A comparative study of the axillary sclerites in Coleoptera

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A COMPARATIVE STUDY OF THE
AXILLARY SCLERITES IN COLEOPTERA

A THESIS
SUBMITTED TO THE FACULTY OF THE
DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY
BRIGHAM YOUNG UNIVERSITY

IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE
MASTER OF SCIENCE

BY
HOWARD P. SHURTLEFF
MAY, 1961
This thesis by Howard P. Shurtleff is accepted in its present form by the Department of Zoology and Entomology as satisfying the thesis requirement for the degree Master of Science.

May 1961

Signed
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INTRODUCTION

There exist many structures in Coleoptera that are indicative of phylogeny which have been overlooked in studies of the comparative morphology of the order. Structures which have been neglected, at least in part, include the tentorium and gula of the head, the pro- and mesothoracic endosternites, the central nervous system, and the internal male and female genitalia. Another set of structures previously unstudied is the axillary sclerites.

The axillary sclerites are a series of small scleritized plates between the tergum and the bases of the wing veins in the articulating membrane of the meso- and metathoracic segments. It is through the manipulation of these plates, and of the epipleurites, by various muscle attachments, that the beetle is enabled to extend and retract the wing, fold it, and use it in flight. The highly variable folding patterns of the flight wing in various groups of beetles suggest that the structure of the axillary sclerites should also vary while maintaining definite relationships to the structures with which they articulate.

It is the purpose of this study to describe and compare the metathoracic axillary sclerites of various families of
Coleoptera, to determine their usefulness in phylogeny, and to show their relationships to the veins of the flight wing.
REVIEW OF LITERATURE

One of the earliest workers to describe and name the axillary sclerites was Straus-Dürkheim (1828). The axillary sclerites were then largely ignored until Snodgrass (1909) published his paper on the thorax of insects and the articulation of the wing. Snodgrass described the axillary sclerites in the various orders of insects and defined the relationships of their various parts more accurately than had been done previously.

Since the work of Snodgrass, although several authors working with the morphology of a single species, genus, or family have briefly described or figured the axillary sclerites, there has been no specific study of them. Generally, workers studying the morphology of the thorax have considered the axillary sclerites as part of the wing, while authors studying wing venation have either considered them as part of the thorax or have entirely ignored them. Snodgrass regarded them as part of the wing. The axillary sclerites have been described or illustrated in the beetle families Scolytidae (Hopkins, 1909), Cerambycidae (Swain and Hopping, 1928), Carabidae (Bostick, 1945), and Alleculidae (McDonald, 1960). They have been used as a guide in studies on wing venation by Saalas (1936) in his
work on Cerambycidae and by Balfour-Browne (1944) in his study of wing venation in Adephaga.

Crampton (1918) compared the morphology of the axillary sclerites and tergum in a number of orders and attempted to relate the orders on the basis of their similarity. However, he erroneously concluded that the Coleoptera and Dermoptera were related.

Although the wing veins in Coleoptera have been studied more extensively than have the axillary sclerites, there have been few attempts to relate or describe the veins of the flight wing on the basis of their relationships to the axillary sclerites. This is somewhat unusual since Snodgrass (1935) stated that they "have definite and constant relations both to one another and to the bases of the veins."

One of the earliest studies of wing venation showed that members of the Adephaga possess common characters of venation (Burmeister, 1842). Ganglebauer (1903) described the wings of the Coleoptera and proposed three basic venational patterns within the order. They were the Adephagan type, characterized by the presence of many longitudinal veins with many cross veins and oblongum cell; the Staphylinoid type, characterized by the absence of the cross veins and basal part of the media; and the Chalcid type which has cross veins and a hooked media.

The Coleoptera was divided into three suborders on the basis of wing venation (and other characteristics) by Kolbe (1901). These were the Adephaga (including Cupedidae), four
groups of Heterophaga, and the Rhyncocephora. In his discussion of the wings he followed Adolph's (1880) theory of alternate convex and concave veins which has since been discounted by Forbes (1922) and Ganglebauer (1903) on the basis that it is not valid in Coleoptera.

An extensive description of the wings was given by Kempers (1899-1909) in his classification of the Coleoptera based on wing venation. D'Orchymont (1921) classified the beetles into two suborders, the Adephaga and Polyphega; in his study of wings he recognized only two venational types, the Adephaga and Cantharid types.

The most recent, major studies of wing venation are those of Graham (1922) and Forbes (1922). Neither author divided the Coleoptera on the basis of venational patterns, although Graham did give four venational groups—the Lampyrid, Cerambycid, and Carabid types and a fourth group (not named) too highly specialized to indicate relationships. Both Graham and Forbes proposed a hypothetical pattern of venation for the primitive wing. Their systems differ, however, in the number of veins and in the names given to each. Current authors tend to follow the system used by Forbes.

The ontogenetic development of the wings was described by Powell (1904-05). Comstock (1918) described and named the veins by using their ontogenetic developmental sequence and relationships as a basis. The extensive work of Comstock largely standardized the terminology used for the wing veins of all
insects. Since many of the early studies of the wing veins contained various sets of names for the veins, Oertel (1924) made an attempt to homologize or unify the terminology of a number of authors with respect to the Adephaga; Balfour-Browne (1944) also attempted to standardize and correct the terminology of the same group.

In order to evaluate the usefulness of wing venation in taxonomy, several authors have made studies of the variation, and consistency of venational patterns, in various groups. Wilson (1934), in a study of a Chrysomelid beetle, showed how the venation can vary slightly in a single species, and even vary between the right and left wings of a specimen. Another study demonstrated how the venation and size of the wing in Dryopidae varies with the habitat (Segal, 1933), while Darlington (1936) discussed extensively the variation and atrophy of the flight wing of Carabidae. In his study, Darlington concluded "that flying wings have frequently tended to atrophy among Carabidae of diverse sorts except in ecological groups where the wings are observably useful to the insects." He also stated that "in view of the extraordinary variation which occurs not only among closely related species but within a single species, the state of the wings must be used as a taxonomic character only with the greatest care, after examination of a long series." Darlington's study also indicated that the basal portion of the wing is subject to less modification or reduction than the rest of the wing.
Many authors have stated that the venation in the flight wing tends toward reduction as the size of the beetle becomes smaller (Darlington, 1936; Forbes, 1926; Parsons, 1943).

In spite of the variation present, the venational patterns are sufficiently constant that Cockrell and Harris (1925) were able to construct a key to some of the Meloid beetles based on wing venation. Good (1925), Wilson (1920), and Saalas (1936) used the wing venation for determining the phylogeny of the Buprestidae, Cucujoida, and Cerambycidae respectively. Goodlife (1939), in his study of the Bytisoidae, concluded that the wings provided excellent characteristics for determining the tribes and genera of the family. In a study of some Cerambycidae, Swaine and Hopping (1928) state "that the wing venation of the Lepturini present excellent group and generic characters and may be utilized, in places, for the identification of species."

The folding patterns of the flight wing were worked out by Forbes (1926). Forbes presented a hypothetical folding type and its modifications, then demonstrated relationships between the families and higher groups based on their folding patterns. However, he stated that some families show more than one type of folding pattern. Darlington later showed that the amount of folding decreases as the specimen becomes smaller. Balfour-Browne in his work with Adephaga concluded "that the mechanical strains play a large part in the arrangement of the veins..."
flight wing. Among them are the studies of Hopkins (1909), Blood (1935), Forbes (1942 a, b), Bostick (1945), Selander (1957, 1959), and McDonald (1960). For the most part, these are either morphological studies of a species or phyletic studies.
METHODS AND MATERIALS

In this study, the axillary sclerites of more than 200 specimens representing 52 families of Coleoptera were examined. Prior to study the dried specimens were soaked in a ten percent solution of cold potassium hydroxide (KOH) for varying lengths of time depending on the size of the specimen and the amount of sclerotization in the wing base. When soft enough to manipulate, the specimens were placed in water, the right elytron pulled forward, and the flight wing pinned out at a right angle to the body.

The axillary sclerites, the base of the wing, and a portion of the tergum were then drawn on onion-skin paper, with an underlying sheet of graph paper, with the aid of an ocular grid and stereoscopic microscope at a magnification of 10, 20, 40, or 80 times. All drawings were made approximately the same size to emphasize the relationships of the parts to one another. They were later transferred to a more permanent paper with the aid of a tracing table, and then inked.

Permanent mounts of the wings were prepared by removing the left flight wing with its axillary sclerites, floating it onto a microscope slide with the wing spread into position, then removing it from the water and carefully removing the excess water before mounting. Various mounting media were
used (Hoyers, polyvinyl alcohol, Harleco synthetic resin, clerite, and Canada balsam), however, clerite and polyvinyl alcohol were found to be the best because of their fast drying qualities and hardness when dry. The wing veins were later drawn from these slides as they were needed.

The following alphabetical list of families of Coleoptera includes the names of species examined during this study:

Amphizoidae: *Amphizea lecontei* Matthews
Anobiidae: *Vrilletta murrayi* LeConte
Anthribidae: *Phoenicobiella chamaeropis* Le Conte
Belidae: *Ithycerus noveboracensis* (Forster)
Bostrichidae: *Dinapate wrightii* Horn
Brentidae: *Brentus* sp.
   *Eupsalis minuta* Drury
Buprestidae: *Hippomelass phenicus* (LeConte)
Byrrhidae: *Byrrhus laramiensis* Casey
Cantharidae: *Chauliognathus* sp.
Carabidae: *Brachinus* sp.
   *Calosoma tepidum* LeConte
   *Chlaenius* sp.
Cebrionidae: *Cebria bicolor* Fabricius
Cerambycidae: *Prionus* sp.
   *Tetraopes canescens* LeConte
Chrysomelidae: *Chelymorpha* sp.
   *Chrysochus cobaltinus* LeConte
Cicindelidae: *Cicindela oregona* LeConte
Cleridae: *Trichodes ornatus* Say
Coccinellidae: *Anatis lecontei* Casey
Cucujidae: *Cucujus* sp.
Cupedidae: *Copea concolor* Westwood

**Priaecma serrata** LeConte
Curculionidae: *Calandra ochrea* (LeConte)

*Cyphus placidus* Horn
*Laconopus argus* Reiche
*Rhynchophorus* sp.

Dascillidae: *Dascillus davidsoni* LeConte
Dermestidae: *Dermestes marmoratus* Say

Dryopidae: *Helichus striatus* LeConte

*Lara avara* LeConte
Dytiscidae: *Dytiscus marginicollis* LeConte
Elateridae: *Alaus oculatus* (Linné)
Erotylidae: *Megalodacne fasciata* (Fabricius)
Gyrinidae: *Dineutus sublineatus* Chevrolat
Heteroceridae: *Heterocerus* sp.

Histeridae: *Hister* sp.

*Hololepta* sp.
Hydrophilidae: *Hydrous triangularis* (Say)

Lampyridae: *Photinus* sp.

*Photuris* sp.
Lucanidae: *Pseudolucanus maxima* Le Conte
Lycidae: *Lycostomus loripes* (Chevrolat)
Lymexylidae: *Atractocerus* sp.
Melandryidae: Eustrophinus sp.
Meloidae: Lytta vulnerata cooperi LeConte
Melyridae: Collops bipunctatus Say
Mordellidae: Tomoxia bidentata (Say)
Nitidulidae: Phenolia grossa (Fabricius)
Oedemeridae: Asclera excavata LeConte
Ostomatidae: Temnochila chorodia (Mannerheim)
Platypodidae: Platypus jansoni Chapuis
Rhipiceridae: Rhipicera tessellata Westwood
                              Sandalus petrophylla Knoch
Rhipiphoridae: Rhipiphorus sp.
Rhysodidae: Rhysodes hamatus LeConte
Scarabaeidae: Polyphilla lineata Say
Scolytidae: Dendroctonus engelmanni Hopkins
                      Dendroctonus monticola Hopkins
                      Dendroctonus valens LeConte
                              Ips guildi Blackman
Silphidae: Neorophorus marginatus Fabricius
Staphylinidae: Creophilus maxillosus villosus (Gravenhorst)
Stylopidae: Lychnocolax mindore Bohart
                              Myrmecolax rossi Bohart
                            Tricogera mexicana Pierce
Tenebrionidae: Tenebrio obscurus Fabricius
Trogidae: Trox sp.
Description of a Typical Beetle

The axillary sclerites in Coleoptera (fig. 1) consist of three flattened scleritized plates called the first, second, and third axillary sclerites. Associated with them is a number of accessory sclerites including the median plates, pleural disc, and myodisc.

The first axillary sclerite (1Ax) is a flattened, generally bilobed structure with the anterior lobe or head connected by a narrow neck to the posterior lobe or base. The head articulates to the base of the subcostal vein (Sc) on the distal side and the anterior notal wing process on the basal side. The base articulates to the anterior notal wing process (ANP) on the lateral margin of the tergum, on its basal side and to the second axillary sclerite along its distal margin.

The second axillary sclerite (2Ax) serves as a pivot for the wing base and rests upon the pleural wing process. It generally is triangular with its basal margin articulating to the base of the first axillary sclerite and its distal margin articulating to the median plates (MP). Anteriorly it usually is connected by means of a narrow bridge, called the axillary bridge (Ax B), to the base of the radial vein (R1). The
posterior angle of the triangle may just meet the median edge of the crest of the third axillary sclerite or taper out and end before reaching it. This sclerite functions in drawing the wing in toward the body.

The third axillary sclerite (3Ax) articulates to the posterior notal wing process (PNP) along part of its basal margin and distally to the anal veins. Anteriorly it articulates to, or is connected to, the second median plate. It may consist of a broad anterior head and an elongate tapering shaft. The head usually bears a small process or knob at its antero-median corner. The sloping curved portion just anterior to this process forms the crest of the head. Muscle attachments cause the outer edge of this axillary sclerite to lift and fold the anal portion of the wing.

The myodisc (MD), or muscle disc, is a small sclerite immediately anterior to the anterior notal wing process of the metathorax. Snodgrass (1909) and Crampton (1918) both called it the muscle disc and not a tegula as might be assumed. Crampton also stated that muscles which function in flight are attached to it.

Located in the axillary membrane between the third axillary sclerite and the tergum is a small, round, and generally ignored sclerite, the pleural disc (PD) (Hopkins, 1909). It serves no observable function except perhaps that of an articulative buffer surface to prevent wearing of the membrane by the process of the third axillary sclerite.
There are two median plates which articulate to the lateral margin of the second axillary sclerite and are fused to the bases of the medial (M₁) and cubital (Cu₁) veins, or are connected to them by a median bridge (MB). The anterior, or first median plate (1MP), is fused with, or separated to various degrees from, the posterior or second median plate (2MP), which articulates to the crest of the third axillary sclerite.

The axillary sclerites, median plates, and pleural disc are located in the axillary membrane (AxM). The membrane extends from the tergal margin to the base of the wing veins.

The wing veins maintain definite relationships to the axillary sclerites and median plates and may be named from the consistency of their connections, although this has been ignored by most authors.

The costa (C₁) does not connect basally with any of the sclerites, but is connected by a membrane to the subcosta to the first axillary sclerite, and to the parts of the tergum. The distal part of the vein is either fused to the subcosta or lost.

The base of the subcosta (Sc) articulates to the head of the first axillary sclerite. The base of the subcosta also connects to the base of the radius (R₁), which in turn connects to the axillary bridge, when it is present.

The media (M₁) either fuses to the median plates or to a large plate formed by its fusion with the cubitus (Cu₁). This
fused plate is connected to the median plates by means of a single or divided median bridge (NB). The media and radius are often connected to one another by a small cross vein just distal to the fusion plate of the media and cubitus.

The first anal vein (1A) is persistent in beetles, and one or more additional anal veins may be present, although these latter anal veins either may be lost or else represented by thin, indefinite scleritized areas. The first anal vein usually articulates to the distal point of the head of the third axillary sclerite. Its base often extends anteriorly to fuse with the base of the cubitus, and posteriorly to the other anal veins. This latter connection is often very indistinct.

Group Modifications

Archostemata.--(Figs. 1 and 2). The first and second axillary sclerites follow the general description given above. The third axillary sclerite, however, is a comparatively small irregularly shaped triangle which articulates only by its posterior tip to the posterior notal wing process. The large median plates, at their point of articulation to the second axillary sclerite, are separated by a small membranous area. The posterior notal wing process is an anteriorly projecting lobe from the tergum, which extends anteriorly to articulate to the posterior tip of the third axillary sclerite. Except for the first anal vein, and a second anal vein in the wing of
Cupes, the anal veins are absent. An axillary cord is present and there is a lightly scleritized area extending anteriorly from it which connects the anal veins together, and to the cubitus.

Adephaga.--(Figs. 3 to 8). The first axillary sclerite is normal except for the median portion of the base which is elongated posteriorly to extend beyond the anterior tip of the lobe-like posterior notal wing process, and the deeply constricted neck. The third axillary sclerite is small and irregularly present to triangular shaped. The third axillary sclerite articulates to the posterior notal wing process by its posterior tip only. An axillary cord is present with a scleritized area extending anteriorly from it connecting the numerous anal veins. In Geadephaga (figs. 6 to 8), the axillary bridge is absent, except for Rhysodidae (fig. 6). The axillary bridge is present in Hydradephaga (figs. 3 to 5). The articulatory surface between the second axillary sclerite and median plates is reduced in Hydradephaga to a narrow area, and absent in Geadephaga. In Rhysodidae, the median plates and bases of the wing veins are reduced, and the posterior notal wing process is present only as a small, knob-like process of the tergum.

Staphyliniformia.--(Figs. 9 to 12). The first and second axillary sclerites follow the general description, except that the base of the first axillary sclerite has a posterolateral slope. The third axillary sclerite, however, varies con-
siderably in the series. In Hydrophilidae (fig. 9), the head is large with an irregular anterior margin while the shaft is long and narrow; in Staphylinidae (fig. 11), the head is small and in line with the shaft; in Silphidae (fig. 10), the solerite is larger, but resembles that of Staphylinidae; and in Histeridae (fig. 12), the solerite is a very large square structure. The median bridge is divided. In Staphylinidae the anal vein is absent, while in the other families a second anal vein is present. The bases of the veins are enlarged with extensive fusion taking place between them to result in large scleritized areas, particularly in the Histeridae. The posterior notal wing process is an anteriorly projecting point with a wide articulatory surface connecting to the third axillary solerite.

**Elateriformia.**—(Figs. 13 to 20). The axillary solerites of Byrrhidae (fig. 13) and Dryopidae (fig. 14) are similar to one another and follow the general pattern for the axillary solerites. The median plates are small and the median bridge is undivided. The posterior notal wing process is an anteriorly projecting point and has a wide surface articulating to the third axillary solerite. There is a second anal vein present throughout the series, although it is reduced in Lycidae (fig. 20). In Buprestidae (fig. 15) the first axillary solerite has a laterally elongate base which almost touches the posterior notal wing process. The second axillary solerite and median plates are reduced to narrow
structures, while the third axillary sclerite is broadly rectangular. The first and second axillary sclerites of Cebrionidae (fig. 16) and Elateridae (fig. 17) fit the general description. In Elateridae the axillary bridge is broken or subdivided. The shaft of the third axillary sclerite is broader than is the head and there is a small sclerotized connection with the head of the anal vein from the sclerite. A small membranous area is present in the fusion plate of the media and cubitus. In Rhipiceridae (fig. 18) the third axillary sclerite has a slight lateral elongation of the base, the head of the third axillary is wider than is the shaft, and the median plates appear divided. A membranous area is present in the fusion plate of the media and cubitus. The posterior notal wing process of Rhipiceridae, is lobe-like and a second anal vein is present. The articulating surface between the second axillary sclerite is wide, extending the length of the second axillary sclerite, as it does in most Polyphaga. The distinctive features of Cantharidae (fig. 19) are the broad triangular third axillary sclerite and lobe-like posterior notal wing process. It lacks the membranous area in the fusion plate of the media and cubitus; it has un-divided median plates and median bridge; and has a second anal vein. The family Lycidae has a lobe-like posterior notal wing process, a membranous area in the fusion plate of the media and cubitus, but lacks the second anal vein.

Scarabaeiformia.--(Figs. 21 to 24). The family
Dasoilidae (fig. 21) follows the general pattern except that the base of the first axillary sclerite is elongated laterally and the median plates and median bridge are divided. The third axillary sclerite is broad and angular. The posterior notal wing process is a large anteriorly projecting point, and a second anal vein is present. The axillary bridge is absent in Lucanidae (fig. 22) and Scarabaeidae (fig. 24). The third axillary sclerite in Lucanidae is roughly triangular, in Trogidae (fig. 23) it is slightly curved, and in Scarabaeidae it is almost rectangular. There is a small process from the fusion plate of the median and cubital veins which extends toward the crest of the third axillary sclerite, and in Scarabaeidae meets with the crest. There is another process from the same fusion plate which extends anteriorly to meet with the radius. The third axillary sclerite has a broad articulation to the posterior notal wing process which is an anteriorly projecting point. A second anal vein is present in Lucanidae and absent in Trogidae. Scarabaeidae has a number of anal veins.

Bostrichiformia.--(Figs. 25 to 27). In Bostrichidae (fig. 27) the base of the first axillary sclerite slopes posterolaterally, but is normal in other representatives of the series. The third axillary sclerite varies from an irregularly shaped crescent in Dermestidae (fig. 25), a rough trapezoid in Anobiidae (fig. 26), to almost linear in Bostrichidae. In Dermestidae and Anobiidae, the median plates
and median bridge are divided and there is a membranous area in the fusion plate of the media and cubitus; in Bostrichidae the median plates and median bridge are also divided but there is no membranous area in the fusion plate of the media and cubitus. In Dermestidae, the bases of the posterior veins are reduced and in Anobiidae, the bases are almost completely absent, but in Bostrichidae the vein bases are distinctly present, and there are several additional anal veins present. In Bostrichidae the posterior notal wing process is reduced to a crest on the margin of the tergum; it is a laterally projecting point in the other families.

*Oculosoma*—(Figs. 28 to 49). Among the Oculosomatidae the axillary sclerites are generally alike and usually resemble the general pattern. Generally though, the two posterior points of the base of the first axillary sclerite are on the same plane, the third axillary sclerite is usually elongate and slightly curved, and there is a broad articulation between the posterior notal wing process and the third axillary sclerite. Other features common in this series include the presence of a cross ridge in the fusion plate between the medial and cubital veins, and a lateral indentation which partially separates the median plates. There is also a second anal vein, or indication of one, throughout the series. The axillary sclerites in *Lymexylidae* (fig. 37) are small, the axillary bridge is absent, the third axillary sclerite is roughly linear, the posterior notal wing process is reduced to
to a small rise on the margin of the tergum, and an axillary cord is present. The family Stylopidae has Coleoptera-like axillary sclerites, although they are very small and reduced. The Cleroidea possess typical axillary sclerites except in the family Cleridae (fig. 39) in which the third axillary sclerite is roughly trapezoidal. In Cerambycidae (fig. 40) the first axillary sclerite has a large head and base with a narrow neck. The second axillary sclerite is normal in the Chrysomeloidea, but lacks the axillary bridge in Cerambycidae. Also in Cerambycidae the third axillary sclerite is long and comparatively slender. In the Chrysomeloidea the posterior notal wing process is a small slightly posteriorly sloping process. The Curculionoidea (figs. 43 to 49) follow the general pattern for the Cucujiformia. The first and second axillary sclerites are normal but the third axillary sclerite tends to become thinner and crescent shaped with a hook on the distal end of the head. The axillary bridge is present but the median bridge is narrow and only lightly scleritized (except in Rhynchophorus and Lachnopus). The second anal vein tends to be reduced and is lost in the Scolytidae, in Calandra, and in Rhynchophorus.
DISCUSSION

The suborders Adephaga and Archostemata may be distinguished from the suborder Polyphaga by a combination of characters. For example, the posterior notal wing process in Adephaga is a lobe-shaped structure (except in Rhysodidae), while in the Polyphaga the process generally is a simple anteriorly projecting point, and is lobed only in the Staphylinidae, Rhipiceroidae, and Cantharoidae.

The first axillary sclerite of the Adephaga and Archostemata is generally more constricted in the neck region than in the Polyphaga, while the lateral margin of the base is more deeply indented or angled in Adephaga than in Polyphaga in which the posterior margin of the base is usually a smooth arch with the ends of the arch level with each other.

The second axillary sclerite is basically the same among all beetles and undergoes only slight variations.

The third axillary sclerite of the Adephaga and Archostemata is comparatively smaller and more irregularly shaped than in Polyphaga. It is elongate and larger in Polyphaga, but short and broad in Adephaga. In Polyphaga the third axillary sclerite articulates with the posterior notal wing process along a part of its medial margin, while in Adephaga and Archostemata the sclerite articulates by its
blunt posterior point to the anterior point of the posterior notal wing process.

Among the Adephaga and Archostemata, there is a tendency for the medial point of the base of the first axillary solerite to extend posteriorly until it is almost on the same level as the anteriorly projecting posterior notal wing process.

Other distinguishing features of Adephaga and Archostemata include the presence of an axillary cord (or its remnant), and a large scleritized area extending anteriorly from the tergum and axillary cord connecting the anal veins and bases of the radius and media. In Polyphaga the anal veins may be fused with the radius and media in a large scleritized plate but the scleritization does not extend to the tergum.

In Adephaga and Archostemata there may be no connection between the median plates and second axillary solerite, each median plate may connect separately with the second axillary solerite with a small membranous area between their ends, or there may be only a single narrow articulation. In Polyphaga the articulation usually extends the length of the lateral margin of the second axillary solerite.

The Archostemata (Cupedidae) may be distinguished from the Adephaga by a number of characters. The Archostemata possess a more lobe-like posterior notal wing process; the median plates are separated at their point of articulation to the second axillary solerite; they have a reduced number of
anal veins; and the scleritization of the anal area of the wing is reduced. These characters all vary in the Adephaga.

Within the Adephaga, the Hydradephaga can be readily distinguished from the Geadeaphaga. The Hydradephaga all have an exillary bridge, and there is a narrow articulation between the median plates and second axillary sclerite, while in Geadeaphaga there is no axillary bridge and no articulation between the median plates and second axillary sclerite.

The family Rhysodidae appears to represent a separate branch of the Adephaga, and not a part of the Geadeaphaga. It has a closer resemblance to Cupes (Cupedidae) than to other Adephagans. The second axillary sclerite of Rhysodes resembles Cupes or Hydradephaga more than it does Geadeaphaga. It has an axillary bridge unlike the Geadeaphaga, and the third axillary sclerite has a greater resemblance to Cupes than to Adephaga. The absence of the anal veins and the posterior notal wing process helps set it apart as a separate group also.

Within the Polyphaga there are no definitely reliable characters which may be used to separate the various series or superfamilies. There are only a few general trends in the development or reduction of one structure over another.

The series Staphyliniformia is typified by the presence of a divided, or partially divided, median bridge and the generally posteriorlateralally sloping of the base of the first axillary sclerite. The Histeridae appear to be an aberrant
form within the series; the third axillary sclerite and median plates are enlarged out of proportion to the other structures; and the first axillary sclerite and the enlarged costal head resemble those of Silphidae, while the second axillary sclerite resembles Hydrophilidae.

The Blateriformia has no uniform differences which separate it from other closely allied groups of beetles. The Buprestidae, whose axillary sclerites differ from those of other beetles, has an elongate first axillary sclerite with the narrow median portion of the base extending past the anterior point of the posterior notal wing process, a narrow second axillary sclerite, median bridge, and median plates, all of which are the same width, and a large, almost rectangular third axillary sclerite. The Rhipiceroidea and Cantharoidea possess similar characteristics. Their axillary sclerites are of the same general shape, but their distinguishing feature is the lobed posterior notal wing process.

The remaining families of Blateriformia also have similar characteristics.

The two series Scarabaeiformia and Bostrichiformia have many characteristics in common. In Trogidae and Anobiidae the first and second axillary sclerites are almost identical. A general trend within these two groups is for the axillary bridge to be split, or at least partially so, or to possess a process extending from the fusion plate of the medial and cubital veins toward the crest of the third axillary sclerite.
which appears to form the divided axillary bridge. These two series also have similarities to some other groups of beetles; the axillary sclerites of Dascillidae are almost identical to those of Ripipoteridae, and the third axillary sclerite of Bostriichidae is similar to that of Cucujiformia. The lack of an axillary bridge and the broad posteriorly tapering third axillary sclerite demonstrates the close relationship between Lucanidae and Scarabaeidae. The family Trogidae appears to be an intermediate group between Dascillidae and Scarabaeidae, as is seen in the resemblance of its third axillary sclerite to Dascillidae and its median plates for Scarabaeidae.

There are few distinguishing features of the large series Cucujiformia except for the presence of a heavy scleritized ridge in the fusion plate of the medial and cubital veins, the tendency for the third axillary sclerite to become elongated and thinner through the head region than that of other beetles, and for the median plates to be indented or divided along their lateral edge. Within the Cucujiformia there are few characteristics which serve to divide one group from another. The family Lymexylidae may be distinguished by the reduction of its axillary sclerites, and its elongate, almost linear third axillary sclerites. The Cerambycidae are distinguished by the formation of a hooklike process formed by the curving of the distal tip of the head of the third axillary sclerite. Other than these, the Cucujiformia possess rather uniform characteristics.
A brief study of the wings themselves indicates that as the size of the species decreases, the venation undergoes reduction and becomes less complex. This, however, is dependent upon the initial amount of venation in the group and on the comparison of specimens of the same size in various groups having varying degrees of venation.

The study also indicates that although there is interspecific variation and may be some intraspecific variability, the venational patterns of the wing base are of value in the determination of some genera and families, and may be useful in the analysis of phylogeny in certain groups of Coleoptera.
CONCLUSIONS

1. There is considerable variation in the general form of the axillary sclerites in the order Coleoptera.

2. The suborders Archostemata, Adephaga, and Polyphaga may be distinguished from one another by a combination of axillary characters.

3. Within the Adephaga the Geadephaga may be distinguished from the Hydradephaga, except that the family Rhysodidae appears to represent a separate branch of the adephaga.

4. Within the Polyphaga major groups may be distinguished from each other. However, in most cases variations in the axillary sclerites are too inconstant to provide useful criteria for determining the phylogeny of these Coleoptera.

5. Generally the venation of the wing base undergoes reduction as the size of the specimen decreases, but this evidently has little effect on the form of the axillary sclerites.

6. Venational patterns are of some value in determining some families and genera, such as Meloidae, Cerambycidae, and Buprestidae, and may be useful in determining the phylogeny of some groups.
LITERATURE CITED


A COMPARATIVE STUDY OF THE AXILLARY SCLERITES
IN COLEOPTERA

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BY
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This abstract by Howard P. Shurtleff is accepted in its present form by the Department of Zoology and Entomology as satisfying the abstract requirement for the degree Master of Science.

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ABSTRACT

The axillary sclerites of 69 species representing 52 families of the order Coleoptera were examined and illustrations prepared of most of them. A description is given for the typical axillary sclerites and the deviations in form from this pattern are discussed for the major groups of beetles.

The phylogenetic relationships between some families, and other groups, are pointed out based on the morphology of the axillary sclerites. Phyletic groups in Adephaga are characterized by the axillary sclerites, but in the Polyphaga variations are too numerous and inconsistent to be useful in determining phyletic trends.