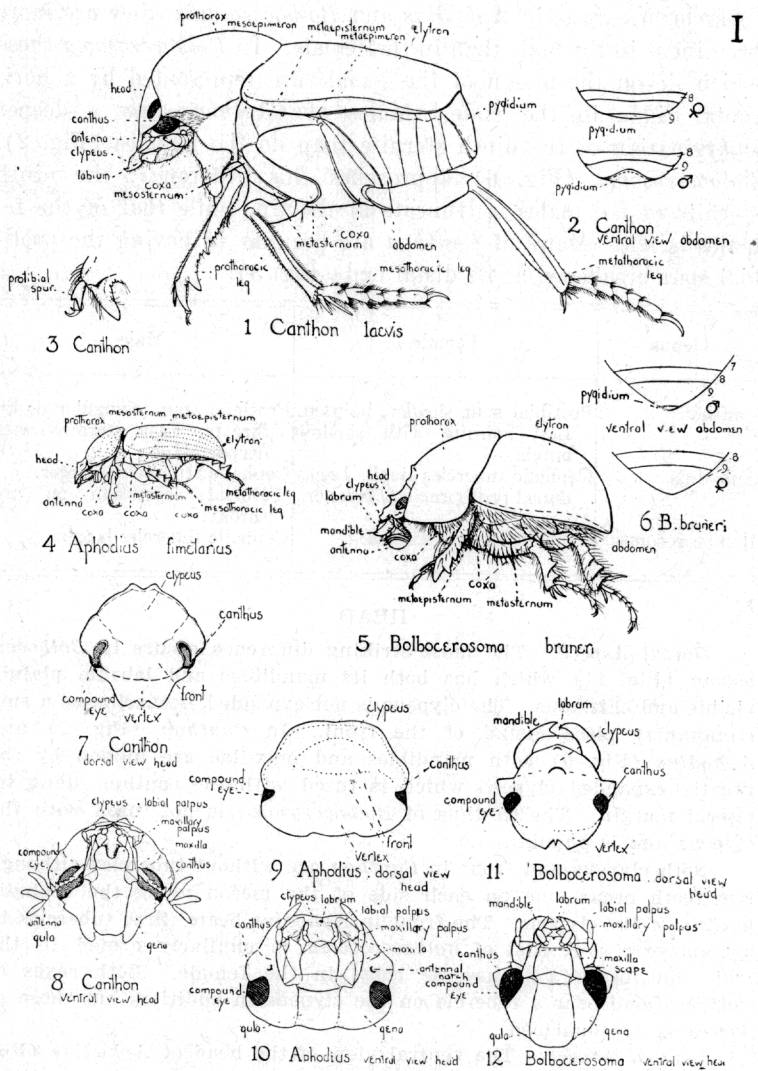


PLATE I.

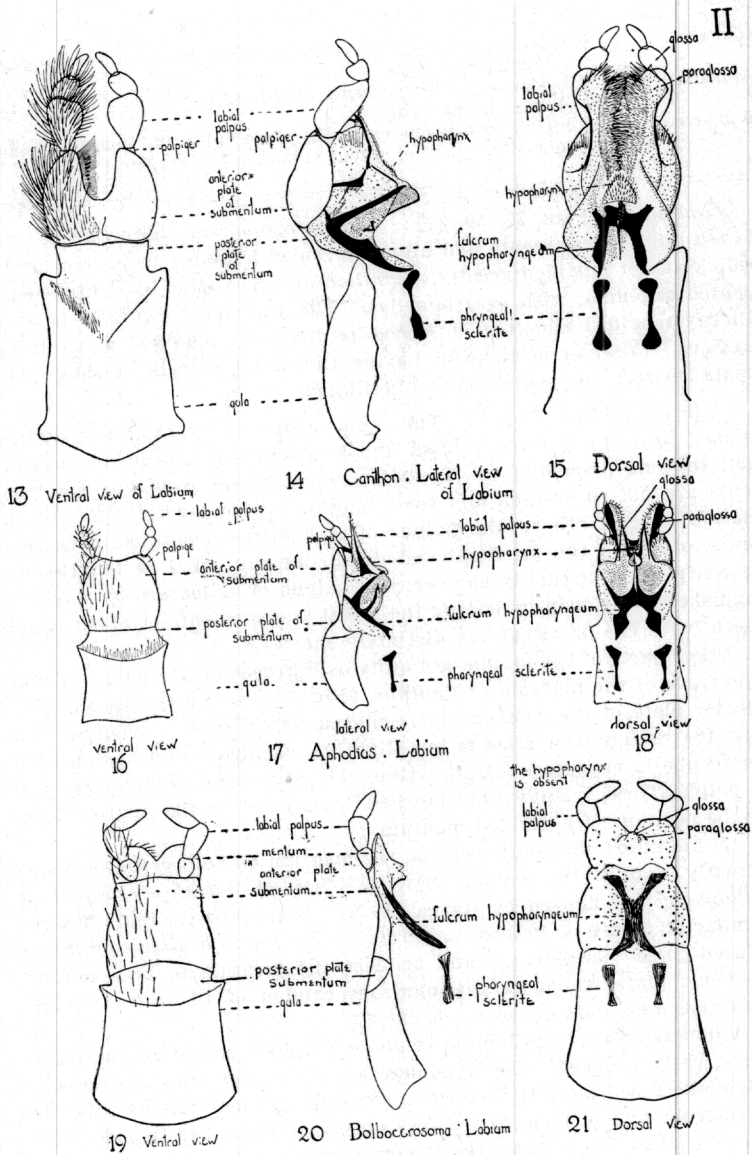


PLATE II.

Genus	Head characters
Canthon.	Clypeus expanded, covering mouthparts, base of antennae hidden by maxillae.
Aphodius.	Clypeus expanded covering mouthparts, base of antennae not hidden by maxillae.
Bolbocerosoma.	Clypeus not much expanded, mandibles and labrum visible dorsally. Base of antennae hidden by maxillae.

Antennae (Figs. 35, 36, 37): *Bolbocerosoma* is unique in having eleven antennal segments and almost circular lamellae in its club. Its pedicel is not modified greatly. *Canthon* and *Aphodius* have nine segmented antennae with oval lamellae. The pedicel of *Canthon* is only slightly modified and that of *Aphodius* distinctly modified as a larger segment. *Canthon* is alone in having the distal margin of those segments between the pedicel and club dilated.

Labrum (Figs. 13-21): The labial palpi of *Canthon* are distinguished by being greatly swollen and in having each segment shorter than the one preceding it. In *Bolbocerosoma* and *Aphodius* the segments are not so swollen and their lengths are somewhat different in relation to each other: the palpus of *Aphodius* consists of three segments, of which the proximal and distal one are equal in length and the central one distinctly shorter; the palpus of *Bolbocerosoma* is distinguished in its turn by having the distal two segments of about equal length, with the proximal one distinctly shorter.

Other parts of the labium are quite as different as the palpi: There is no trace of the mentum of *Canthon* (Fig. 13) in ventral aspect. The anterior plate of the submentum is enormously bilobed. In *Aphodius* (Fig. 16) the anterior plate is but slightly emarginate and has on each laterocephalic margin a distinct triangular plate upon which are born the palpi. These triangles are labelled "palpifers" in the figure. They may be portions of a divided mentum.

If this interpretation is correct, the mentum of *Bolbocerosoma* is as distinctly visible in ventral view as that of *Lachnosterna* (now *Phyllophaga*) as figured by Hayes (1922). Hardenberg (1907) figures a similar structure of *Bolboceras farctus* (now *Bolbocerosoma farctum*) as fused galea (paraglossa) and believes the mentum to be a narrow transverse plate which he distinguishes caudad of it. Such a plate seems absent in *Bolbocerosoma bruneri*.

A dorsal view of the labium of *Bolbocerosoma* shows all the structures greatly reduced: the hypopharynx is reduced, the glossae and paraglossae fused mesally to form a three lobed membranous tubercle. The fulcrum hypopharyngeum shows only a straight bar in side view.

In *Canthon* the hypopharynx is a triangular chitinous plate bearing spines and in *Aphodius* it is less chitinous and bears soft hairs. In *Canthon* the paraglossa of either side is partially fused with the glossa. Both form a long tongue-like lobe, chitinized on its outer margin and bearing an abundance of soft hairs on the inner margin.

Those of *Aphodius* are fused throughout their length, are chitinized on the outer margin, and sparsely setaceous on the inner margin. In side view, the fulcrum hypopharyngeum is v-shaped.

Maxillae (Figs. 22, 23, 24): The chitinous distagalea sets *Bolbocerosoma* in its own class. In the other two species it is a membranous lobe heavily setaceous on its dorsal surface. The lacinia of *Bolbocerosoma* is different, being a slightly curved spur whereas that of *Canthon* and *Aphodius* is membranous and setaceous on the dorsal surface. The lacinia of the latter two differ slightly: that of *Canthon* consists of a single lobe while that of *Aphodius* is bi-lobed. The subgalea of *Bolbocerosoma* is peculiar, having a sharp tooth, if my interpretation is correct. Hardenberg (1907) believes this to be a portion of the lacinia, but I find no suture separating it from the subgalea, hence believe it a prolongation.

The maxillary palpi are strikingly different: the proximal segment of the palpi of *Canthon* is acutely elbowed; that of *Aphodius* is cylindrical and only very slightly bent; while that of *Bolbocerosoma* almost escapes observation, being very short and straight. *Canthon* is also peculiar in that the distal segment is longer than the second by one-third while that of the others does not greatly exceed the second in length.

The remaining parts of the maxillae are not greatly differentiated although the proxagalea and stripes of *Canthon* are connected. The general shape of the maxillae of *Bolbocerosoma* is narrow; that of *Aphodius* short and broad; and that of *Canthon* intermediate.

Mandibles (Figs. 25, 28, 29, 30): The mandibles of *Bolbocerosoma* are different in being almost entirely chitinized, the membranous acia being the exception. Each bears a suprabrustia. Dentes are present on the inner apical portions and fit those of the opposing side. In *Canthon* and *Aphodius*, the entire apical half is membranous with its caphalo-mesal portions fitted with soft setae. A prostheca is present on the mandibles of both. Probably the most striking likeness between the three species is the convexity of the right mola and the concavity of the left.

Labrum-epipharynx (Figs. 31, 32, 33, 34): Some interesting differences occur in the development of the labrum-epipharynx. The dorsal view of this structure, or labrum proper will first be treated. It is membranous and bears cephalic setae in *Canthon* (Fig. 31) and *Aphodius* (Fig. 33). The labrum of *Aphodius* is essentially like it. The clypeus is dilated over it, hiding it from dorsal view. In *Bolbocerosoma* (Fig. 34) the labrum is entirely chitinous and half of its length is exposed cephalad of the clypeus, but it is attached to the clypeus on its ventral surface much as that of the other two and bears cephalic and lateral margins, besides a few others irregularly placed on its flat surface. *Canthon* (Fig. 31) and *Aphodius* are different in having this surface membranous and strengthened by chitinous arches and plates. The setae are more definitely arranged, each epipharynx having a row of mesally directed ones near its lateral margin with others scattered laterad and mesad of them. A set of spines on the

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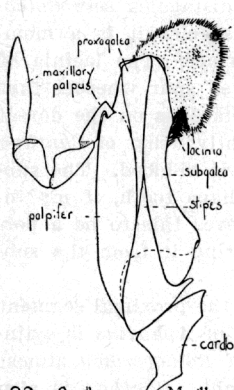
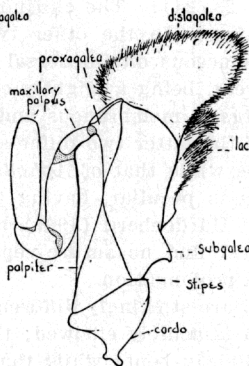
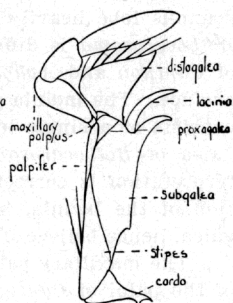
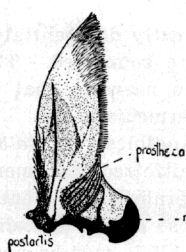
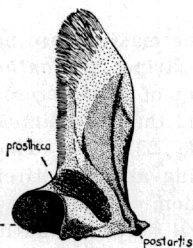
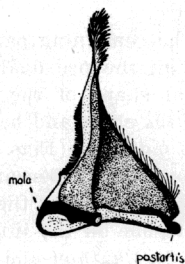
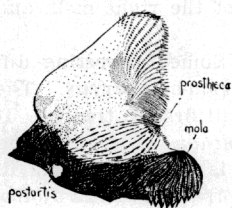
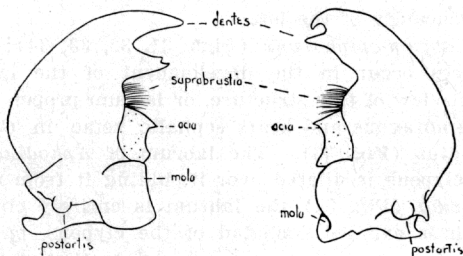
22 Carilhon : Maxilla
ventral view23 Aphodius Maxilla
ventral view24 Bolbocerosoma Maxilla
ventral view25 Right Mandible
Carilhon: Ventral View26 Mandible of Carilhon
Ventral View of Left Mandible27 Lateral View Carilhon
Right Mandible28 Right Mandible of
Aphodius
ventral view29 Right Mandible
Mandibles of Bolbocerosoma
ventral view30 Left Mandible
ventral view

PLATE III.

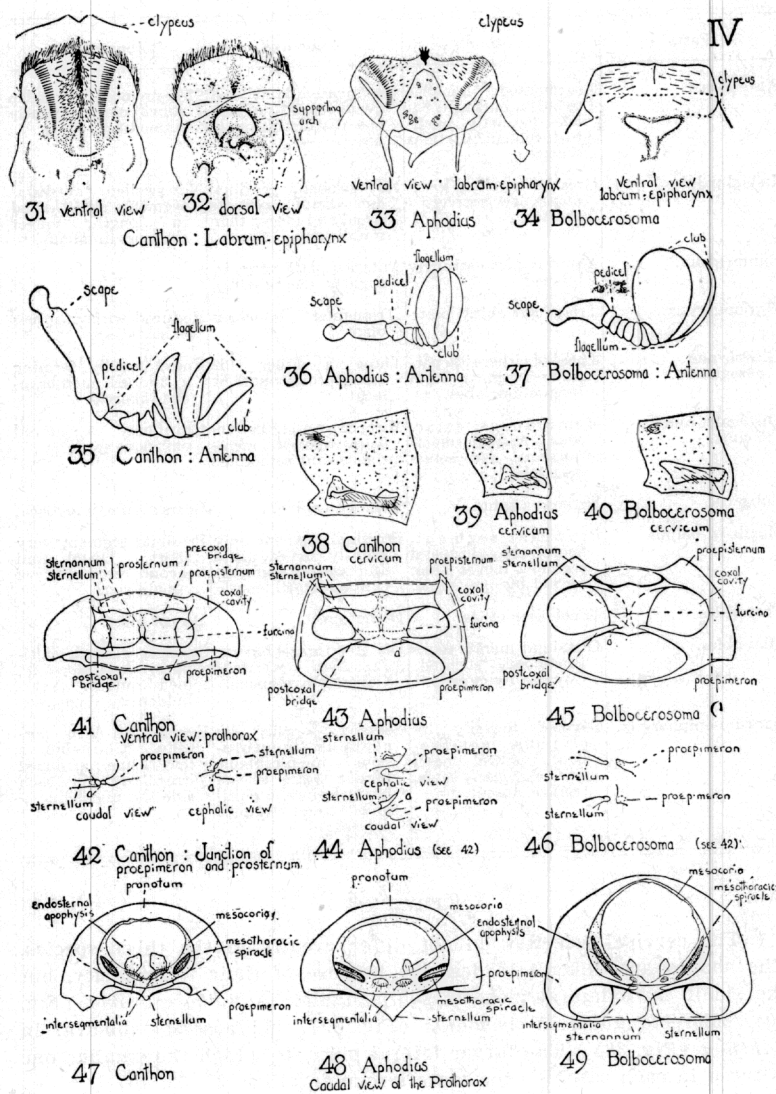


PLATE IV.

meson of the cephalic surface and a mesal, perforated, and triangular plate make the epipharynx of *Aphodius* different from that of *Canthon* which bears a mesal brush-like set of setae.

Parts	Canthon	Aphodius	Bolbocerosoma
Antennae.	9-segmented, lamellae ovoid in outline, pedicel distinctly modified, cephalic portions dilated.	9-segmented, lamellae X ovoid in outline, pedicel distinctly modified.	11-segmented, lamellae subcircular, pedicel unmodified.
Labial palpi.	Greatly swollen, segments successively shorter.	Not swollen, proximal and distal segments equal and longer than middle one.	Not swollen, two distal segments about equal in length, longer than proximal one.
Submentum.	Anterior plate strongly bilobed.	Anterior plate very slightly emarginate.	
Hypopharynx.	Triangular spiny plate	Triangular setaceous plate.	Reduced, without spines or setae.
Glossae and paraglossae.	Those of either side partially fused to form tongue-like lobes.	Those of either side fused throughout their length.	Fused mesally, forming a 3-lobed membranous tubercle.
Distagalea and lacinia.	Membranous, setaceous. A single membranous and setaceous lobe.	Membranous, setaceous, bilobed, membranous and setaceous.	Chitinous. A curved chitinous spur.
Subgalea.	Without a spine.	Without a spine.	Bears a spine-like tooth.
Maxillary palpus.	Proximal segment, acutely elbowed, distal segment longer than second by one-third.	Proximal segment only slightly curved, distal and second segments of about equal length.	Proximal segment very short. Distal and second segments of equal length.
Proxagalea.	Touch each other.	Do not meet.	Do not meet.
Mandibles.	Distal end membranous. Prostheca striated. Covered by clypeus.	Distal end membranous. Prostheca striated. Covered by clypeus.	Strongly curved, chitinous. Acia alone membranous. Not hidden by clypeus.
Labrum-epipharynx.	Covered dorsally by clypeus, membranous, ventral mesal line bears many setae, triangle absent.	Covered dorsally by clypeus, membranous meso-cephalic border bears set of heavy spines, a chitinous mesal triangle present.	Exposed to view dorsally, Chitinous, a few setae arranged irregularly on each side the mesal line.

CERVICUM

The cervical sclerites do not differ greatly in the three species. The shapes are difficult to describe because of their irregularity, but the small caudo-lateral piece is subtriangular in *Bolbocerosoma* (Fig. 40), sub-rectangular in *Aphodius* (Fig. 39), and possibly sub-oval in *Canthon* (Fig. 38). The larger lateral piece, to which the smaller one is fused in each case, is even more irregular (Figs. 38, 39, 40).

THORAX

Prothorax (ventral aspect) (Figs. 41, 43, 45): The narrow prothoracic and subtriangular pleura of *Canthon* are distinctive. The tip of its post coxal bridge (Figs. 42, 44, 46) is bilobed and articulates in a

double branched socket in the sternellum, while that of *Aphodius* and *Bolbocerosoma* consists of a single lobe fitted into a single socket. In *Aphodius* and *Bolbocerosoma*, the pleura are reduced to bands between the ventral edge of the pronotum and the coxal cavities. The outline of the ventral view of the prothorax is subquadrate for *Aphodius* and semicircular in *Bolbocerosoma*.

Prothorax (caudal aspect) (Figs. 47, 48, 49): A caudal view of the prothorax of *Aphodius* (Fig. 38) shows the sternellum greatly bent downward as compared with the other two species. *Bolbocerosoma* (Fig. 49) is peculiar in showing much of the coxal cavities in this view; in having very elongate mesothoracic spiracles and almost minute intersegmentalia. The intersegmentalia of the other species are much larger.

Prothoracic Legs (Figs. 50, 51, 52): The coxa of each bears a transverse ridge near its distal margin. This is most prominent in *Aphodius*, less so for *Bolbocerosoma* and faint for *Canthon*. The femur of the latter bears on its proximal cephalic surface a slight depression from which grows a great brush of soft setae. This is represented in *Aphodius* by a long brush of similar setae and lost in *Bolbocerosoma*. The tibia of each species is characteristic: that of *Canthon* bears three teeth on its lateral margin. Between these, there may or may not be smaller ones, the number varying even on the leg of either side. Between the first prominent tooth and the proximal end of the tibia are about a dozen small ones. The number varies on the leg of either side, and with age or wear. A distal spur, varying in shape with the sex and tarsus of which the first segment is longer than the next three and protected by an expansion of the tibia complete the armature. *Aphodius* also bears three prominent tibial teeth. Smaller ones are present on the proximal portion but none between the larger set. The tarsus is distinct by reason of having its proximal segment shorter than the second and no longer than the third or fourth. The first segment is unprotected. The claws bear two setae between them.

The tibia of *Bolbocerosoma* is distinguished by its armature of approximately eight teeth which become successively larger from the first to the last. Like the previous two species, it bears a single apical spur. Its tarsus is unprotected and the first four segments are of nearly equal length, distinguishing it from *Canthon* and *Aphodius*.

Meso- and Metasterna (Figs. 53, 54, 55): The metaepimeron of *Aphodius* touches the mesocoxal cavity, distinguishing it from both *Canthon* and *Bolbocerosoma*. Both the latter are again distinguished from the first by the fact that the mesoepimeron is prolonged mesally in them so as to reduce the anterior margin of the mesosternum. *Canthon* is in its turn distinguished from *Bolbocerosoma* and from *Aphodius* by having the mesosternum reduced to a narrow band and in having the coxal cavities penetrate deeply into the metasternum.

Mesotergum and Elytra: *Canthon* stands alone in having more parts than the scutellum easily visible dorsally and in having the mesotergum entirely covered when the elytra are at rest. The tip of

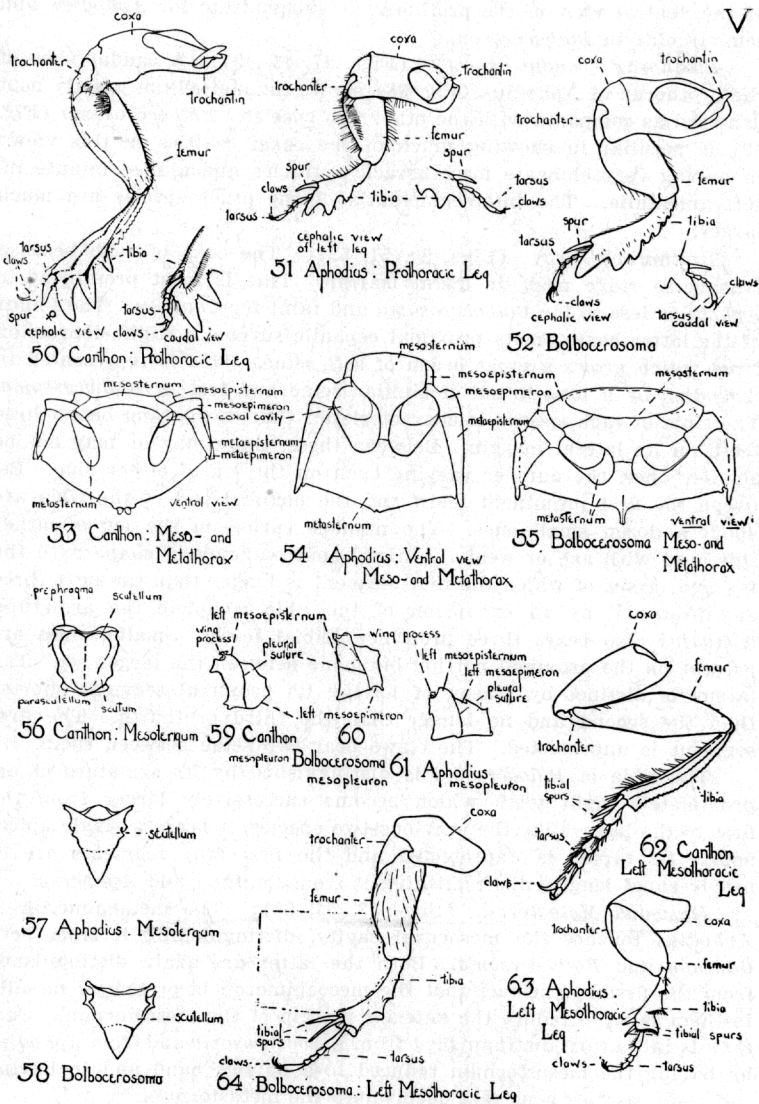


PLATE V.

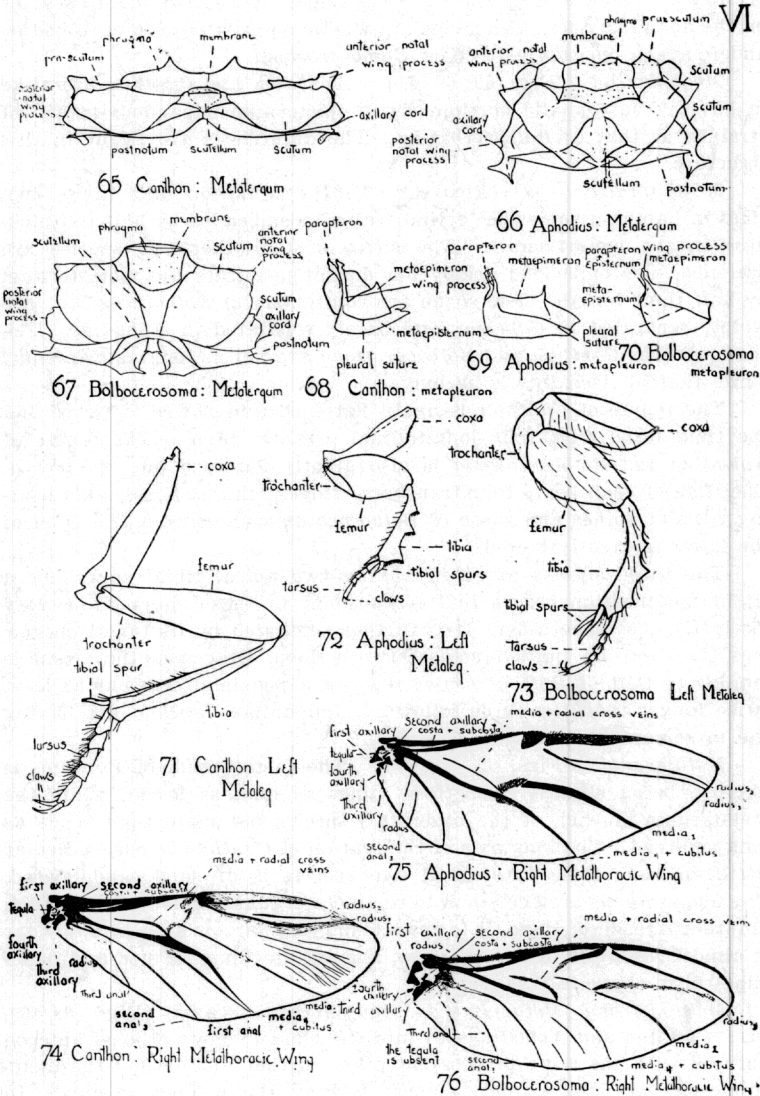


PLATE VI.

the scutellum of the remaining species is exposed and assists in locking the elytra in place.

Each elytron of *Canthon* bears eight very faint striae, of which the punctures are visible only on the inner surface; the elytral striae of *Aphodius* and *Bolbocerosoma* are stronger and the punctures show on the dorsal surface. Ten striae are visible on each elytron of *Aphodius* and fourteen on each elytron of *Bolbocerosoma*.

Mesopleuron (Figs. 59, 60, 61): *Aphodius* and *Canthon* are alike in having the cephalic portion of the episternum expanded instead of straight as that of *Bolbocerosoma*. The differences are slight in this structure.

Mesothoracic Legs (Figs. 62, 63, 64): *Canthon* falls in its own class in having a somewhat cylindrical coxa embedded by half its thickness in the metasternum. The coxae of the other two species are flattened, also embedded deeply but do not penetrate the metasternum by half their length. The coxae are contiguous in *Bolbocerosoma*; are widely separated in *Canthon*, and barely separated in *Aphodius*. The coxae of both *Canthon* and *Bolbocerosoma* are not as long as the femur while that of *Aphodius* is as long.

The femur of *Canthon* is again flattened and bowed upward, and the tibia fitted with four longitudinal crenate ridges. The femur of *Aphodius* and *Bolbocerosoma* is also greatly flattened but not bowed. The tibia of each bears four transverse ridges; those of *Aphodius* bearing rows of spines and those of *Bolbocerosoma* unarmed. The tibia of the latter is greatly bowed.

The three species agree in having two apical tibial spurs but a slight modification occurs in *Canthons* one of these spurs being very distinctly above the other. It is further separated by its tarsal characters, the claws having two setae between them. Otherwise the tarsus is similar to that of *Bolbocerosoma*, having a proximal segment at least twice longer than the three following, and unlike *Canthon* not having the tarsomeres compressed.

Metatergum (Figs. 65, 66, 67): The metatergum of *Canthon* is narrow, being slightly over three times as long as broad, while the metatergum of each of the other two species not more than twice as long as broad. The long axis of the scutum of *Canthon* is perpendicular to the meson; that of the next two species is directed caudo-mesad. The membranous area common to the metatergum of coleoptera is much different in each of these, it forms a short and narrow area in *Canthon*; is almost square in *Bolbocerosoma*, and intermediate in size and quadrilateral in shape in *Aphodius*.

Metapleurona, *Metaepimeron*, and *Metaepisternum* (Figs. 68, 69, 70): *Canthon* and *Aphodius* fall into one class in having the parapteron unfused with the wing process but differ in that in *Canthon* the metaepimeron does not extend caudally beyond the metaepisternum. In *Bolbocerosoma* they end on the same line and the parapteron is closely fused with the cephalic portion of the wing process.

Metathoracic Legs (Figs. 71, 72, 73): Some very distinct variations occur. When in position in the body, the coxa of *Canthon* is

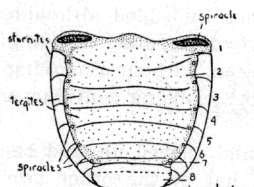
deeply imbedded between the third abdominal segment and the metathorax so that it barely breaks the regular outline. It is not as long as the femur. Two abdominal sternites are entirely concealed from view by it, leaving six exposed. It stands alone in this respect: the coxa of *Aphodius* being longer than the femur; that of *Bolbocerosoma* exactly as long; and both being flattened but not imbedded although they do extend backward so that in *Aphodius* two sternites are concealed and in *Bolbocerosoma* four may not be seen without removing the coxa. The coxae of the three species are alike in being contiguous on the meson.

The femur of *Canthon* is slightly flattened and curved upward being nearly four times as long as broad while that of the other two species is not more than one-third longer than broad, greatly flattened and not curved upward.

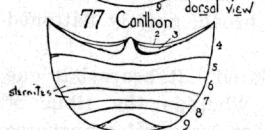
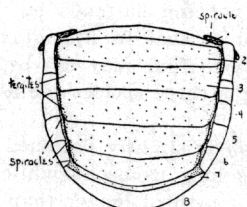
Tibial characters again leave *Canthon* isolated. It bears but one spur and four longitudinal, crenate ridges, whereas the tibia of *Aphodius* and *Bolbocerosoma* bears two spurs and several transverse ridges. The likeness of the latter two ends here: the ridges on the straight tibia of *Aphodius* number three and each bears a single row of spines; four unarmed transverse ridges cross the tibia of *Bolbocerosoma* which is it greatly bowed inwardly.

Parts	Canthon	Aphodius	Bolbocerosoma
Prothoracic intersegmentalia. Prothoracic legs.	Intersegmentalia prominent. First tarsal segment protected by expanded tibia and exceeds the combined length of the next three. Paired erect setae are not found between the claws.	Intersegmentalia prominent. First tarsal segment unprotected, shorter than the second and equal in length to the third and to the fourth. Two erect setae between the claws.	Intersegmentalia minute. First tarsal segment unprotected, and equal in length to each of the next three. Paired erect setae are absent between the claws.
Meso and Metasterna.	Metaepimeron fails to touch the mesocoxal cavity. Mesoepimeron prolonged mesally reducing the anterior portion of the mesosternum. Coxal cavities penetrate deeply into the metasternum.	Metaepimeron touches the mesocoxal cavity. Mesoepimeron not modified so as to restrict the anterior portion of the mesosternum. Coxal cavities do not penetrate deeply into metasternum.	Metaepimeron fails to touch the mesocoxal cavity. Mesoepimeron prolonged mesally reducing the anterior portion of the mesosternum. Coxal cavities do not penetrate deeply into metasternum.
Mesotergum and Elytra.	Scutellum covered entirely when wings are closed.	Part of scutellum visible when wings are closed.	Part of scutellum visible when wings are closed.
Mesothoracic legs.	Coxae cylindrical widely separated. Tibial spurs of unequal length, set on same level. Tarsomeres compressed.	Coxae flattened, nearly touch mesally. Tibial spurs of nearly equal length. One set above the other. Tarsomeres not compressed.	Coxae flattened, touch mesally. Tibial spurs of nearly equal length. Tarsomeres not compressed.
Metathoracic legs.	Coxae imbedded over two abdominal tergites, hiding them. Bear only one tibial spur. Tarsal segments compressed and the proximal one hardly longer than the next three. Lacks two erect setae between the claws.	Coxae compressed, not embedded, but conceal two abdominal tergites. Bear two tibial spurs. Tarsal segments not compressed, and the proximal one being at least twice as long as any of the next three. Bears two erect setae between the claws.	Coxae compressed, not embedded, but conceal four abdominal tergites. Tarsal segments not compressed and the proximal one being at least twice as long as any one of the next three. Lacks two erect setae between the claws.
Metathoracic wing.	Tegula present.	Tegula present.	Tegula absent.

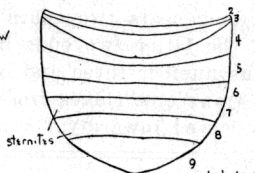
VII



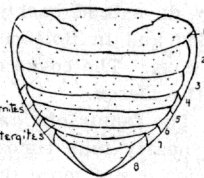
77 Canihon

78 Canihon: Abdomen
of Male83 Canihon: Female
Genitalia

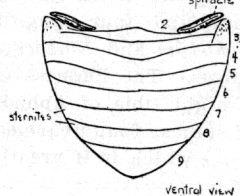
79 Aphodius: Abdomen



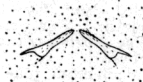
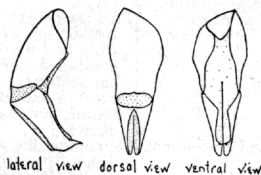
80 Aphodius: Abdomen



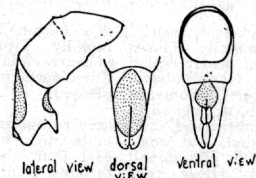
81 Bolbocerosoma



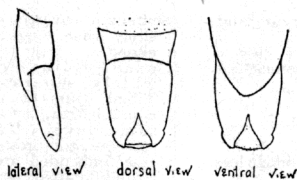
82 Bolbocerosoma: Female

85 Bolbocerosoma
Female Genitalia

87 Aphodius: Male Genitalia



86 Canihon: Male Genitalia



88 Bolbocerosoma Male Genitalia

The tarsal segments of *Canthon* are compressed and the proximal one is barely longer than three distad of it. The proximal segment of the other two species is at least twice as long as any one of the three following it. *Aphodius* is distinct in bearing two setae between the claws.

Metathoracic Wing (Figs. 74, 75, 76): The metathoracic wings of *Canthon* and *Aphodius* bear tegulae; that of *Bolbocerosoma* is without. The anterior margin of the costa of *Canthon* bears setae on its apical half. None occur beyond the weak point at which the wing folds. In *Aphodius* these setae are shortened to form a sawlike edge. A few hairlike ones are found beyond the "joint" or weak point. This portion of the wing of *Bolbocerosoma* is similar. *Bolbocerosoma* stands alone in having a few fine setae on a vein which is labelled "second anal₂." It again stands alone in having but one radical branch whereas, *Canthon* and *Aphodius* have radius₂ and radius₃ present. *Canthon* is peculiar in showing a well-developed first anal vein and in having between radius₂ and media, many fine veins, *Bolbocerosoma* bears some thickening at this point which are not figured because of some uncertainty that they are veins.

Abdomen (Figs. 77, 79, 81): The abdomen of each species is as broad as long. In *Canthon* and *Aphodius*, it is terminally blunt; in *Bolbocerosoma* it terminates rather sharply. Eight tergites are present. In *Canthon* they are almost membranous except the last which is chitinous in the three species; in *Bolbocerosoma* almost as chitinous as its tergites; and in *Aphodius* somewhat intermediate in chitination. The first tergite of *Canthon* is broader than any of those following and is not completely marked off by a suture from the second. The first tergite of *Bolbocerosoma* is almost incompletely marked off by a suture, but differs from *Canthon* in having only a mesal portion visible dorsally, being somewhat reduced. The first tergite of *Aphodius* is completely marked off and is narrow as compared with any of the following six, but not as narrow as the seventh. The pygidium or eighth tergite is chitinous, triangular, and exposed only in *Canthon* when the elytra are at rest.

The abdominal spiracles number seven pairs for each species and are found on the membrane connecting the sternites with the tergites. When the elytra are at rest, they are covered except for the peculiar first pair of *Bolbocerosoma*. The first spiracle on either side is narrowly oval and transverse. Its position for each of the three species is significant. It is very evidently dorsal in *Canthon*; in *Bolbocerosoma* it is very evidently ventral; while in *Aphodius* its position is intermediate but still to be seen in dorsal as well as lateral aspect.

The six remaining spiracles are small and circular in the three species. They are very plainly exposed in *Canthon*, but in *Bolbocerosoma* much manipulation is necessary in order to see them, for the tergites are expanded laterally covering them deeply. In *Aphodius* the condition is somewhat intermediate, but none of its spiracles are visible without some manipulation.

The sternites (Figs. 78, 80, 82) number eight for each species, and these, according to Hayes (1922), represent the second to the ninth, the first having become reduced. The second and third bend abruptly inward as a provision for the metathoracic coxae and are embedded partially between the metathorax and third sternite. They are not as heavily chitinized as those which are exposed. In *Canthon*, the ninth and last is deeply notched, so that the tip of the pygidium is exposed, the notch being greater for the male than for the female. In *Bolbocerosoma* this segment is triangular in the female, preventing a ventral view of any part of the pygidium, but for the male it is somewhat truncate showing a bit of the pygidium. In *Aphodius* there is no sexual difference evident and the pygidium is not to be seen in ventral aspect.

Parts	<i>Canthon</i>	<i>Aphodius</i>	<i>Bolbocerosoma</i>
Abdomen.	The eighth tergite exposed when the wings are closed. First abdominal spiracle dorsal in position. Sternites closely fused.	The eighth tergite covered when the wings are closed. First abdominal spiracle dorso-lateral. Tergites articulate freely.	The eighth tergite covered when the wings are closed. First abdominal spiracle ventral in position. Tergites articulate freely.

Female Genitalia (Figs. 83, 84, 85): Homologies seem not difficult to make. Paired chitinous plates occur on each side of the meson. Those of *Canthon* are one third as broad as long and are club-shaped; those of *Aphodius* are strap-like and twisted each approaching an S in shape; and those of *Bolbocerosoma* are somewhat triangular, half as wide as long at the broadcast point and sparsely setaceous.

Male Genitalia (Figs. 86, 87, 88): Without examination of a number of intermediate forms, it is not well to attempt to homologize the parts of the male genitalia of *Bolbocerosoma* (Fig. 88) with those of the other two species, which are very evidently similar. Possibly the distal segment is homologous with the distal segment of the other two. This part differs chiefly from the other two in being greatly depressed.

There can be no doubt about the homologies of the genitalia of *Canthon* and *Aphodius* (Figs. 86, 87). The basal pieces are homologous and also the distal pieces. These differences occur: The basal piece is caudally asymmetrical in *Aphodius* and the chitinous portion is not closed ventrally. In *Canthon* it is symmetrical and closed. A dorsal membranous area connects both pieces in *Aphodius*; in *Canthon* the entire connecting area is chitinous. In *Aphodius* the dorsal portion of the distal piece is membranous to its caudal end, in *Canthon* the membrane is limited caudally by a chitinous bar arising from the lateral chitination. The ventral membrane of the same piece is terminated only at its distal end by a sharp terminal tooth arising from each lateral chitination in *Aphodius*; in *Canthon* it is limited at about the middle by a similar tooth.

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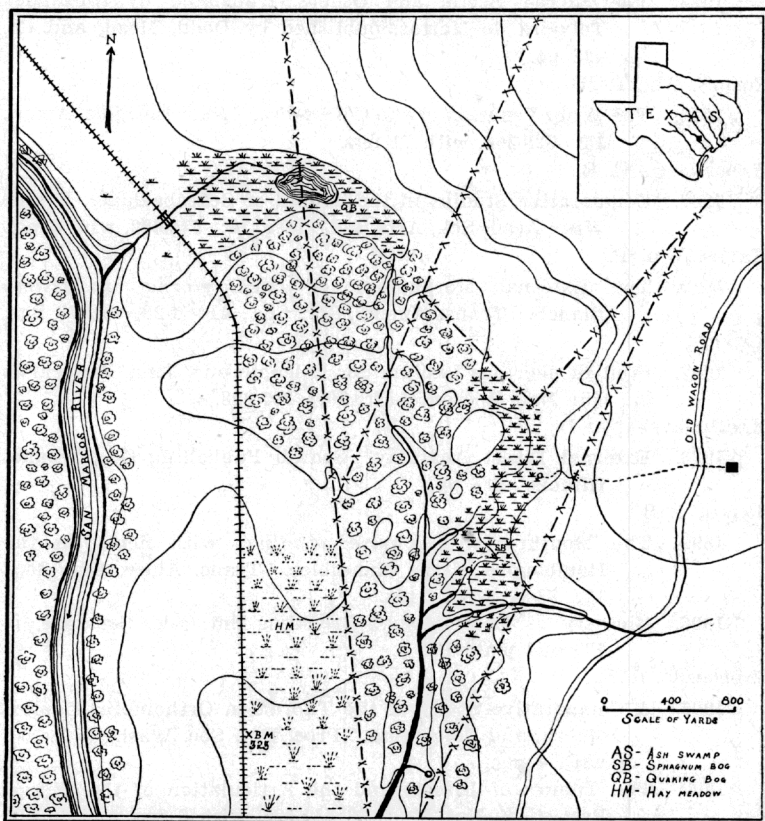
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Sketch map of bog area.