The external male genitalia of some Rhynchophora

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INTRODUCTION

Today there is an increasing recognition among taxonomists of the importance of consideration of the complete morphology of insects in classifying them and in arranging them in their logical phylogenetic sequence. Regarding the Rhynchophora, with which this paper is concerned, some progress toward a more complete understanding has been made. In 1912 Sharp and Muir made a study of the male genital tube of the Coleoptera in general and observed that the various specializations they noted in the forms of Rhynchophora examined would doubtless be of future significance. Tanner in 1927 made a similar important study of the female genitalia and subsequently has included both the male and the female genitalia in descriptions of new species, as noted in his study of the subtribe Hydromoni. Stickney in 1923 examined and reported his findings on the head capsule. Boving and Craighead in 1931 published the results of their studies of the larval forms. Ting in 1936 reported the results of a rather comprehensive study of the mouth parts of the Rhynchophora alone.

The purpose of this study has been twofold:
1. To examine the external genitalia of as many varied forms as time would permit and to interpret, insofar as is possible, the phylogenetic relationships that exist. It is also proposed to determine to what extent the results of this study are in agreement with investigations that have been made concerning other parts of the anatomy of Rhynchophora.

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2. To determine if the morphological differences that exist between the genitalia of different species within the same genus are significant enough to warrant serious consideration of this structure in classification.

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SPECIES STUDIED

The following species that have been studied are listed as they appear in the first edition of Leng's Catalogue of the North American Coleoptera along with the two species from the Islands of the Pacific.

Family Brentidae

_Eupsalis minuta_ Drury. Figs. 3 a & b.

_Ectocnemus 10-maculatus_ Montr. P. Islands. Figs. 4 a & b.

Family Platystomidae

_Ischnocerus infuscatus_ Fabr. Figs. 12 a & b.

_Antheplus cornutus_ Say. Figs. 13 a & b.

Family Belidae

_Ithycerus norboracensis_ (Forst.) Figs. 2 a & b.

Family Curculionidae

Sub-family Rhynchitinae

_Rhynchites aeacus_ Boh. Figs. 6 a & b.

_Rhynchites bicolor zeickhami_ Clkl. Figs. 5 a & b.

Sub-family Atelabinae

_Atelabus bipustulatus_ Fab. Figs. 7 a & b.

Sub-family Pterocolinae

_Pterocolus ovatus_ (Fab.) Figs. 8 a & b.

Sub-family Cyladinae

_Cylas formicarius_ (Fab.) Figs. 9 a & b.

Sub-family Apioninae

_Apion pensylvanicum_ Boh. Figs. 15 a & b.

_Apion turbulentum_ Sm. Figs. 14 a & b.
Sub-family Otiorhynchinae

*Eupagoderes sordidus* (Lee.) Figs. 17 a & b.

*Dyslobus wasatchensis* Tamm. Figs. 16 a & b.

*Endiagopus pulcher* Fahr. Figs. 18 a & b.

*Coleccerus marmoratus* Horn. Figs. 29 a & b.

*Tanyneicus confertus* (Gyll.) Figs. 20 a & b.


Sub-family Curculioninae

*Phytonomus posticus* (Gyll.) Figs. 1 a, b, & c.

*Phytonomus nigriostris* (Fab.) Figs. 34 a & b.

*Hypera punctata* (Fab.) Figs. 36 a & b.

*Notaris puncticollis* (Lee.) Figs. 10 a & b.

*Notaris aethiops* (Fab.) Figs. 11 a & b.

*Dorytomus brevisetosus* Csy. Figs. 24 a & b.

*Tycheius lineellus* Lee. Figs. 38 a & b.

*Magdalis gentilis* Lee. Figs. 21 a & b.

*Magdalis lecontei tenebrosa* Fall. Figs 22 a & b.

*Balaniaus baculi* Chitt. Figs. 30 a & b.

*Anthonomus grandis* Boh. Figs. 31 a & b.

*Anthonomus squamosus* Lee. Figs. 32 a & b.

*Anthonomus eugenii* Cano. Figs. 33 a & b.

*Dinocles albovestitus* Csy. Figs. 26 a & b.

*Cleonus calandroides* (Rand.) Figs. 27 a & b.

*Lixus terminalis* Lee. Figs. 25 a & b.

*Odontocoryinus scutellum-album* (Say). Figs. 23 a & b.

*Mononychus vulpeculus* (Fab.) Figs. 28 a & b.

*Ceutorhynchus sulcicollis* (Payk.) Figs. 37 a & b.

*Rhinonecus pyrrhopus* Boh. Figs. 39 a & b.

*Cryptorhynchus pachyrhachis* (Hbst.) Figs. 35 a & b.

Sub-family Calendrinae

*Rhodobaenus tredecimpunctatus* (Ill.) Figs. 45 a & b.

*Scyphophorus yuccae* Horn. Figs. 44 a & b.

*Calendra parvulus* Gyll. Figs 40 a & b.

*Calendra destructor* Chitt. Figs. 41 a & b.

*Calendra zeae* Walsh. Figs. 43 a & b.

*Calendra ochreus* Lee. Figs. 42 a & b.

Family Scolytidae

Sub-family Scolytinae

*Scolytus ventralis* Lee. Figs. 46 a & b.

Sub-family Hylesininae

*Dendroctonus valens* Lee. Figs. 47 a & b.
The Rhynchophora examined were museum specimens from the collection at the Brigham Young University. The insects were relaxed by placing them in water and heating it, often to a boil. The abdomen was then removed under a binocular microscope and was placed in a solution of caustic potash, the strength of which was determined by the condition and the age of the specimen. The structure was boiled long enough to remove the fat and muscles. The tergites were removed from the abdomen, exposing the internal structures to full view in-situ. With a pair of hair-spring tweezers the structures were protruded from the abdomen. Since the study was concerned only with the morphology of the external genitalia no attempt was made to study those structures that normally lie within the abdomen during copulation. However, the testis and the ejaculatory duct were noted in many species.

Within the external genitalia are chitinized struts of varying length, the median struts of the median lobe and the tegminal struts. Often parts of these struts rested within the abdomen after the structures had been fully evaginated. In order to show them in their entirety, therefore, it frequently became necessary to detach the genital tube from the abdominal wall.

GENERAL MORPHOLOGY

The external genitalia of the Rhynchophora consists essentially of a tube, part of which is drawn within itself and has become chitinized to varying degrees. The innermost tube extends anteriorly where it joins another smaller tube of different origin, the ejaculatory duct, which extends into the abdomen where it branches to the testes. The outermost tube, which makes up the copulatory apparatus is attached to the eighth abdominal segment.

The origin of the external male genitalia has been the subject of much study and conjecture. Sharp and Muir speculated that since the genital tube lies posterior to the anus, no tergite could reasonably enter into its composition. They further assume that since the eighth sternite is the last plainly visible, the chitinized Y shaped rod (spiculum gastrale) that is found on the floor of the abdomen represents the ninth sternite.

Snodgrass states that the membrane which makes up the genital tube is the posterior part of the venter of the ninth primary somite, with the Y shaped rod (spiculum gastrale) representing the 9th sternite. He locates the anus within the dorsal remnant of the tenth.
Metcalf traced the development of the external genitalia in one of the curculionids, *Anthonomus pomorum* L., and in three other species of Coleoptera. The conclusions are not at wide divergence with those of Snodgrass or the speculations of Sharp and Muir. By making longitudinal sections of the developing genitalia in both the larval and pupal stages Metcalf was able to trace the development of the tube, including the formation and the chitinization of the various segments into which it subsequently becomes divided. On the basis of these investigations and a thorough review of the literature, including the work of foreign investigators, Metcalf has concluded that the external genitalia, including the spiculum gastrale that lies within the abdomen during copulation, develops from the endopodites of the ninth sternite and that, as such, this structure is homologous with the parameres of other insects.

In the adult, then, the external genitalia is attached to the eighth abdominal somite. When at rest the tube lies folded upon itself within the abdomen, being extruded at the time of copulation. Figure 1 illustrates the general form and method of attachment of the genitalia of *Phytomonos posticus* Gyll, one of the curculionids as it appears when extruded from the abdomen by the artificial method described. Viewed from both the dorsal and the lateral aspects the relationship of the various structures to each other can be discerned.

Insofar as it has been possible the terminology used to designate the various parts of the external genitalia is that used by Bissell in his paper on the study of the reproductive system of the pecan weevil. When terminology other than that used by Bissell was needed, the work of Sharp and Muir was relied upon. In the main the names used in the two studies are in agreement with specific differences noted as they occur. One term, inter-aedeagal structures, was coined by the author.

In a normal extruded genital structure the most posterior part of the tube is the median lobe (ml) which is essentially a chitinized portion of the tube itself. This structure varies considerably within the Rhynchophora from a simple trough in the Scolytidae and some Curculionidae to paired “plates” in the Brenthidae and others. Often these “plates” do not resemble such structures at all but are referred to as such for the purpose of clarity and uniformity.

Attached to, or articulating with, the median lobe are paired rods called the median struts (ms) that extend anteriorly. Their size, shape, and their method of attachment is variable. Bissell points out that these structures serve as points of attachment for some of the muscles used to manipulate the structure.
Within the median lobe, generally in a membranous area, is the median orifice (mo). This marks the place where the tube folds back within itself. The innermost tube is referred to as the internal sac (is). Sharp and Muir have indicated that in *Sphenuhornus obscurus* this sac develops as an extension of the genital tube, and that it is not evaginated into the median lobe until the pupa is ready to emerge. This being the case the median orifice is often very difficult to locate, particularly in the smaller specimens. The lines in the figures used to indicate the location of this opening do not necessarily indicate its size and shape since this is often impossible to determine with accuracy. Often the median orifice is bordered by one or two chitinized plates, the orificial plates (op). Their presence aids materially in the location of the orifice.

The apex of the internal sac where it connects with the ejaculatory duct (ed) is called the flagellum (f). In many species parts of the flagellum as well as parts of the internal sac are chitinized in various ways and to different degrees. Since these chitinized areas are not uniform, and since no name has been applied to them, I have labeled them as inter-aeогдаal structures (int. st.) since they occur in varying positions within the genital tube, which Bisell has called the aedeagus. In two species, *Rhinoscaphia lequilloui* Guer. and *Ithyereus nataebraecepis* (Forst.) this sac has been evaginated by grasping its sides through the median orifice and pulling it outward. This structure has been noted in connection with the narrative descriptions of both species and in one it has been illustrated.

Sometimes the ejaculatory duct can be discerned at its point of attachment to the flagellum and occasionally it can be traced throughout much of the aedeagus, but more often it cannot be identified with certainty beneath the membrane. At times the internal sac is not easy to locate, sometimes it cannot be seen. This is particularly true in those structure where the median lobe is tube-like or where the edges are inflexed dorsally. In some species the sac extends well beyond the ends of the median struts while in others it is very short. Sharp and Muir have indicated that during copulation in some species the internal sac is evaginated and consider this behavior to be the general rule. Since no species were observed in copula no additional light can be thrown on this by this study.

Anterior to the median lobe is another chitinized structure, the tegmen (tg) which may be present as a simple ventral plate, as a fork, as a simple ring with a ventral strut, or a ring with a strut ventrally and paired lobes or a pronounced cap-piece on its dorsal surface. The
ventral strut when present is referred to as the tegminal strut (ts).

Connecting the tegmen to the median lobe is the second connecting membrane (cm 2) referred to as the first connecting membrane by Sharp and Muir, Metcalf & Wilson. Since it is customary to number the abdominal segments from the anterior to the posterior, it seems reasonable that the connecting membranes should be numbered in a similar manner. Therefore the system of Bissel is adopted in this paper and the most posterior will be called the second. The membrane which connects the tegmen with the abdominal wall is the first connecting membrane (cm 1). In those forms where the tegmen is Y shaped or reduced to a ventral plate, the two membranes are continuous dorsally and laterally. In such cases the separation of the two is an arbitrary one, based on their location in relation to the tegmen. A similar situation is noted when the dorsal portion of the median lobe is membranous. This membrane is essentially a posterior extension of the second connecting membrane and is referred to as such, although it is recognized as being a part of the median lobe.

In some forms (Calendrinae) the first connecting membrane has become chitinized to varying degrees to form a “sleeve” around the tegmen. The degree of this chitinization is variable and sometimes is so slight that it is difficult to distinguish it from the adjoining membrane.

In many of those forms that possess a dorsal cap-piece or have paired lobes on the tegmen, the first connecting membrane is attached in such a manner that the ends of the cap-piece, or the lobes, are pulled upward and sometimes completely over as the aedeagus is drawn from the abdomen. Whether such an extreme condition as this occurs during copulation is questionable, but this adaptation is doubtless of some value during the performance of that act.

Within the abdomen, and lying on its ventral wall is a third chitinized structure referred to by Sharp and Muir as the “spicule” and by Wilson, Bissell and Metcalf as the spiculum gastrale (sg). Metcalf insists that this structure arises as a part of the aedeagus and that it serves as a basis of attachment for the powerful muscles that manipulate the external genitalia. Since it is normally not extruded with the external genitalia it has not been included in this study. An exception to this exists in the Calendrinae where, as a simple rod, it is attached to the ventral surface of the chitinized “sleeve” from which it extends anteriorly and slightly dorsally.
EXPLANATION OF PLATES

All drawings were made with the camera lucida attached to a binocular microscope. The drawings of Apion were doubled in size with dividers after the original tracings were made. Those areas that are stippled represent membrane, or very light chitin that cannot readily be distinguished from the membrane adjacent to it. Where this situation exists it has been noted in the narrative descriptions of the species involved. Those areas that are chitinized are indicated in two ways, either a solid black line or as clear areas. The choice of which to use has largely been determined by the comparative size of the structures involved as viewed from both the dorsal and lateral views. Dashed lines are generally used to indicate the borders of the internal sac and the sacs themselves are stippled more densely than the other membranous structures. The straight lines on the right side of the paired figures represent 1 mm.

As has been previously noted, it became necessary to detach some of the structures from the abdomen in order to see the anterior terminus of the median and tegmental struts. Therefore, for the sake of uniformity, all structures, with the exception of Figure 1, have been illustrated in that manner, that is, their point of attachment to the abdominal wall has not been shown since it did not appear to serve any particular purpose to include it.

In the following descriptions the various species that were examined have been grouped in what seems to be their most logical sequence on the basis of the external genitalia alone. It will be noted that the family Platystomidae is described following a group that includes some of the Sub-families of Curculionidae according to the arrangement of Leng’s Catalogue and that other Sub-families of Curculionidae follow the platystomids. The reasons for this arrangement are noted later in the paper.

In the figures those that are labeled “a” represent the dorsal view of the structure and those that are labeled “b” indicate that the figure illustrates the lateral aspect. The following abbreviations have been used:

- ml—median lobe
- ms—median strut
- mo—median orifice
- op—orificial plate
- is—internal sac
- f—flagellum
- int. st.—inter-acedagal structure
- sg—spiculum gastrale
- ej—ejaculatory duct
- tg—tegmen
- ts—tegmental strut
- cml—1st connecting membrane
- cp—cap-piece of tegmen
- cm2—2nd connecting membrane
DESCRIPTIONS OF STRUCTURES STUDIED

Family Belidae

Ithyergus novaboracensis (Forst.) Figs. 2 a & b.

The median lobe consists of two chitinized portions, the lower is a shallow trough, the upper a single strap-like piece that terminates in a U-shaped loop beyond which the membrane protrudes. This membrane contains the median orifice which is flanked by orificial plates. The dorsal strap piece forks anteriorly, each fork joining with a lateral extension of the ventral plate to form the median struts. The tegmen is a ring with a dorsal cap-piece which is roughly X shaped, the anterior forks of which are hirsute. The internal sac extends beneath and anterior to the tegmen. By careful manipulation with hair-spring tweezers the sac in this species was evaginated. It is longer than the medial lobe and its struts. On the ventral surface is a narrow chitinized strip that extends into the flagellum and on into the ejaculatory duct. This may be a flattened chitin tube since it appears very loosely attached to a membrane. About midway between the flagellum and the median orifice are two pouches, one dorsal and one ventral that project laterally. These pouches are braced on their margins by narrow strips of chitin which form a V. It is entirely possible that these serve as claspers during copulation or that the sac is normally not evaginated as far as it was by the artificial means used and that these are used in transferring sperms into the spermatheca of the female.

Family Brentidae

Characteristics of the Family: The median lobe consists of two plates, the lower is a shallow trough, fully chitinized laterally, but with a membrane or light chitin ventrally near the median line. The upper plate is chitinized laterally and apically, the center being either membrane or extremely light chitin. The median orifice is located in the terminus of a membranous pouch that extends posteriorly from between the two plates. It is flanked by orificial plates. The median struts fork posteriorly with one branch of each connected to the lateral edges of the dorsal and ventral plates respectively. The tegmen forms a Y ventrally with the forks articulating with the ventral projections of a dorsal cap-piece which is deeply forked posteriorly each of the forks hirsute near the apex. Inside the lateral edges of this cap-piece is a small chitin strip that is attached to the median struts on either side and serves to bind the tegmen to the median struts. The first connecting membrane is attached in such a manner as to pull the hirsute
ends of the cap-piece upward as the aedeagus is drawn from the abdomen. In both species the ejaculatory duct is visible as a small chitinitized tube which enters the flagellum near the anterior end of the aedeagus.

*Eupsalis minuta* Drury. Figs. 3 a & b.

The ventral plate of the median lobe is chitinized laterally, blending to membrane near the center. The dorsal plate is narrowly chitinized peripherally the balance being entirely membrane. The cap-piece of the tegmen is deeply forked and the hirsute ends are rather pointed:

*Ectocnemus 10-maculatus* Montr. Figs. 4 a & b.

The ventral plate of the median lobe is chitinized except for a very narrow strip mid-ventrally. The dorsal plate is largely chitin except for a membranous lumen medially. The median struts and the tegmental struts are both rather large. The hirsute forks of the dorsal cap-piece are rounded.

**Family Curculionidae**

Sub-families: Rhynchitinae, Attelabinae, Pterocolinae, Cyladinae.

Genus *Notaris* (Curculioninae).

**Characteristics of the Group:** The median lobe consists of two plates, the amount of chitinization of both variable. The median struts are forked posteriorly, one branch attached to the lateral edges of each of the plates. The tegmen is a ring with a dorsal cap-piece which normally projects posteriorly although it is sometimes pulled upward and anteriorly by the first connecting membrane as the aedeagus is drawn from the abdomen. The cap-piece has either a single or a double lobe.

*Rhynchites bicolor wickhami* Ckll. Figs. 5 a & b.

The lower plate of the median lobe is very lightly chitinized medially. The upper plate is narrow and thin, the chitin blending into membrane laterally. The median orifice lies below and behind the apex of this plate. The dorsal cap-piece of the tegmen was pulled anteriorly by the action of the first connecting membrane in some specimens of this species. Cap-piece is hirsute terminally.

*Rhynchites aeneus* Boh. Figs. 6 a & b.

The lower plate of the median lobe is chitinized ventrally, the upper is rather broad. The median orifice lies in the membrane between the two plates at their apex. Tegmen, as drawn, illustrates how
the first connecting membrane pulls the cap-piece anteriorly as the aedeagus is drawn from the abdomen. Cap-piece is hirsute terminally.

*Atteles bipustulatus* Fab. Figs. 7 a & b.

The lower plate is rather heavily chitinized ventrally and is about half the length of the rather broad upper plate. The median orifice lies in the membrane between the two plates near their apex. An inter-aedeagal structure lies in the flagellum. Cap-piece is hirsute terminally.

*Pterocolus ovatus* (Fab.) Figs. 8 a & b.

The lower plate of the median lobe is chitinized laterally with light chitin present on its ventral surface near the tip. The narrow upper plate is chitinized. The median orifice is located in the terminus of the membrane which lies between the two plates. The cap-piece with a single lobe is directed posteriorly. The internal sac can be traced throughout the body of the aedeagus.

*Cylas formicarius* (Fab.) Figs. 9 a & b.

The ventral plate of the median lobe is chitinized laterally and peripherally, but is membranous medially. The dorsal plate is very narrow and rounded at the apex. Between the two plates apically and within the membrane the median orifice is found. An inter-aedeagal structure is present within the internal sac. A double forked cap-piece which normally points posteriorly was inverted by the action of the first connecting membrane as the aedeagus was drawn from the abdomen lies dorsally on the tegmen. The internal sac can be traced throughout the structure and anteriorly the ejaculatory duct can be discerned entering the flagellum.

*Notaris puncticollis* (Lec.) Figs. 10 a & b.

The lower plate of median lobe is chitinized laterally, terminally and lightly so medially. Dorsally this plate is largely membrane with a single orificial plate overlying the median orifice. The upper plate is narrow, and short with the chitin confined to the periphery. The tegmental cap-piece which was inverted by the action of the first connecting membrane is slightly notched apically with the notch filled in with much lighter chitin which rounds off the structure.

*Notaris aethiops* (Fab.) Figs. 11 a & b.

The lower plate of the median lobe is broad, short and fully chitinized ventrally and laterally. Dorsally this plate is largely membranous with a pair of orificial plates near the terminus which flank the median orifice. The upper plate is short, pointed and chitinized on the
periphery only. The cap-piece of the tegmen is undivided with a slight incurving at the tip. The cap-piece was prevented from being inverted during evagination by holding it firmly to the rest of the structure with the tweezers. The internal sac and the ejaculatory duct are very evident anteriorly.

Family Platystomidae

Characteristics of the Family: The median lobe is a single scoop-shaped structure which is chitinized ventrally and laterally. Dorsally the second connecting membrane extends to the apex where the median orifice is found, overlain by orificial plates or a plate. The median struts are attached to the dorsal and lateral edges of the median lobe. The tegmen is a ring with a single dorsal cap-piece which normally projects posteriorly. The cap-piece is spade shaped. The terminal strut is very short.

Ischnocerus infuscatus Fahr. Figs. 12 a & b.

Median lobe as described, the orificial plates are paired. The first connecting membrane reversed the direction of the cap-piece as the aedeagus was drawn from the abdomen.

Anthribus cornutus Say. Figs. 13 a & b.

Median lobe as described, the orificial plate single. The tip of the cap-piece is very lightly chitinized.

Sub-family: Apioninae

Characteristics of the Sub-family: The degree of chitinization of the median lobe is very difficult to ascertain since the structures are so tiny. Both specimens appear to be chitinized ventrally and laterally. The median struts are attached to the dorsal edge of the median lobe in a distinctive manner for each of the two species examined. The median orifice cannot be located with any degree of certainty. The tegmen is a ring with a comparatively large dorsal cap-piece. The connecting membrane cannot be discerned except briefly in one specimen. No internal sac can be discerned.

Apion turbidens Sm. Figs. 14 a & b.

The median lobe appears to be a tube composed of lightly chitinized material. The median orifice could not be located. The median struts are attached to the dorsal anterior edge of the median lobe. The tegmen is a ring with large dorsal cap-piece which terminates posteriorly in a double point and anteriorly in a single one. The connecting membrane that was discernable under a compound microscope is fragmental.
Apion pennsylvanicum Boh.  Figs. 15 a & b.

The median lobe appears to be a chitined trough. Ventrally and laterally the chitin is rather evident, but dorsally the medial area that is indicated as being membranous may in reality be light chitin. Certainly it is of different consistency than are the edges or the bottom of the trough. The median orifice has been tentatively located in this membranous (?) area. The median struts are attached to the lateral edges of a short dorsal extension of the median lobe. The tegmen is a ring with a dorsal cap-piece which is rather bluntly pointed posteriorly and rather sharply pointed anteriorly. No connecting membranes were discerned on any of the specimen's of the species that were examined.

Sub-families: Otiorrhynchinae & Curculioninae

Characteristics of the Two Sub-families: No sharp line of demarcation exists between these two sub-families as they are listed in Leng's Catalogue. Some of the members of one group appear closely akin to those of the other on the basis of the external genitalia. Consequently they will be described as one group, within which there is much variation.

The median lobe is either a simple trough or a tube. The tegmen may be a Y, a ring, or a ring with lobes. Often the internal sac is impossible to discern. The first and second connecting membranes often cannot be separated dorsally, but literally and ventrally they are divided by their attachment to the forks of the tegmen.

Dyslobus wasatchensis Tanner.  Figs. 16 a & b.

The median lobe is a chitined tube as long as the second connecting membrane and rather pointed apically from the lateral aspect. Mid-dorsally there is a depression in the chitin immediately anterior to which the internal sac protrudes with a single orificial plate overlying it. The median orifice is in the tip of this pouch. The tegmen is a ring with short, pointed projections that were anteriorly as the aedeagus was drawn from the abdomen.

Eupagoderes sordidus (Lec.)  Figs. 17 a & b.

The heavier chitin of the median lobe forms a trough, but mid-dorsally there is a membranous area which contains the medial orifice which is overlain by a single orificial plate of light chitin. Anterior to this membrane a light chitin band connects the two sides. The median struts are attached to a mid-lateral extension of the median lobe. The
tegmen is a ring with two small lobes that are pulled upward by the first connecting membrane.

_Eudiagogus pulcher_ Fahr. Figs. 18 a & b.

The median lobe is a short, round, chitinized tube the sides joined (?) together with the point of this juncture (?) very evident. The median orifice can easily be discerned in the membranous area at the tip of the tube. Median struts are attached laterally to a ventral plate-like extension of the median lobe. The tegmen is a ring, slightly lobed dorsally.

_Rhinoscapha leguilloui_ Guer. Figs. 19 a, b & c.

The median lobe is a chitinized tube which is longer than the second connecting membrane. Immediately behind a posterior dorsal depression of the lobe is a membranous lumen with the median orifice situated in its apex. The median struts appear as lateral extensions of the ventral aspect of the lobe. The tegmen forms a ring with the flagellum normally pointing posteriorly, but which have been pulled to an anterior position by the first connecting membrane as the aedeagus was pulled from the abdomen. The internal sac has been pulled from its position and is shown in Figure 19 c. Various parts of it are chitinized as is indicated. It is probable that those chitinized structures which are noted in many species and termed inter-aedeagal structures are similar chitinized parts of the internal sac.

_Tanymecus confertus_ (Gyll.) Figs. 20 a & b.

The median lobe is a chitinized trough the lateral edges extending dorsally and medially leaving a narrow extension of the second connecting membrane running down the center. A rather large median orifice marks the terminus of this membranous area. Median struts are attached to the ventral lateral edges of the median lobe. The tegmen is a ring with two projections which were pulled upward by the first connecting membrane. Inter-aedeagal structures are present within the flagellum.

_Magdalis gentilis_ Lec. Figs. 21 a & b.

Ventrally and laterally the median lobe is chitinized, the lateral edges inflexed some what dorsally. The balance of the dorsal surface is occupied by a posterior extension of the second connecting membrane which contains the median orifice near the apex. Paired orificial plates are found immediately anterior to the orifice. The median struts are short extensions of the sides of the median lobe. The tegmen is a ring with paired cap-pieces which project posteriorly.
Magdalis lecontei tenobrosa Fall. Figs. 22 a & b.

Ventrally and laterally the median lobe is chitinized, the lateral edges somewhat inflexed dorsally. The balance of the dorsal surface is occupied by a posterior extension of the second connecting membrane which contains the median orifice near the apex. Paired orificial plates which are attached to the sides of the median lobe and appear as lighter continuations of it. The median struts are short extensions of the sides of the median lobe. The tegmen is a ring with paired cap-pieces that project posteriorly.

Odontocorynus scutellum-album (Say). Figs. 23 a & b.

The median lobe is lightly chitinized ventrally, much more densely so laterally. Dorsally the second connecting membrane extends throughout the entire distance of the median lobe and beyond the terminus of the chitinized sides for some little distance. The median orifice cannot be located with certainty, but it appears to be situated in this membranous tip. The median struts are attached to a ventral plate-like extension of the median lobe. The tegmen is a ring with paired and pointed cap-pieces that have been pulled anteriorly by the first connecting membrane as the aedeagus was drawn from the abdomen. The internal sac can be traced posteriorly as far as the median lobe.

Dorytomus breviscostosus Csy. Figs. 24 a & b.

The scoop shaped median lobe is chitinized ventrally and laterally. Dorsally the second connecting membrane extends into the median lobe to near its apex where it bears the median orifice which is flanked by two small orificial plates. Median struts are attached to a small ventral plate-like extension of the median lobe. The tegmen is a ring with paired and pointed cap-pieces projecting posteriorly. Within the internal sac is a chitinized tube, probably an extension of the ejaculatory duct, which can be followed posteriorly to near the median orifice.

Lixus terminalis Lec. Figs. 25 a & b.

The median lobe is chitinized ventrally and laterally. On the dorsal-anterior edge the sides meet, but do not join. Posteriorly an ever-widening membrane lies between the sides at which terminus the median orifice is found. An inter-aedeagal structure that marks the anterior end of the internal sac is located within the median lobe. The median struts are short extensions of the lateral edges of the median lobe. The tegmen is a ring with short dorsal knobs that project posteriorly.
Dinoecius abovestitus Csy. Figs. 26 a & b.

The median lobe is densely chitinized ventrally and laterally. Dorsally the chitin is much lighter and occupies most of the area between the heavy chitin sides. The median orifice is located in a membranous area near the tip and is flanked by orificial plates. The median struts are short extensions of the sides of the median lobe. The tegmen is a ring with two short dorsal knobs which project posteriorly. The terminal strut is very short.

Cleonus calandroides (Rand). Figs. 27 a & b.

The median lobe is densely chitinized ventrally and laterally. Dorsally and anteriorly there is membrane which blends soon into chitin which is considerably lighter than that at the sides. No membranous area is found apically, rather the median orifice seems to be present beneath the chitinized cover near the apex. The median struts are short extensions of the lateral edge of the median lobe. The tegmen forms a simple ring with a slight notch in the mid-dorsal surface.

Mononychus vulpeculus (Fab.) Figs. 28 a & b.

Ventrally the median lobe is chitinized at the periphery, a light chitin strip connecting the heavier sides anteriorly. Dorsally the chitin is confined to the sides and to a rather pointed apex. The second connecting membrane extends well into the median lobe dorsally with the location of the median orifice questionable. It appears to be about two-thirds of the way back from the apex. Immediately behind, and within the internal sac, is a lightly chitinized inter-aedeagal structure. The median struts articulate with ventral-lateral extensions of the median lobe. The tegmen forms a substantial ring.

Colecerus marmoratus Horn. Figs. 29 a & b.

The median lobe is trough like, chitinized ventrally and laterally. The second connecting membrane extends into the lobe dorsally and terminates near the apex where the median orifice is located. Orificial plates flank the orifice. Median struts are attached laterally to a ventral plate-like extension of the median lobe. The tegmen forms a thin ring around the median struts.

Balanimus baculi Chitt. Figs. 30 a & b.

The median lobe is long, narrow, and chitinized ventrally and laterally to form a trough. Dorsally the second connecting membrane extends to near the apex where the median orifice is located. It is flanked by orificial plates. The median struts are attached to a ventral plate-
like extension of the median lobe. The tegmen forms a thin ring, its strut very short.

*Anthonomus grandis* Boh. Figs. 31 a & b.

The median lobe is a shallow chitinized trough, lightly chitinized ventrally, laterally and on the dorsal apex for about one-third its length. Dorsally the second connecting membrane continues posteriorly to the chitinized area. Although there are no chitinized plates to mark its position the median orifice appears to be at the apex of this membrane. The median struts are attached to ventral-lateral extensions of the median lobe. The tegmen forms a thin ring, its strut very short.

*Anthonomus squamosus* Lec. Figs. 32 a & b.

The median lobe is fully chitinized ventrally and laterally. Dorsally the chitin is confined to the apex and to an area behind a membranous lumen that bears the median orifice in its distal end. Median struts are attached laterally to a ventral-like extension of the median lobe. The tegmen is a Y with long forks that flank the median struts.

*Anthonomus eugenii* Cano. Figs. 33 a & b.

The median lobe is a long, narrow, and fully chitinized ventrally and laterally. Dorsally the chitin is confined to a rather blunt apex and to an area behind a membranous lumen which bears the median orifice. This orifice is bordered by a lightly chitinized orificial plate. The median struts are lightly attached to the ventral surface of the median lobe. The tegmen is a large, but slender ring that surrounds the median struts.

*Phytonomus nigrirostris* (Fab.) Figs. 34 a & b.

The median lobe is a broad chitinized scoop, the second connecting membrane extending into it dorsally for about half its distance. A large median orifice lies in the terminus of this membrane. The median struts articulate with the ventral surface of the median lobe. The tegmen is a Y the forks flanking the median struts. An inter-aedeagal structure is present within the flagellum.

*Cryptorhynchus parochus* (Hbst.) Figs. 35 a & b.

The median lobe is a chitin trough with the second connecting membrane extending into it dorsally for most of its distance. The median orifice, flanked by orificial plates, is near the apex of this membrane. Immediately behind the plates and within the internal sac is an inter-aedeagal structure. The median struts are attached to the ventral-lateral edge of the median lobe. The tegmen is a Y with the forks flanking the median struts.
*Phytonomus posticus* (Gyll.) Figs. 1 a, b & c.

The median lobe is a chitin scoop with the second connecting membrane extending into it mid-dorsally with the median orifice located in the apex of this membrane. The median struts articulate with a ventral extension of the median lobe. The tegmen is a Y with the forks extending dorsally to flank the median struts. A U shaped inter-aedeagal structure is present within the flagellum.

*Hypera punctata* (Fab.) Figs. 36 a & b.

The median lobe is a chitinized scoop over one half as broad as it is long. The second connecting membrane extends into it dorsally to near its apex where the median orifice is found. It is flanked by the orificial plates. The tegmen is a Y, the forks flanking the median struts which in turn articulate with the ventral-lateral edges of the median lobe. A large inter-aedeagal structure is noted.

*Centorhynchus sulcicollis* (Payk.) Figs. 37 a & b.

The median lobe is a chitinized scoop with the second connecting membrane extending into it for about one half of its distance. The median orifice is found near the apex of this membrane. There are numerous inter-aedeagal structures which are presumed to be a part of the internal sac. The tegmen is a Y with the forks flanking the median struts which are attached to a ventral extension of the median lobe.

*Tycheius lineellus* Lec. Figs. 38 a & b.

The median lobe forms an inverted chitinized trough which is largely chitinized dorsally and laterally, but ventrally the chitin is confined to the periphery. There is, however, a membranous area near the dorsal apex which contains the median orifice. The median struts articulate with ventral-lateral projections of the median lobe. The tegmen is small and Y shaped and lies below the median struts.

*Rhinoncus pyrrhopus* Boh. Figs. 39 a & b.

The median lobe forms an inverted chitin trough, densely chitinized laterally, lightly so dorsally with the ventral largely membranous. A small membranous lumen near the apex dorsally contains the median orifice. Median struts are attached to ventral-lateral points of the median lobe. The tegmen is small and Y shaped with the forks flanking the median struts.

Sub-family: *Calendrinæ*

Characteristics of the Sub-family: The median lobe usually
consists of a dorsal and a ventral plate which are separated laterally by a narrow strip of membrane. The median orifice lies in a membranous or a lightly chitinized area dorsally near the apex and is flanked by orificial plates. In all forms the internal sac can be seen. The amount and degree of chitinization both dorsally and ventrally is variable, often this forms the chief difference between species. The median struts are attached or articulate with the anterior end of the dorsal plate. In most forms the two struts are joined for a variable distance anterior to the point of articulation.

The tegmen forms a Y with the forks surrounding the median struts. The membrane surrounding the tegmen in this area is chitinized, in some species decidedly so. Attached to the ventral aspect of this "sleeve" is the spiculum gastrale a chitin rod that extends anteriorly and dorsally on the right side. The first and second connecting membranes could not be separated one from the other by their attachment to the tegmen as in other forms as the tegmen lies well within the "sleeve." However, Sharp and Muir have noted this and have labeled the membranous area connecting the median lobe with the "sleeve" as the first connecting membrane and the "sleeve" or the chitinized portion as the second connecting membrane. Subsequently Muir reversed this order and Bissell adopted the revision. In this paper the reversed order of Muir & Bissell has been utilized.

*Calendra parvulus* Gyll. Figs. 40 a & b.

The median lobe consists of two plates, the dorsal is membranous terminally, the ventral with an oblong membranous area medially. The median orifice is in the dorsal membranous area and is flanked by orificial plates. Median struts articulate with the dorsal plates and are connected for some distance behind the point of articulation. The first connecting membrane is lightly chitinized but is hardly discernible from the second. The spiculum gastrale is attached to this lightly chitinized "sleeve."

*Calendra destructor* Chitt. Figs. 41 a & b.

The median lobe consists of two plates, both the dorsal and the ventral with membranous areas apically. The median orifice is in the dorsal membranous area and is bordered by orificial plates. Median struts articulate with the median lobe and are connected briefly anterior to the point of articulation. The first connecting membrane is decidedly chitinized with the spiculum gastrale attached to it.

*Calendra ochreus* Lec. Figs. 42 a & b.

The median lobe consists of two plates, the ventral fully chitin-
nized, the dorsal with a membranous area terminally. Within this area lies the median orifice flanked by small orificial plates. Median struts articulate with the dorsal plate and are connected for some distance anterior to point of articulation. The first connecting membrane is discernibly chitinized.

_Calendua zeac_ Walsh. Figs. 43 a & b.

The median lobe consists of two plates, the dorsally fully chitinized although it is much more densely so laterally. The ventral plate is chitinized apically and laterally with a distinct membranous strip extending medially as an apparent continuation of the 2nd connecting membrane. The median orifice which is dorsal and terminal is flanked by orificial plates of denser chitin. Median struts articulate with the dorsal plate and are connected for some distance anterior to the point of articulation. The first connecting membrane is markedly chitinized and bears the spiculum gastrale, and is marked dorsally by a V shaped intrusion of the second connecting membrane. The internal sac is massed on the left side of the aedeagus just anterior to the median lobe. No trace of the ejaculatory duct can be discerned through the membrane.

_Scyphophorus yuccae_ Horn. Figs. 44 a & b.

The median lobe consists of two plates, the ventral fully chitinized, much more densely so laterally. The dorsal plate is chitinized laterally and terminally the center consisting of a posterior extension of the second connecting membrane with the median orifice at the apex where it is flanked by orificial plates. Median struts articulate with the dorsal plate and are attached anterior to the point of articulation by a cross bar, beneath which is found an inter-aedeagal structure. The first connecting membrane is well chitinized with the spiculum gastrale attached to it.

_Rhodobaenus tredecimpunctatus_ (Ill.) Figs. 45 a & b.

The median lobe is a single chitin trough the sides of which meet both anteriorly and posteriorly. Ventrally and laterally the structure is wholly chitinized, but dorsally a membranous strip extends down the center. The median orifice is found in the membranous area near the apex and is flanked by orificial plates. The median struts are attached to a dorsal plate-like extension of the median lobe. Both connecting membranes are lightly chitinized and the “sleeve” although present, is not readily distinguished from the second connecting membrane. The point of attachment of the spiculum gastrale and the location of the
Family Scolytidae

Characteristics of the Family: The median lobe consists of a single chitinized plate the sides of which are inflexed to form a trough. The median orifice is located in a dorsal membranous area and an orificial plate is present. The median struts are attached differently in each of the two specimens examined. The tegmen is present as a simple ventral plate. Dorsally and laterally the connecting membranes are continuous and cannot be distinguished except in reference to their position to the tegmen.

Scolytus ventralis Lec. Figs. 46 a & b.

The median lobe is a relatively deep chitinized trough, the edges almost meeting mid-dorsally. The median orifice is located in a membranous area dorsally and apically and is overlain by an orificial plate. The median struts are mid-lateral extensions of the anterior margins of the median lobe. The tegmen is a flat chitinized plate, slightly forked anteriorly.

Dendroctonus valens Lec. Figs. 47 a & b.

The median lobe is a chitinized trough with parts of the edges extending dorsally as paired "wings." Dorsally the second connecting membrane continues through the median lobe to its apex. An orificial plate lies near the apex in this area with the median orifice located immediately posterior to it. Anterior to the plate and within the internal sac are two inter-aedeagal structures. The median struts are lightly attached to the mid-lateral edges of the median lobe and appear to be joined at their points of origin anteriorly. The tegmen is a flat, V shaped sclerite.

Taxonomy and Phylogeny

In grouping the Rhynchophora on the basis of the study of the external genitalia of a limited number of species alone, the writer is aware of the definite limitations that exist. Even if the genitalia of the entire group had been examined no final conclusions regarding the taxonomy and phylogeny could be reached. As Macgillivary points out, all structures must receive serious consideration in determining the phylogeny of insects. This does not, however, rule out the wisdom of making studies of individual characteristics or of making interpretations of the information secured in such investigations since it is through such studies properly correlated with those of other parts, that
the eventual complete understanding of the various groups will be attained. The interpretations that follow are not intended as representing the final word in phylogeny of the species studied. Rather it is hoped that they will contribute to the general morphological knowledge of those species and the groups to which they belong.

On the basis of the external genitalia the Rhynchophora examined seem to fall into eight groups, the relationships of which are noted below. They are separated on the basis of the two chitinized segments of the aedeagus, the median lobe and the tegmen, with other parts considered when a marked variation occurs.

The Belidae, the Brentidae and the group which includes the Attelabinae, Rhynchitinae, Cyladinae (?), Pterocolinae, the and genus Notaris (Curculioninae) are all alike in one respect, that is, the median lobe is composed of both a dorsal and a ventral "plate" each of which is attached to a posterior fork of the median strut. The Belidae are set apart from the rest of the group by the distinctive strap-shaped dorsal piece of the median lobe as well as the large X shaped cap-piece of the tegmen. The Brentidae are distinctive in that the cap-piece is not firmly attached to its base, rather it articulates with it. The reduced cap-piece attached to a solid ring is characteristic of the Attelabinae group.

In none of the other forms examined was the median strut divided posteriorly. These forms with the single median struts are separated as follows: The Platystomidae are distinctive in that the tegminal cap-piece has a single posterior projection and is hirsute terminally. The Apioninae are set apart by a large tegminal cap-piece and a simple median lobe. The Calendrinae are separated from the
others on the basis of the partial or pronounced chitinization of the first connecting membrane to which the spiculum gastrale is attached. The similarities of the Otiorhynchinae and the Curculioninae have been noted. The median lobe may be either a trough or a tube while the tegmen varies from a simply Y to a ring, often with paired lobes that normally point posteriorly. The Scolytidae are by far the simplest of all the forms studied, the distinctive plate-like tegmen without a strut being sufficient to separate it from all others. The median lobe likewise is reduced to a simple trough with the lateral edges rather high.

Boving & Craighead after a study of the larvae of numerous Coleoptera have broken the Rhynchophora down into two large groups, the Platystomidea and the Curculionidea, the latter being divided into the families Brentidae, Proterhinidae, Attelabidae, (Rhynchitinae and Attelabinae), Apionidae, Curculionidae, (Curculioninae & Lissorhoptrinae), Calendridae, Platypodidae, and Scolytidae. Belidae was not studied.

Ting, in his study of the mouth parts of Rhynchophora is in general agreement with Boving and Craighead. He does, however, add the Rhinomacerinae and the Pterocolinae to the Attelabidae of Boving and Craighead, presuming that the larval stages of these groups were not studied by those two investigators. Although one species of Clyladinae, *Cylas formicarius* (Fab.) was studied by Ting, he did not include it in with the Attelabidae. The same species was studied in this investigation and has been tentatively included in with the Attelabidae, although it does differ from the rest in that the tegminal cap-piece is bifurcate, while all the others are essentially undivided. Whether this characteristic is distinctive enough to separate it from the others is problematical, therefore its inclusion is only tentative.

There is no record of the genus Notaris being studied in either of the two investigations noted above. On the basis of the external genitalia it is more like the Attelabidae than it is the Curculionidae. The dorsal plate of the median lobe is considerably reduced, however, and a slight tendency toward the division of the tegminal cap-piece was noted. It may be that Notaris is an intermediate form between the two groups.

Within the Otiorhynchinae and the Curculioninae, which includes the balance of the Curculionidae investigated in this study according to the classification of Boving and Craighead, which has been noted in the third supplement of Leng’s Catalogue, the arrangement of the species differs somewhat from the arrangement adopted in the first edition. It should be noted, therefore, that this does not imply that
such an arrangement of the family should be adopted. The reduction of the tegmen from a bilobed ring to a simple Y shaped strut is easy to follow, but this is not always in agreement with a similar simplification of the median lobe.

SUMMARY

1. On the basis of the comparative morphology of the external genitalia the Rhynchophora investigated seem to fall into eight groups. In general this is in agreement with that suggested by Boving and Craighead and by Ting.

2. The genus Notaris seems to be more closely related to the Attelabidae than to the Curculionidae.

3. The Cyladinae show similarities to the Attelabidae, but also show differences that make its inclusion within the group questionable.

4. Assuming that the common opinion that structures have become more simple as structures have evolved, or more specifically that the statement by Muir that the evolution of the genitalia in Coleoptera has been from the complex to the simple, is correct, the Belidae, Brentidae and the Attelabidae group are the most primitive and the Scolytidae are the most recent.

5. Where closely related species of the same genus were investigated, discernible differences were noted in the construction of the external genitalia. It appears, therefore, that investigation of the genital structures should be utilized as a means of identifying the various species of Rhynchophora.

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PLATE I

Figs. 1 a & b. *Phytynomus posticus*, dorsal & lateral aspects of external genitalia & abdomen c. spiculum gastrale.

Figs. 2 a & b. *Ithycerus novaboracensis*, dorsal & lateral aspects.

Figs. 3 a & b. *Eupalis minuta*, dorsal & lateral aspects.

Figs. 4 a & b. *Ectocemus 10-maculatus*, dorsal & lateral aspects.

Figs. 5 a & b. *Rhynchites bicolor wickhami*, dorsal & lateral aspects.
PLATE II

Figs. 6 a & b. *Rhynchites aeneus*, dorsal and lateral aspects.
Figs. 7 a & b. *Attelabus bipustulatus*, dorsal & lateral aspects.
Figs. 8 a & b. *Pterocolus ovatus*, dorsal and lateral aspects.
Figs. 9 a & b. *Cylas formicarius*, dorsal & lateral aspects.
Figs. 10 a & b. *Notaris puncticollis*, dorsal & lateral aspects.
Figs. 11 a & b. *Notaris aethiops*, dorsal & lateral aspects.
Figs. 12 a & b. *Ischnocerus infuscatus*, dorsal and lateral aspects.
Figs. 13 a & b. *Anthribus cornatus*, dorsal & lateral aspects.
Figs. 14 a & b. *Apion turbulentum*, dorsal and lateral aspects.
Figs. 15 a & b. *Apion pennsylvanicum*, dorsal & lateral aspects.
Figs. 16 a & b. *Dyslobus wasatchensis*, dorsal & lateral aspects.
PLATE III

Figs. 17 a & b. *Eupagoderes sordidus*, dorsal & lateral aspects.
Figs. 18 a & b. *Eudiagogus pulcher*, dorsal & lateral aspects.
   c. internal sac.
Figs. 20 a & b. *Tanymecus confertus*, dorsal & lateral aspects.
Figs. 21 a & b. *Magdalis gentilis*, dorsal & lateral aspects.
Figs. 22 a & b. *Magdalis lecontei tenebrosa*, dorsal & lateral aspects.
Figs. 23 a & b. *Odontocorynus scutellum-album*, dorsal & lateral aspects.
Figs. 24 a & b. *Dorytomus brevisetosus*, dorsal & lateral aspects.
Figs. 25 a & b. *Lixus terminalis*, dorsal & lateral aspects.
PLATE IV

Figs. 26 a & b. *Dinoclaus albocostatus*, dorsal & lateral aspects.
Figs. 27 a & b. *Cleonus calandroides*, dorsal & lateral aspects.
Figs. 28 a & b. *Mononyxus vulpeculus*, dorsal & lateral aspects.
Figs. 29 a & b. *Colecerus marmoratus*, dorsal and lateral aspects.
Figs. 30 a & b. *Balaninus baculi*, dorsal & lateral aspects.
Figs. 31 a & b. *Anthonomus grandis*, dorsal & lateral aspects.
Figs. 32 a & b. *Anthonomus squamosus*, dorsal & lateral aspects.
Figs. 33 a & b. *Anthonomus eugenii*, dorsal & lateral aspects.
Figs. 34 a & b. *Phytonomus nigrostris*, dorsal & lateral aspects.
Figs. 35 a & b. *Cryptorrhynchus parochus*, dorsal & lateral aspects.
Figs. 36 a & b. *Hypera punctata*, dorsal & lateral aspects.
PLATE V

Figs. 37 a & b. *Ceutorhyncha sulcicollis*, dorsal and lateral aspects.
Figs. 38 a & b. *Tychius lineellus*, dorsal & lateral aspects.
Figs. 40 a & b. *Calendra parvulus*, dorsal & lateral aspects.
Figs. 41 a & b. *Calendra destructor*, dorsal & lateral aspects.
Figs. 42 a & b. *Calendra ochreus*, dorsal & lateral aspects.
Figs. 43 a & b. *Calendra zea*, dorsal & lateral aspects.
Figs. 44 a & b. *Scyphophorus yuccae*, dorsal & lateral aspects.
Figs. 46 a & b. *Scolytus ventralis*, dorsal & lateral aspects.
Figs. 47 a & b. *Dendroctonus valens*, dorsal & lateral aspects.