Relationships within the Family Chrysomelidae (Coleoptera) as Indicated by the Male Genitalia of Certain Species

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Introduction

The last quarter century has seen the use of the genital characters of insects come into prominence as a means of accurate identification of species. The increased use of such characters has been due, in part, to the ineffectiveness of color and other superficial differences which are affected by environment, such characters having been used in many early contributions to the taxonomic literature. The adult genitalia, which in many groups lie wholly within the insect body, except during copulation and oviposition, are less liable to be affected by environmental factors and, therefore, should supply more reliable characters for species distinction. In addition to the internal position of these structures, especially in the Chrysomelidae, they are usually heavily chitinized and would not be easily modified.

A study of these structures as they are found in the males of certain species of the Chrysomelidae has been made by the author. The distinctions between different species have not held his interest so much as the broader investigation of the relationships which must exist within the group. If species differences in the genitalia are found to be definite it seems logical to suppose that from them phylogenetic relations could also be determined with some degree of accuracy. It has been with this latter aim in view that the present study has been made.

A review of the literature on the subject reveals that many workers with insect genitalia have shown that these genitalia are derived from originally paired structures. Notable among the contributions which support this fact are those of the following: Christophers and Cragg (1921-1922) in Hemiptera (Cimex), Singh-Pruthi (1925) and George (1928) in Homoptera, Christophers (1922) in Diptera (Mosquito), Haviland (1921), Kraeplin (1873), Kulagin (1897-1898) and Michaelis (1900) in Hymenoptera, Zander (1900, 1901, 1903) in Hymenoptera, Trichoptera, and Lepidoptera, Verson and Bisson (1896) in Lepidoptera, and Newell (1918) in insects in general; Singh-Pruthi (1924) and Metcalfe (1932) have studied the development of the genitalia in Coleoptera and agree as to the exact structures from which the genitalia are derived. Muir (1918) who has also studied the development of the genitalia states that the "median lobe" (intromittent organ, penis, aedeagus) develops as an unpaired median element.

If the findings concerning the double origin are true, it would seem that the adult genitalia which show the most indications of such origin should first

1 Studies from the Zoological Laboratory, University of Nebraska, No. 208.

be determined and from this tentative ideas of phylogenetic relationships made. This would necessitate that the adult genitalia be well investigated and then checked with their embryological development. The former has been the plan of the present study. It is hoped that future investigations upon the development of some genitalia discussed herein may be made.

Originally the plan of this investigation included the study of male genitalia from one species of each genus within the family Chrysomelidae as found in North America. The difficulties involved in obtaining representatives of all genera, — due to restricted distribution, scarcity and the impossibility of exchanging and collecting certain species needed, — accounts for the limitation to those species which could be procured. Several species of certain genera have been included to give indications of relationships which must exist within these smaller groups. Although the results concerning relations existing between the genera cannot be as conclusive as was desired it is hoped that this study may contribute toward a better understanding of this large family of beetles.

The nomenclature of the species is that of Leng's "Catalogue of the Coleoptera of America, North of Mexico" (1920) with a few recent changes indicated by Barber and Bridwell (1940). All of these changes are plainly indicated in the section on the Descriptions of the Genitalia. The descriptions and drawings are arranged in the order given in the above mentioned publication.

The writer wishes to acknowledge his indebtedness to the late Dr. Robert H. Wolcott of the University of Nebraska under whom this study was first begun; to Dr. David D. Whitney for helpful suggestions during the preparation of the manuscript; to Dr. H. W. Manter for suggestions concerning drawings and for aid with the photographic work entailed; to Dr. George Hudson who generously donated specimens for study; and to the Department of Zoology of the University of Nebraska for the provision of facilities for the progress of the work and also for the purchase of certain specimens which were not otherwise available. Helpful suggestions were also made by Professors Myron H. Swenk, Don B. Whelan, and Raymond Roberts of the Department of Entomology of the University of Nebraska. The names of several specimens were verified or corrected by Mr. H. S. Barber of the Division of Insect Taxonomy of the United States National Museum. Such species are indicated (B) in the manuscript and acknowledgment of indebtedness to this source of reliable information is here made. Due credit is also given to Dorothy M. Powell who, in addition to the care of six children, found time to aid with the reading of the manuscript and to offer encouragement so necessary for the completion of such work.

Materials and Methods

The specimens used in this study were obtained from various sources throughout the United States and Canada. A considerable number were Nebraska specimens collected by the author during the last ten years. Others taken in various parts of the United States were donated by friends or were obtained by exchange or purchase. Of the one hundred seventeen genera listed by Leng (1920), representatives of fifty-one genera including seventy-two species were studied. All subfamilies were included except four, namely, Sagrinae, Megascelinae, Lamprosominae, and Halticinae. The first three of these groups are small ones containing a total of seven species whose distribu-

tion is limited to southwestern United States. The fourth, Halticinae, is a large subfamily with many species of wide distribution but also many of such small size that the time involved in the dissection of the genitalia made it impossible to include them. Pinned specimens were used for the most part since they were more convenient to handle. Unpinned matrial was relaxed and pinned. Fresh specimens of local species were also studied.

A serial number was given to each specimen (consecutive numbers to those of a species) and placed on pins and vials used. A progressive record with serial number, collection data, and of the following treatment was kept for each specimen. Additional notes were recorded as a check against mistakes. Various methods of procedure were studied and tried; a combination of those used by Metcalf (1921) and DeLong (1931), with some alterations to meet the needs of the author, was found most suitable.

Relaxation of specimens was accomplished in boiling *distilled* water. The time needed for the different species varied with the chitinization but twenty-five to thirty minutes were required to soften the exoskeleton of the heavier insects. No appreciable injury to the colors was noted by this method.

Dissection was done under a binocular dissecting microscope with the aid of various types of curved needles made by the author. In most cases the complete abdomen, or a part thereof, was severed from the body. The remainder was carefully saved on its pin with collection data and serial number. The place formerly occupied by the abdomen was filled with clear shellac to add support to the specimen and was kept for future reference. Such mutilation of the specimens seemed justified since the external abdominal characters were usually not important ones and the extraction of some of the genital parts could be accomplished in no other manner.

During the remainder of the procedure the parts from different specimens were kept separate in one dram vials which were plainly marked with serial numbers of each. The time allowed for the baths in the different solutions was varied slightly according to the chitinization of the material, less time being required for that with less chitin.

The abdomens were placed in sodium hydroxide, 10 to 15% strength, and allowed to remain for twenty-four to thirty-six hours until almost clear. Upon removal they were thoroughly washed in distilled water. They were then placed in glacial acetic acid for a few hours to remove any fat and to neutralize any sodium hydroxide which remained after the washing. They were then thoroughly washed in distilled water as before.

The staining required from eight to twenty-four hours (depending on the chitinization) in acid fuchsin of the following formula (Metcalf, 1921): acid fuchsin, 1 gram; hydrochloric acid, 10% strength, 25 cc.; distilled water, 500 cc. Specimens usually were heavily stained since a gradual destaining occurred in further handling; a final light stain, best for differentiation for study of parts, was thus obtained.

Upon removal from the stain, the parts were washed and the genitalia were dissected from the abdomens. Delaying the final dissection of the genital

parts until this time reduced the loss of the minute structures desired. A thorough washing in distilled water followed after which the genitalia were stored in one-half dram vials containing glycerin. Each vial was marked with a gummed label on which was printed in waterproof ink the serial number of the specimen, Leng's checklist number, and the name of the species. A coating of collodion was painted over the label as an extra precaution against loss.

Containers for storing the vials, patterned after Schmidt insect boxes, were made from wooden cigar boxes and masonite (synthetic wood). The latter was placed in the bottom of the container and holes of appropriate size and equally spaced were made in it to allow for the insertion of the vials. Lined on the inside with white paper and covered on the outside with heavy black paper these made convenient and permanent receptacles for storage.

A binocular dissecting microscope, a compound microscope, and a deep-well slide were utilized in the study of the genitalia. The specimens were placed in the pit of the slide and submerged in glycerin. This method, since the structures could be turned at any angle, was found much more convenient than permanently mounting them in balsam or damar. When drawings were to be made the specimens were quickly washed in distilled water and fastened in the desired position to the bottom of the well by means of fine lines or smears of LePage's glue before the glycerin was added. When dorsal or dorso-caudal views of curved specimens were needed a small platform was constructed in the well from small pieces of glass slide and the specimens attached to its edge. At first, some difficulties with this method were encountered but with practice they were easily overcome.

Simple line drawings were made with the use of a camera lucida. Such drawings appeared to be easier to understand than many of the complex drawings found in much of the literature which was reviewed. The views chosen seemed to illustrate sufficiently the points desired.

Homology and Terminology

The great variation in the character of the genitalia in the different orders of insects has, no doubt, been responsible for the confusion of terms which have been used for these structures as a group and also for the individual parts. Attempts by many authors to homologize them have somewhat alleviated this situation but much work along this line still remains to be done. The author makes no attempt to give a detailed discussion on this subject but would refer those interested to the contribution of Metcalfe (1932) in which considerable literature is reviewed and a clear discussion of the homologies is given. Since the above mentioned investigation involved the development of genitalia in Coleoptera and included that of *Gastrophysa* (=*Gastroidea* auth.) *polygoni* L., one of the Chrysomelid beetles, the terminology suggested by that author has, in the main, been adopted for the structures considered in this paper.

Investigations into the development of Coleoptera have shown that the posterior segments of the abdomen of the larvae are retracted into the body

and parts and appendages of this retracted portion have been variously modified to form the genitalia of the adult. The name, *genital pocket,* has been used by Singh-Pruthi and Metcalfe for this invaginated portion of the body wall. The other parts of the genitalia are in close relationship to the above structure and, in this paper, have been named the *aedeagus* (Metcalfe, Blake, 1932), the *tegmen* (Sharp and Muir, Metcalfe), and the *spiculum gastrale* (Sharp and Muir, also Singh-Pruthi, and Metcalfe).

The first of these has also been called the median lobe by Muir and Singh-Pruthi. It lies within the genital pocket and consists of a median tubular piece, variously shaped and curved in the Chrysomelidae. A portion of the genital pocket near the middle of the aedeagus is chitinized and forms the *tegmen* which partially or wholly surrounds the aedeagus. In most specimens studied by the writer, this structure has the form of a Y with its lateral forks extending from below around the aedeagus while the remainder, the *strut,* projects anteriorly below the aedeagus. In *Macroplea* (=*Haemonia* auth.) *nigricornis* (Kby.), *Donacia piscatrix* Lac., *Orsodacne atra* var. *childreni* Kby. (Pl. 1, Figs. 1, 2, and 3 respectively), and *Timarcha intricata* Hald. (Pl. 6, Fig. 28) the tegmen is united above and forms a *tegmental cap* over the apical (posterior) portion of the aedeagus. Sharp and Muir (1912) have found this condition in many Coleoptera. In the posterior ventral portion of the genital pocket is the *spiculum gastrale,* a Y-, V-, or U-shaped chitinous structure which varies in size and shape. A generalized explanation of the aedeagus and its internal structure, since the latter is not fully represented in the drawings, will clarify the descriptions which follow in a later section.

At its apical end the aedeagus possesses an opening which is here called the *apical orifice* (median aperture of Sharp and Muir). This is usually situated dorso-caudally due to the fact that, in general, its ventral wall forms a more or less, single or double, pointed apex. The median dorsal wall of the aedeagus is usually thinly chitinized in the posterior half. A *basal foramen* (median foramen of Sharp and Muir), which varies in size, is found on the ventral side of the anterior portion. The roof above this latter opening varies in the amount of chitinization and also in extent. In *Orsodacne* and *Timarcha* two elongated plates are separated by a median opening which extends from near the middle to the extreme anterior or basal tip of the aedeagus. Sharp and Muir have also shown that species of these two genera, other than those studied by the author, show this particular character. The same feature, but not developed to such a marked degree, has been noted in other genitalia discussed in this paper.

An *internal sac* (Sharp and Muir) lies within the aedeagus and posteriorly is continuous with it at its apical orifice. The walls of this sac may be membranous (very lightly chitinized) or, as in many cases, provided with chitinized plates. A distinctly chitinous projection from the junction of the internal sac and the dorsal wall of the aedeagus may extend posteriorly above the apical orifice. This structure, which the author has called the *apical hood,* apparently cannot be retracted into the aedeagus. In other species there may be retractile dorsal plates, dorso-lateral plates or no chitinous structures at this point. The

internal sac extends anteriorly within the aedeagus, the distance varying in different species. An *ejaculatory duct* pierces the sac at its closed anterior end and may extend posteriorly within it. In many species, particularly noticed in the subfamily Chrysomelinae (Figs. 28-58 incl.), the ejaculatory duct connects with or passes through a heavily chitinized and larger tube-like structure, the *flagellum* (Sharp and Muir). At or near the closed end of the sac in other species may be found a pair of elongated plates which, because of their position and structure, have been called *ejaculatory guides* by the writer.

The variations of the internal sac and the flagellum, while indicating species differences, have not been studied sufficiently to judge their full significance as to phylogenetic relationships. For this reason the general character of the aedeagus, the tegmen, and the spiculum gastrale are used mainly in further discussion and are fully illustrated and described.

Descriptions of the Genitalia

Macroplea (=*Haemonia* auth.) *nigricornis* (Kirby) (Pl. 1, Figs. 1a, b, c)

Aedeagus with considerable curve; apex elongated and pointed; apical orifice rather large. Basal foramen large, occupying about one-third of the ventral surface; its borders with thinly chitinized edges which at the anterior tends to curve upward forming a slight pocket. Tegmen ring-like; the strut large and keel-like which when viewed from the side has the shape of the foot of a sock; the lateral, slender and rod-like forks extend dorso-laterally and posteriorly above the aedeagus and join to form a single lobed tegmental cap above the apical orifice; under surface of the tegmental cap curved upward at the tip and bearing long bristle-like hairs. A dorsal plate with two tapering chitinized extensions which curve basally and laterally into the aedeagus is present in the sac at the orifice.

Donacia piscatrix Lacordaire (B) (Pl. 1, Figs. 2a, b)

Aedeagus large, tubular and curved with an elongated and tapering apex. Apical orifice large, occupying about two-fifths of the upper surface. Basal foramen about equal in length to the apical orifice; its posterior edge rather well chitinized and projecting ventrally; the remainder of its border thinly chitinized with anterior edge slightly cupped. Tegmen ring-like, possessing a sock-shaped keel; tegmental cap broad and flattened, divided by a median slit anterior to the tip; the latter bearing long hairs. The internal sac with a median apical hood at the orifice.

Orsodacne atra var. *childreni* Kirby (Pl. 1, Figs. 3a, b, c)

Aedeagus dorsoventrally flattened and only slightly curved. Apex with two pointed lobes. Apical orifice about one-fourth the length of the aedeagus. Basal foramen occupies about one-fourth of the ventral surface, its roof separated by a median slit into two elongated lateral plates. Tegmen ring-like with the strut in the form of a small keel; lateral forks rounded and rod-like and connected dorsally by a transverse rounded ridge; tegmental cap posterior to the ridge having an apex of two pointed lobes, the tips of which are covered with long

hairs. The spiculum gastrale large and Y-shaped, composed of rounded chitinized rods which curl anteriorly upward at their junction. Internal sac large and generally membranous, with a slightly chitinized apical hood, and extending almost the length of the basal foramen beyond the basal tip.

Crioceris asparagi (Linnaeus) (Pl. 1, Figs. 4a, b)

Aedeagus tubular and curved. Its apex blunt and divided into two broad lobes. Apical orifice almost terminal. Basal foramen about one-third the length of the aedeagus, its anterior margin recurved and forming a pocket. The tegmen Y-shaped with a large keel-like strut possessing a tooth on its dorsal margin. (A spiculum gastrale was not found although several specimens were examined carefully for this particular structure. If present, it must be very small and closely attached to the genital pocket.) Internal sac short; a narrow, median dorsal plate and a prominent lateral plate at each side of the orifice.

Lema trilineata (Olivier) (Pl. 1, Figs. 5a, b)

Aedeagus considerably curved with its diameter the least in its mid-section; the floor posterior to the middle sharply bent downward to form the prominent anterior border of the basal foramen. The latter occupying approximately the anterior third of the ventral surface. Apex pointed with its tip curved slightly upward. The tegmen Y-shaped with an elongated keel which curves upward at the anterior. Internal sac approximately one-half the length of the aedeagus; broad median dorsal plate which bends ventrally into the orifice and then anteriorly to form laterally curved projections in the upper wall of the sac; a ribbon-like lateral plate on each side of the orifice, similar to but not so prominent as those in Crioceris.

Antipus laticlavia (Forster) (Pl. 1, Figs. 6a, b, c)

Aedeagus slightly curved; apical orifice large, approximately one-third the length of the aedeagus, its lateral walls sloping gradually toward the pointed apex. Floor of the orifice with median groove. Basal foramen large but less than one-half the length of the adeagus. Tegmen Y-shaped with small lateral forks and a much broadened strut which almost completely fills the foramen and is truncated at the tip. The spiculum gastrale Y-shaped and composed of much flattened but rather heavily chitinized elements. The internal sac very short, complexly folded, and with chitinized ribbon-like plates at the orifice. A slender chitinous flagellum extending into the sac from its closed end.

Megalostomis subfasciata (Leconte) (Pl. 2, Figs. 7a, b, c)

Aedeagus broad, the basal half the broader; slightly curved. Apex flattened in a horizontal plane and truncated at the tip. Lateral walls of the orifice with a distinct lobe projecting posteriorly; a distinct notch below each lobe. Two groups of hairs on each lobe, the smaller group attached to the inner border dorsal and anterior to the tip, the larger group on the outer surface of its lower corner. The basal foramen approximately one-half the length of the aedeagus. Tegmen Y-shaped, the lateral forks curving upward and anteriorly,

the strut broad, slightly elevated in the median line and practically filling the foramen. Spiculum gastrale Y-shaped, composed of rather heavy rod-like elements; the strut approximately twice as long as the lateral forks and only faintly showing a fusion line of its component parts; ends of the lateral forks blunt. A broad, slightly bilobed, apical hood present. The internal sac, below the apical hood, heavily chitinized and tapering to surround a small opening at the posterior. A slender chitinized plate extends posteriorly and towards the median line along each side of the pointed portion. A large ribbon-like lateral plate extends posteriorly on each side from near the prominent lobe of aedeagus, curves toward the median line, then anteriorly and ventrally toward the interior of the aedeagus.

Babia quadriguttata (Olivier) (Pl. 2, Figs. 8a, b, c)

Aedeagus with much the same appearance from the lateral view as *Megalostomis* but slightly more curved. Apex tapering quickly to a rather blunt point. The apical orifice almost terminal in position. A group of long hairs attached to the inner border of the apical orifice slightly above the middle. The basal foramen two-thirds the length of the aedeagus. Tegmen Y-shaped with fairly broad lateral forks curving upward and with a broad strut tapering toward a truncated tip and roundly elevated in the median line. The spiculum gastrale Y-shaped, possessing an anterior keeled strut and pointed lateral forks. Walls of the internal sac more chitinized throughout and with chitinized plates extending into the orifice and consisting of the following: (a) two flattened dorso-lateral plates below which the membrane curves anteriorly and posteriorly bearing a (b) broad median apical hood with diagonal projections which connect anteriorly with (c) chitinized lateral plates near the lateral wall of the orifice.

Urodera crucifera Lacordaire (Pl. 2, Figs. 9a, b, c)

Aedeagus somewhat dorsoventrally flattened, broader at the posterior, and very slightly curved. Apical orifice almost terminal with two groups of hairs on its lateral borders; the more ventrally situated group of small hairs attached to the outer surface, the longer hairs more dorsal and on the inner surface of the orifice wall. The apex with a broad squared point, intermediate in width between *Megalostomis* and *Babia*. Tegmen Y-shaped with rather heavy lateral forks curving dorsally and anteriorly and with a broad strut truncated at the tip. Spiculum gastrale more triangular than Y-shaped, with the membrane chitinized between its lateral forks but with an elongated keel-like strut. Internal sac at orifice similar to *Urodera crucifera* in having dorso-lateral and lateral plates and an apical hood chitinized. The chitinization of sac walls similar in general to Urodera.

Saxinis omogera Lacordaire (Pl. 2, Figs. 10a, b, c)

Aedeagus broader at apical portion and with considerable ventral curvature approximately one-fourth from the tip, the remaining three-fourths with little curve of ventral surface. Apical orifice almost terminal with an irregular row of long hairs attached to the upper inner surface of each lateral wall. Apex

slender, bluntly pointed and with a ventrally curved tip. Basal foramen large, approximately three-fourth the length of the aedeagus. Tegmen Y-shaped with posteriorly curved tips and a flattened strut, crudely truncate at its tip. Spiculum gastrale small with lateral forks barely shorter than the strut which is slightly keeled. The walls of the internal sac rather well chitinized throughout; a pair of curved dorso-lateral plates at the orifice beneath which are other complexly looped chitinous plates. No distinct apical hood present.

Exema conspersa var. *dispar* Lacordaire (Pl. 2, Figs. 11a, b, c)

Aedeagus considerably curved with posterior margin of the basal foramen chitinized and projecting abruptly downward anterior to the middle; a prominent hump directly above on the dorsal surface. The apical portion gradually tapering to a rounded and ventrally curved tip; its ventral surface supplied with hairs anterior to the tip. The basal foramen less than half the length of the aedeagus. Tegmen Y-shaped with rather heavy lateral forks and with a strut, much narrower than in *Saxinis*, elevated in the median line and rounded at the anterior. Spiculum Y-shaped with forks shorter than the strut which is slightly keeled at the anterior. A median dorsal plate present, its under fold forming a dorsal thickening in the wall of the sac. The closed end of the sac chitinous and boxlike through which a slender flagellum passes.

Griburius equestris (Olivier) (B) (Pl. 3, Figs. 12a, b, c)

Aedeagus broader at posterior half and with a rather marked ventral curve one-fourth of the distance from the distal end. The lateral walls of the apical orifice sloping gradually to the rather narrow truncated point; a group of long hairs on each side of the under surface of the apex anterior to the tip. Basal foramen large, approximately one-half the length of the aedeagus; the anterior border rather heavily chitinized but not with abrupt ventral curve. Tegmen Y-shaped with dorso anteriorly curved forks and a large strut elevated in the median line; its tip pointed and curved upward toward the posterior giving a bilobed appearance. Spiculum with lateral forks much shorter than the strut; the latter quite rod-like and exhibiting greater fusion of its component elements. Opening of the internal sac large; the walls of the sac supported by looped dorsa-lateral plates (lp); one on each side, which almost touch in the median line at the posterior, with a strap-like thickening in the median line of the ventral wall, a slender dorsal plate (dp) in the median line above the posterior ends of the dorso-lateral plates. The closed end of the sac pointed and extending posteriorly; its ventro-lateral portion with an elongate plate, ejaculatory guide, on each side.

Pachybrachis luridus (Fabricius) (B) (Pl. 3, Figs. 13a, b, c)

Aedeagus with posterior two-fifths broader and rather sharply curved ventrally. Apical orifice more terminal. Apex broad and tapering toward a rounded point; its side walls somewhat elevated to form a broad groove and its undersurface possessing groups of hairs, two lateral and one medio-posterior near tip. Basal foramen large, over half the length of the aedeagus. Tegmen