SPECIES VARIATION IN THE HIND WINGS OF COLEOPTERA AS EXEMPLIFIED BY THE GENERA _SILPHA_ AND _SAPERDA_

By

EDWIN WALLACE KING

A Major Thesis Submitted to the Graduate Committee

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

in

Entomology

Approved:

Course Adviser

Head, Department of Biology

Dean of Agriculture

Virginia Polytechnic Institute

1947

Frontispiece-----The Wings of *Silpha* and *Saperda*

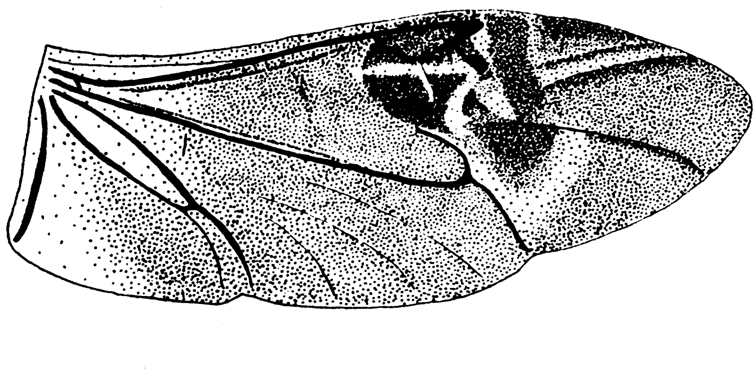


TABLE OF CONTENTS

List of Plates

List of Tables

SPECIES VARIATION IN THE HIND WINGS OF COLEOPTERA AS EXEMPLIFIED BY THE GENERA SILPHA AND SAPERDA

INTRODUCTION

Coleopterous wing venation has been used for some time as an aid in indicating phylogenetic trends among families and, in some cases, genera (see Review of Literature). It has been thought by the writer that certain characters may be sufficiently constant to justify their use in differentiating species. The value of such a study lies not in its immediate utilization for the identification of beetles——that can usually be accomplished by means of more readily available organs——but in the fact that the hind wings may possess characters which, when taken in conjunction with other structures of the insect, will enable the systematist to describe a specimen more completely and to determine more accurately its taxonomic relationships.

The investigation discussed in this paper was undertaken, therefore, with two objectives: first, to determine the constancy and value of such specific characters, should they be found to exist; and second, to attempt to correlate the characteristics of the wings with the established relationships of the species concerned.

Two genera were chosen for study: the genus *Silpha*, of the family Silphidae, and the genus *Saperda*, of the Cerambycidae. These two genera are well separated phylogenetically; the Silphidae, while not considered among the most primitive families of Coleoptera, are nevertheless much less advanced than are the highly specialized Cerambycidae. Neither *Silpha* nor *Saperda* is entirely confined to North America, although both genera are well represented on this continent; and since ten of the fifteen North American *Silpha* species and fifteen of the eighteen North American *Saperdas* were available for study, it seemed likely that the purposes of the investigation could be fulfilled by limiting it to the North American species of both genera.

REVIEW OF LITERATURE

Literature dealing with the hind wings of Coleoptera is not extensive, and that which considers species variation is apparently almost non-existant. Swaine and Hopping (17) describe in detail the venation of a few species of Lepturinae (Cerambycidae) but their discussion is limited to venation in the rather variable anal field, and no attempt is made to reach a definite conclusion. G. R. Hopping, working with the tribe Clytini (Cerambycidae) states* that he was unable to find reliable specific characters in those members of that group whose wings he investigated. The writer (10) succeeded in separating by a difference in coloration the wings of two species of the genus Cyllene (Cerambycidae).

In the general works dealing with insect wing venation little space is usually devoted to the order Coleoptera. Comstock (1), Needham (14), and Woodworth (18) offer little that is pertinent to the present problem. All are concerned with ordinal venational characters.

Two papers may be considered to be of basic importance, however. Forbes (3) and Graham (6) each present a theory to account for the basic venational types among the families and superfamilies of Coleoptera. Their theories are compared in detail in another part of the present paper. The sequel of the Forbes discussion, (4) dealing with wing folding patterns, considers another phase of wing taxonomy and throws more light on family relationships.

Good (5) and Saalas (15) have carried the subject one step further, the former having keyed out the wings of the American genera of the Bu-

---

*Private communication.

prestidae and the latter many genera of European Cerambycidae. Both papers demonstrate what may be accomplished in family studies, and have served as prototypes for the present study at generic level. Both papers utilize only venation, and find it adequate for generic determination.

Reference will be made to a few structures and terms which have been treated in general works not primarily concerned with wings. Two such general sources are Snodgrass (16) and McIndoo (13).

Since any taxonomic study necessarily depends on some understanding of the groups concerned, the following taxonomic material was relied upon: for Saperda, Felt and Joutel's Monograph of the Genus Saperda (2); for Silpha, Horn's Synopsis of the Silphidae (7); and LeConte's Synopsis of the Silphales (11). Final authority for validity and nomenclature of all species was Leng (12).

A small part of the material presented lends itself to statistical analysis. The references used in this connection were Kendall (9) and Hotelling and Pabst (8).

PROCEDURE

Techniques of Preparation

The technique used in mounting the wings is comparatively simple. Relaxation of a specimen is easily accomplished by autoclaving for 30 minutes at 15 pounds pressure or by several days in a relaxing jar. When thoroughly relaxed, the elytron is raised and the wing gripped firmly across the basal sclerites with a pair of fine forceps. Since a beetle is conventionally pinned through its right elytron, the left wing is taken in nearly all cases. A steady pull removes the basal sclerites from their attached muscles without tearing either the wing or the thorax. The elytron may then be allowed to return to its normal position, and the specimen is externally uninjured.

The wing is washed thoroughly in absolute alcohol for several minutes, unfolded, and spread by means of forceps. Held in a spread position, it is then immersed in xylene for a minute or two. Small wings may be removed immediately at this point and placed on a slide; larger wings must be allowed to dry for two or three minutes, still held by forceps in a spread position, before being released. On the slide, the basal sclerites are cut away based to the arculus, and the wing given its final spreading and orientation.

Both balsam and clarite have been used as media, the latter being preferred because of its great transparency except in cases where the wing is itself transparent.

Fundamental Characters

As might be expected in organs not in continual use, the wings of Coleoptera show a certain amount of individual variation. For that reason a series of from three to twenty-two specimens was used for each species, and only characters which were constant throughout an entire genus were considered. To reduce further the chance of introducing variable characters into the keys, characters which were observed to be unreliable in one species were avoided, or reduced to only secondary importance, in the description of another species.

Three major groups of characters must be considered in examining the wings of Coleoptera for species determination: venation, coloration, and chaetotaxy. These categories will be discussed in detail as their immediate applications arise, but, to avoid duplication, fundamental definitions and evaluations common to both _Silpha_ and _Saperda_ will be reviewed at this point.

Venation appears to be of little value as a specific character. It is quite constant in both genera, and shows little variation among species. Only in _Silpha discicollis_ is venation alone depended upon to separate a species. Since nearly all other characters are located by reference to a vein, however, a thorough knowledge of venational nomenclature as applied to _Silpha_ and _Saperda_ is essential to the proper use of the keys.

As previously mentioned, two principal systems of interpretation are available concerning the wing venation of Coleoptera: that of S.A. Graham and that proposed by W. T. M. Forbes. They are compared in Table 1.

Table 1.
Comparison of Forbes and Graham Venational Theories

Graham	Corresponds to	Forbes
C	. . . .	C
Sc	. . . .	Sc
R	. . . .	R
Rs	. . . .	Rs
R_2	. . . .	Rs + r
R_{3+4}	. . . .	2nd r-m
No corresponding vein	. . . .	R_3
R_5	. . . .	Mr
r	. . . .	1st r-m
$R_5 + M_{1+2}$	. . . .	M_4 + Cu
No corresponding vein	. . . .	M_1
M_{1+2}	. . . .	Cu
M_3	. . . .	1st A
M_4	. . . .	2nd A_1
Cu_1	. . . .	2nd A_2
Cu_2 + 1st A	. . . .	2nd A_3 + 3rd A_1
2nd A	. . . .	3rd A_2
3rd A	. . . .	4th A

It is not within the scope of the present paper to compare the relative merits of the two theories. As may be readily seen, they differ considerably. Since the Forbes system acknowledges the presence, or recent atrophy, of veins in the apical portion of the wing, and since such veins occur and must be considered in both Silpha and Saperda, it is more applicable to the present study and will be used here. Plate I, fig. 1, and Plate III, fig. 3 illustrate its application to typical wings of the two genera.

Coloration may be divided into (a) ground color and (b) pattern. Ground color is the diffused pigment which covers the entire wing to a greater or lesser extent. It is of considerable value in separating the species of Silpha; of much less value in Saperda. Pattern may be defined as the more or less sharply demarked areas of pigment, usually near the radial cell in Saperda or the stigma in Silpha.

In general, it may be noted that characters dealing with either ground color or pattern are best observed under natural light and with little or no magnification.

Chaetotaxy also presents many characters which are of value. In addition to the microtrichia which cover the entire wing in a rather dense pubescence, setae borne on the hind margin vary in length, position, and diameter.

The olfactory pores described by McIndoo (13) were found on the wings of both Silpha and Saperda, but they were more abundant on wings of members of the former genus. Closely associated with them are strong spinose setae which are quite different from the normal pubescence of the wing and are not figured by McIndoo. The fact that such setae are found to be paired, each with a pore, on a Coccinellid wing (Adalia bipunctata L.) suggests that they are also sensory in nature. However, since in all genera observed they frequently occur at some distance from any vein, and hence from any nerve, it is doubtful whether they are sensory in all cases. Suffice it to say here that, in combination with the groups of olfactory pores, they are of interest as descriptive and secondary taxonomic characters.

A seta normally arises from a specialized area of exocuticle, the alveolus, which remains to mark the spot from which the seta may have been broken. (See plate IV, fig. 6, al.). Setae in the basal part of the wing are particularly prone to breakage, and when this occurs it is impossible to distinguish empty alveoli from atypical olfactory pores by microscopic examination alone. Since pores are sensory they must be directly connected with nerves; and since wing nerves apparently travel only in veins, it may be inferred that structures some distance removed from veins are true alveoli. However, when the questionable alveolus is on a vein, this criterion is lost.

Therefore, in defining setal clusters it has been found necessary to include the olfactory pores in the given area as well as empty alveoli and remaining setae; and the term "setal cluster" as used in this paper connotes the total count of all three structures. It is realized that this interpretation is technically inaccurate, but unless the evidence of histology is investigated every time this relatively minor character is encountered, it is the only means of utilizing even such characters as are available in the pores and setae.

The setal clusters which are of value as taxonomic characters are here defined:

Humeral Cluster. A group of four or five short setae anterior to base of Costa. (Plate I, fig. 2, Hc)

Radial Cluster. A group of setae on or slightly anterior to the apex of the Radial Cell. This cluster is dorsal. (Plate IV, fig. 6, Rcl)

Medial Cluster. A group of setae at the junction of Cu, M_4 + Cu, and Mr. This cluster is ventral. (Plate III, fig. 4, Mc)

Subcostal Cluster. A group of setae on or anterior to the base of Subcosta. (Plate I, fig. 2, Scc)

Prearcular Cluster. A large, elongate group of setae and pores on the base or Radius. (Plate I, fig. 2, Prc)

Postarcular Cluster. A group of setae at the base of Cu, just posterior to arculus. This cluster is ventral. (Plate I, fig. 2, Poc)

Anal Cluster. A group of setae on the base of 2nd A. This cluster is ventral. (Plate I, fig 2, Ac)

In addition to any or all of the above groups, an occasional adventitious cluster may appear in any species. For example, Saperda fayi shows such a cluster on the costal margin, distal to the radial cluster. (Plate IV, fig. 6).

Except where otherwise noted, measurements were made as follows:

Length of wing. Measured in a straight line from arculus to apex.

Width of wing. Measured perpendicular to Radius at the widest part of the wing.

THE WINGS OF *SILPHA* SPECIES

Horn (7) regards the genus *Silpha* as being a rather heterogeneous group, although not exhibiting characters which would justify its subdivision into smaller genera. This fact appears to be verified when the wings of the several species are examined; they may be separated with comparative ease and a tentative plan for their relationships developed. Such a plan, together with Horn's conception of the relationships of the species, will be considered in another part of the present paper; but the wings themselves will be keyed and described before attempting to discuss their phylogeny.

Of the fifteen species of *Silpha* listed by Leng, ten were available in sufficient numbers to give an adequate series for study. These ten species, with the number of specimens of each, appear in Table 2:

Table 2.
Specimens of *Silpha*

discicollis	4	*lapponica*	7
surinamensis	19	*bituberosa*	3
americana	9	*ramosa*	6
inaequalis	13	*noveboracensis*	15
trituberculata	3	*quadripunctata*	3

Venation in *Silpha* is homologized with little difficulty in the Forbes system. Costa is distinct at its base in all species and is represented at its apex by a heavily pigmented streak anterior to the tip of Radius. Subcosta is present and well-defined for its entire length, joining Radius about one-half the distance from arculus to stigma. Radius is a strong vein, curving slightly toward the anterior margin and coming to an abrupt stop at a bullate area just before the stigma, to permit folding of the wing at that point. The stigma, (st) a uniformly pigmented area, shows no veins, but is believed to be bounded by R and Rs + r. A short protuberance on its posterior edge, variable in shape and position, but always on the basal half, may be homologized as 1st r-m. Stigmata of the species of Silpha are illustrated in Plate II. Also in the Radial field, R_2 and R_3 are present, though reduced from true veins to heavily pigmented bands.

The Medial field, at least in the discal portion of the wing, has disappeared entirely, Media being represented only by M_1, a "floating" vein in the apex of the wing, and M_4 + Cu, a heavy vein curving from the tip of Cu (to which it is not directly joined) to the hind margin. In addition to the above veins in the Medial field there occurs in about half the specimens examined, without regard to species, a short crossvein arising from the base of M_1 and extending a little less than half way to the stigma. This vein is not mentioned by Forbes, but is undoubtedly a vestige of one of the r-m crossveins.

Cubitus (Cu) is the third strong vein of the wing. Joined with Radius by arculus at its base, it opens the wing by stretching taut the membrane between itself and Radius.

Ist Anal is a weak vein, regarded by Forbes as being unbranched in all Coleoptera. If Forbes' interpretation is to be followed, the apparent 1st A_2 which occurs in all Silpha wings is in reality 2nd A_1. The true 1st A is broken in all specimens seen. Its position is surprisingly constant, however, and is depended upon for a diagnostic character in one species.

Second A_2 is a strong vein and is almost joined to Cu by a vestigial anal arculus (aa). Third A is a weak vein, unbranched, and not closely associated with 2nd A. Fourth A, hypothetically two-branched, has retained in Silpha only the branch curving toward the tip of the wing---presumably 4th A_2. All veins of a typical Silpha wing are illustrated in plate I figs. 1 and 2.

Considerable use is made of ground color in separating the wings of Silpha. Within a species it has been found to vary somewhat in density but little in distribution, and characters based upon it appear quite constant. As will be seen, it is more useful in indicating relationships than is any other single character, since it shows progress from the dark, smoky, uniformly colored wing of americana to the well-developed streaks, spots, and transparencies of bituberosa and trituberculata.

Chaetotaxy assumes a greater importance in Saperda than in Silpha, and a discussion of the forms of microtrichia will be given in connection with their application to that genus. Setal clusters, as defined in this paper, have already been described (p. 10) and are figured in Plate I, fig. 2.

A key to the wings of ten species of Silpha is presented:

Key to the Hind Wings of Silpha Species

1. Ground color present only along the veins, the entire membrane nearly transparent..........................2
Ground color present on at least part of the membrane 3

2. 1st A reaching hind margin midway between M_4 + Cu and 2nd A_2 (Plate I, fig. 4)...................discicollis
1st A reaching hind margin two-thirds of the way from 2nd A_2 to M_4+ Cu (Plate I, fig. 3)........surinamensis

3. Ground color dark and nearly uniformly covering the entire wing....................................americana
Ground color much lighter on basal portion of membrane than elsewhere..4

4. Apex and basal half transparent; ground color sharply truncate at center of wing (Plate I, fig. 5).......... ....trituberculata
Ground color not as above...........................5

5. Center of stigma distinctly less than half of the distance from arculus to apex..............quadripunctata
Center of stigma near or beyond the center of the line defined above.......................................6

6. Protuberance of 1st r-m arising from basal sixth of a long, narrow stigma; ground color between R_2 and M_1 uniform (Plate II).........................lapponica
Protuberance of 1st r-m arising from basal third of a short, blunt stigma; ground color between R_2 and M_1 usually with transparent spot or streak (Plate I, fig. 6)..7

7. Hind margin from tip of 1st A to tip of M_4 + Cu bearing more than twelve microtrichia....................8
This region bearing less than six microtrichia; usually entirely atrichous...........................9

8. Cu a dark, chocolate brown for at least half its length ....inaequalis
Cu a faded, yellowish brown................bituberosa

9. Cu a dark, chocolate brown for at least half its length ....noveboracensis
Cu a faded, yellowish brown.....................ramosa

Silpha discicollis Brulle

Coloration. Radius stigma, and Cu dark brown; other veins much lighter. Ground color lacking over entire wing, except for a narrow band anterior to M_1 and a similar band anterior to $M_4 + Cu$.

Venation. Costa weak but distinct, one-half as long as subcosta. Subcosta extending freely to hinge between Radius and stigma before joining R. 1st A broken, its distal portion nearly perpendicular to R and reaching the hind margin half way or less from the tip of 2nd A_2 to the tip of $M_4 + Cu$. Vein r-m lacking.

Chaetotaxy. Discal cell and anterior third of apex densely pubescent, the microtrichia separated by less than their own length. The remainder of the wing is more sparsely pubescent, but in no region are the microtrichia separated by more than three times their own length. Marginal setae strong, about five times as long as pubescence of vannus, and separated by less than half of their length. Postarculars, 16-18; subcostals, 14-16; anals, lacking.

Remarks. Length, 18-19 mm. Width, 7 mm. Plate I, fig. 4.

Silpha surinamensis Fabricius

Coloration. Veins light chestnut brown or yellowish. Ground color, as in the preceding species, present only along veins, giving the wing a faded, washed-out appearance.

Venation. Costa short but distinct. Distal portion of 1st A reaching hind margin two-thirds of the way from tip of 2nd A_2 to tip of $M_4 + Cu$. Vein 4th A_2 strong and complete, reaching nearly to hind margin. Vein r-m present in three of the six wings observed.

Chaetotaxy. Pubescence in the vicinity of C and R dense; on the other parts of the wing moderately light. Hind margin glabrous. Postarculars, 12-19; subcostals, 10-21; anals lacking.

Remarks. Wing elongate, hind margin nearly straight; R short, placing center of stigma less than one-half the distance from arculus to apex. Length, 16-20 mm. Width, 6-8 mm. Plate I, fig. 3.

Silpha americana Linnaeus

Coloration. Entire wing dark, smoky brown. Main veins (R, Cu, 2nd A_2) yellowish at their bases. Pattern distinct, an oblique pale streak showing between R_2 and M_1, the ground color distal to this streak somewhat lighter than that basal to it.

Venation. Costa strong near its base and apex. Vein 2nd A_1 well separated from 2nd A_2; at no point closer than twice the width of 2nd A_2.

Chaetotaxy. Dense pubescence over entire membrane; somewhat less dense on vannus, but microtrichia here still separated by less than their own length. Hind margin setiferous, the setae being about three times as long as pubescence, and separated by from two to ten times their own length. Postarculars, 5-14; subcostals, 5-11, usually extended in a single line; anals 2-7.

Remarks. Costal margin nearly straight; apex slightly reflexed. Hind margin rounded, indented at tips of $M_4 + Cu$ and 3rd A. Center of stigma well beyond center of costal margin. Length, 14-15 mm.; width 5-5.5 mm.

Silpha trituberculata Kirby

Coloration. Basal half and apex of wing transparent, the ground color sharply truncate basally along a line through base of stigma, tip of Cu, and tip of 2nd A_2. Veins R and Cu yellow; stigma light brown; other veins yellowish brown or transparent. Stigma only slightly darker than darkest ground color.

Venation. Costa distinct only at base. Stigma relatively short, pointed, three times as long as wide. Vein 2nd A_1 widely separated from 2nd A_2, and strongly sinuate. All anals so faint as to be nearly transparent. Vein r-m lacking.

Chaetotaxy. Pubescence of discal cell and vannus moderately dense, but extremely short; on apex somewhat longer. Marginal setae numerous from tip of 3rd A to tip of M_1, separated in some cases by less than their own length. Postarculars, 4-12; subcostals, 5-10; anals, 6-16.

Remarks. Costal margin nearly straight from base to stigma, thence curving smoothly to apex. Hind margin smooth or very slightly sinuate. Length 8.5-9 mm.; width, 3-3.5 mm. Plate I, fig. 5.

Silpha quadripunctata Linnaeus

Coloration. Ground color yellowish brown, Radius and stigma light chestnut. Other veins yellow. Distribution of ground color extremely irregular, transparent streaks and spots appearing in all cells. A particularly noticeable transparent streak appears obliquely between R_2 and M_1. A similar streak, somewhat less pronounced, is of secondary diagnostic importance in S. bituberosa; however, the larger size and shortened Radius are sufficient to differentiate the wing of quadripunctata from that species. Cell 2nd A_2 transparent, bordered apically with a distinct yellow band of ground color.

Venation. Costa present at base. Stigma truncate at base, bluntly pointed at apex. Vein r-m present in two out of three specimens observed.

Chaetotaxy. Pubescence of discal cell and vannus short and dense; on apex somewhat longer. Tubercles prominent in all areas; nearly as long as the microtrichia they support. Marginal setae numerous, unequal in length. Pubescence extending to hind margin at times and mingling with marginal setae. Subcostals, 1-11; postarculars, 0-5; anals, 3-4.

Remarks. Apex unusually long, placing stigma at or before the center of costal margin. Hind margin slightly and evenly indented at the apices of veins M_1, M_4 + Cu, 2nd A_2, and 3rd A. Length, 13 mm.; width, 4.5 mm.

Silpha lapponica Herbst.

Coloration. Ground color uniform light brown, extending from tip of wing over its entire width as far based as tip of 3rd A and exhibiting little variation in density among the specimens seen. Stigma darker than R and Cu.

Venation. Venation normal, 4th A well-developed. Stigma extremely narrow, five or six times as long as wide, the protuberance of 1st r-m arising from it about one-sixth of the way from base to apex, much farther based proportionally than in any other species. Vein r-m present in five out of seven wings observed.

Chaetotaxy. Wing densely and uniformly pubescent, the microtrichia reduced to mere pointed tubercles on discal cell and vannus. Hind margin with a narrow glabrous band, moderately setiferous over its entire length. Subcostals, 0-10; postarculars, 5-10; anals, 2-15.

Remarks. Length, 9-10.5 mm.; width, 4-4.5 mm.

Silpha inaequalis Fabricius

Coloration. Radius, Cu, and stigma dark brown; R_2 and M_1 yellowish brown. Ground color uniform, moderately light brown. Discal cell, jugum, and basal fourth of vannus transparent.

Venation. Costa distinct often at base and always at apex. Stigma bluntly pointed, not more than five times as long as wide. Vein 2nd A_1 well separated from 2nd A_2; 4th A_2 short, slightly curved. Vein r-m present in two-thirds of the specimens observed.

Chaetotaxy. Densely pubescent on discal cell and apex; vannus and jugum sparsely pubescent. Marginal setae short, stout; scattered along hind margin from base of wing to apex of $M_4 + Cu$. Subcostals, 6-10; postarculars, 2-6; anals, 7-10.

Remarks. Hind margin sinuate, indented at apices of M_1, $M_4 + Cu$, and 2nd A_2; expanded between 2nd A_2 and $M_4 + Cu$. Length, 10-11.5 mm.; width, 3.5-4.5 mm.

Silpha bituberosa LeConte

Coloration. Ground color limited to apical half of wing, though not sharply truncate. Characteristic transparent streak extends from a point two-thirds of way from base of R_2 to point at tip of M_1. Veins exhibit in general less pigmentation than do those of the preceding species, though stigma ranges from light tan to dark brown. Vein $M_4 + Cu$ appreciably darker than R_2 and M_1. Anals distinct.

Venation. Venation normal, 1st A nearly entire; 2nd A_1 more sinuate than in most other species, typically as in plate I, fig. 1. Apex of stigma poorly defined, bluntly rounded. Vein r-m present in all specimens seen.

Chaetotaxy. Pubescence uniform and dense, occasionally extending to hind margin. Microtrichia in cell R_2 slightly longer than those of the corresponding region of ramosa, i. e. about four times the length of their tubercles. Hind margin sparsely setiferous along its entire length. Subcostals, lacking; postarculars, 2-15; anals, 5-19.

Remarks. Length, 9.5-10.5 mm.; width, 4.2-4.5 mm.

Sialis novaboracensis Forster

Coloration. Ground color uniform, moderately dark brown, and distributed as in inaequalis. Radius and Cu yellowish at their bases, apical half dark brown and concolorous with stigma. Apical veins (R_2, M_1, and M_5 + Cu) lighter than R and Cu. Apex of R often darker than stigma.

Venation. Costa distinct only at apex, elsewhere only a pigmented line. Other venation normal.

Chaetotaxy. Entirely and densely pubescent. Hind margin glabrous, except for an occasional seta. Subcostals, 3-10; postarculars, 0-9; anals, 12-19.

Remarks. Costal margin smoothly rounded; apex slightly reflexed. Wing widest at a point on hind margin between 1st A and 2nd A_1. Hind margin straight from tip of 1st A to apex; slightly indented at tips of M_5 + Cu and at M_1. Length, 10-11 mm.; width, 4-4.5 mm.

Sialis [illegible] Say

Coloration. Both ground color and venational pattern vary considerably in density from nearly transparent to a moderately dark brown. Radius and stigma distinctly darker than ground color. Basal half to two-thirds of wing transparent, though color not sharply truncate as in *triangulata*. Color extending along hind margin as far based as tip of 2nd A_2, though nearly the entire remainder of cell Cu may be transparent. Anals light brown to yellow.

Venation. Costa well-defined for nearly half its length; poorly demarked at apex. Stigma approaching the elliptical in some specimens, tending to become somewhat rounded on both its anterior and posterior margins and having the protuberance of 1st r-m greatly reduced. Vein r-m weak but present in the six specimens observed.

Chaetotaxy. Microtrichia greatly reduced in size, though not in number, appearing as little more than pointed tubercles. The longest (in cell R_2) are not more than twice as long as the tubercles which support them. Hind margin sparsely setiferous in cells 2nd A_2 and 3rd A. Anal setae strong when present. Subcostals, 0-7; postarculars, 0-1; axals, 0-3.

[illegible]. Length, 10-11.5 mm.; width, 3-4.8 mm.

THE WINGS OF SAPERDA SPECIES

The wings of Saperda may be characterized as being parallel, sometimes lanceolate, in outline; radial cell closed, small, very little longer than wide, and situated slightly beyond the midpoint of the costal margin. Vein 1st r-m is never longer than width of the radial cell, often completely atrophied. The Medial recurrent (vein Mr) does not extend basad farther than base of the radial cell. Veins of the vannus are typically parallel, unconnected, and three in number. The vein in the position of 4th A is believed, for reasons already noted (see p. 13) to be 4th A_1, since its curvature in all wings seen is toward the base of the wing. Color pattern is unusually well-defined, and is illustrated in plate III, fig. 1, which may be considered typical of the genus as regards outline, pattern, and venation.

Of the major categories of characters previously mentioned, the most important in Saperda appear to be those of chaetotaxy. Spinose setae are found in several areas of nearly all wings, and their presence, size, and number, as well as their location, is quite constant in several species. The setae of the greatest value are those on the costal margin of favi, distal to the radial cluster (plate IV, fig. 6) and those of the medial cluster of mutica.

In addition to the larger setae, microtrichia of the pubescence are used to divide the genus into two main groups of species. Microtrichia appear to be of two types, as illustrated in plate III, fig. 6. Both types may occur on a single wing, but in the area just anterior to M_1 one or the other greatly predominates. By examination of these microtrichia, *calcarata*, *mutica*, *noralnea*, *concolor*, *hornii*, and *obliqua* may be separated from the other species of the genus.

Morphology of the microtrichial attachment in the *calcarata* group is uncertain. A microtrichium at its base is bifid, with one projection slightly longer than the other. Below the bifid base, the surface of the wing is apparently everted, forming a small villus or tubercle to support the microtrichium. The whole is approximately one-tenth as long as the diameter of M_1.

Microtrichia in the corresponding area of any species other than those mentioned above are distinctly and obliquely truncate at the base, the area in contact with the wing being slightly larger than the greatest possible cross-section. No villus-like protuberance occurs, and such microtrichia are elliptical in cross-section, slightly curved, and from one-fifth to one-fourth as long as the diameter of M_1. (Plate III, fig. 6).

Setae on or near the hind margin of the wing offer useful secondary characters in *lateralis*, *tridentata*, *indiana*, *vestita*, and *discoidea*; and their presence on a vein is significant in one species (*mutica*).

Coloration, as applied to the wings of *Saparia*, may be venational, ground color, or pattern. Venational pigmentation is of great value in the subcosta, arculus, Media, and $M_4 + Cu$ of several species. Ground color is used in the identification of *calcarata*, *vestita*, and *discoidea*, and offers good secondary characters in other species. It is of particular value in separating *calcarata*, since its absence, always from two regions of, and usually from the entire hind margin, gives that margin a hazy appearance which is characteristic of the species. Pattern is of little value in separating the wings of *Saperda* except as a secondary character.

Venation in *Saperda* is relatively constant. Some variation occurs in the shape of the radial cell, the length of 1st r-m, the tendency of the anals to show adventitious branches, and the angle of the M-Cu-M_4 + Cu fork. None of these characters is sufficiently reliable to be considered in isolating any species. However, since a clear understanding of venation as it applies to *Saperda* is essential for correct interpretation of many characters, the vein in a typical *Saperda* wing are briefly reviewed below:

Costa lies along the anterior edge of the wing, and in the larger species may be distinguished for a short distance. Unlike the costa of *Silpha*, it is not preceded by a membrane.

Subcosta is a weak vein, parallel at its base to Radius, and uniting with Radius before the midpoint of that vein.

Radius is the first strong vein of the wing. It extends from one-half to three-fourths the length of the wing, and terminates in a hemispherical to semi-ovoid radial cell, homologous with the stigma of *Silpha*, and formed by the veins Rs and r. Two cross-veins extend posteriorly from Rs; the 1st and 2nd r-m cross-veins. Vein 1st r-m varies in length in different species; it may be nearly as long as the shortest diameter of the radial cell, or reduced to a mere stump. Vein R_3 is represented in all Cerambycidae by a thickened, darkly pigmented line anterior to, and half the length of, M_1.

The medial field, as in *Silpha*, exhibits a floating M_1 and M_4 + Cu, the latter vein attached to the tip of Cu. In addition, a strong vein arches up from the tip of Cu and curves basad, receiving at its tip the posterior end of 2nd r-m. This vein is the Medial recurrent, designated in figures by Mr.

Cubitus occurs exactly as in *Silpha*---a strong vein in the center of the wing and continuing to the hind margin as $M_4 + Cu$.

The anal field of *Saperda* is rather complicated, due to the branching of the 2nd and 3rd anals and the atrophy of their bases. Three veins may be taken as a unit for definition purposes only: 1st A, 2nd A_1, and 2nd A_2. Each is unattached basally, and 1st A is unbranched. Vein 2nd A_1 may rarely be found united with 2nd A_2 but never with a larger vein. Vein 2nd A_3 is a strong vein, analogous to 2nd A_2 in *Silpha*. It is paralleled basally by third A, which branches at its midpoint. Vein 3rd A_1, after crossing the short distance to 2nd A_3, unites with that vein for the remainder of its course, and 3rd A_2 continues as a free vein. Vein 4th A is a single strong vein, probably not homologous with the 4th A of *Silpha*, since its curvature is in the opposite direction and it would appear to be 4th A_1 rather than 4th A_2. Veins of a *Saperda* wing are illustrated in plate III, fig. 3.

The species of *Saperda* recognized by Felt and Joutel (2) are listed in Table 3, together with the number of specimens of each which were examined in the present study.

Table 3.
Specimens of *Saperda*

mutica	7	*cretata*	5	*tridentata*	19
hornii	3	*candida*	22	*puncticollis*	3
fayi	8	*lateralis*	11	*discoidea*	8
obliqua	5	*populnea*	6	*vestita*	8
calcarata	6	*concolor*	8	*imitans*	3

A key to the wings of fifteen species of *Saperda* is presented:

Key to the Hind Wings of *Saperda* Species

1\. Predominating microtrichia anterior to M_1 bifid or tuberculate at base, 1/10 to 1/8 as long as diameter of M_1 2
Microtrichia of this region obliquely truncate at base, 1/5 to 1/4 as long as diameter of M_1. (plate III, fig. 6) 6

2\. Small colorless spots at tips of M_4 + Cu and 2nd A_3+3rd A_1; these often connected by narrow colorless band on vannal margin. (plate III, fig. 5).......... *calcarata*
Ground color extending to hind margin................. 3

3\. Some spinose setae of medial cluster 3-4 times as long as diameter of Cu; a patch of microtrichia on discal side of fork. (plate III, fig. 2)............... *mutica*
Setae of medial cluster typically only slightly longer than diameter of Cu, rarely enlarged; few microtrichia on discal side of fork. (plate III, fig. 4).......... 4

4\. Subcosta darker at base than at apex; size large (13-17 mm.).. 5
Subcosta not darker at base than at apex; size small (7-10 mm.).................................... {*concolor* / *populnea*}

5\. Arculus lighter than that part of Cu immediately posterior to it. (plate IV, fig. 1)............... *hornii*
Arculus not lighter than that part of Cu immediately posterior to it. (plate IV, fig. 2)............. *obliqua*

6\. With 1-3 strong spinose setae on costal margin distal to radial cell. (plate IV, fig. 6).................. *fayi*
Without setae in this region.......................... 7

7\. Indentation at tip of 2nd A_3 + 3rd A_1 lacking or at most indicated by a slightly sinuate line................. 8
Both marginal indentations distinct.................... 9

8\. Mr as dark as, or darker than, Cu; apex of wing slightly reflexed.. *imitans*
Mr lighter than Cu; apex not reflexed.... *puncticollis*

9. *Wing sparsely pubescent anterior to M_1. (plate IV, fig. 3).......................................10
Wing densely pubescent in this region, never more than a narrow glabrous band appearing. (plate IV, fig. 5).......................................11

10. Indentation of hind margin at 2nd A_2 + 3rd A_1 not so deep nor so sharply angled as that at M_4 + Cu...candida
These two indentations similar in depth and angles...cretata

11. Mr bicolorous, darker brown in apical region than at its junction with Cu (excluding bullate area)...12
Mr unicolorous (excluding bullate area).........13

12. Discal cell darkened anteriorly, the darkest portion never lighter than is the tip of the wing; length, 15-20 mm...........................vestita
Discal cell unicolorous, nearly transparent, lighter in color than is the tip of the wing; length, 10-15 mm..................................discoidea

13. Radius distinctly retaining its color as far based as arculus..............................tridentata
Color of Radius fading and being lost a short distance from arculus.......................lateralis

Descriptions of Wings

In the following descriptions an attempt is made to supplement the key and to present such additional characters as may be useful in identification.

Saperda mutica Say

Coloration. Dark brown, little color variation shown in the specimens examined. Radius and Cubitus brown to smoky black, darker than ground color, yellowish at their extreme bases. Ground color uniform, pat-

*With the exception of one aberrant and damaged specimen of candida.

tern distinct, jugum pigmented on posterior two-thirds.

Venation. Venation normal.

Chaetotaxy. Pubescence anterior to M_1 sparse, the tubercles nearly as long as the microtrichia they support. Medial cluster composed of one to four stout setae; two to four slender ones. Radial cluster 18-20. Pubescence of discal cell encroaching upon fork and covering about one-half the intersection. Setae of hind margin short, regular, not closely crowded.

Remarks. Hind margins with indentations equal; a slight expansion distal to tip of M_4+Cu. Length 10-13 mm.; width, 4.5-5.5 mm. Plate III, fig. 2.

Sanerda hornii Joutel

Coloration. Color typically dark brown; center of discal cell and anterior third of jugum transparent. Apical two-thirds of Sc transparent; arculus lemon yellow, Cu dark chestnut brown.

Venation. Radius more than two-thirds as long as wing. Considerable adventitious branching occurs in the anal veins of this species.

Chaetotaxy. Pubescence anterior to M_1 rather close, the bases of the microtrichia often contiguous. Medial cluster 4-5; radial cluster 20-25.

Remarks. Wing widest at jugum, tapering almost without indentation to a rather sharply pointed apex. Length, 13-16 mm.; width, 5.5-6 mm. Plate IV, fig. 1.

<u>Sanerda fasi Bland</u>

<u>Coloration.</u> Ground color light brown, a transparent area present on basal fourth of discal cell and surrounding 2nd A and 3rd A nearly to their tips. Radial cell much darker than ground color. Veins R and Cu slightly darker than radial cell, yellowed at their bases.

<u>Venation.</u> Venation normal.

<u>Chaetotaxy.</u> Microtrichia near tip of M_1 sparse, some specimens showing a rather extensive glabrous area. Marginal setae short and irregular on vannus, becoming crowded on margin of jugum. Medial cluster, 1-4; radial cluster, 1-7. An adventitious cluster of from one to three strong setae occurs on the costal margin, slightly distal to the radials. This group has not been observed in any other specimen, and appears to be an excellent means of isolating this species.

<u>Remarks.</u> Hind margins with indentations equal, sometimes slightly sinuate at tip of M_1. Length, 10-12 mm.; width, 3.5-4.5 mm. Plate XV, fig. 6.

<u>Sanerda obliqua Say</u>

<u>Coloration.</u> Ground color light yellowish brown; veins only slightly darker than ground color, yellowish at their bases. Jugum posterior to 3rd A as dark as ground color in other regions of the wing. In addition to the normal pattern, the area bounded by the radial cell, M_1, and R_3 is nearly transparent, giving the tip of the wing a faded, washed out appearance.

<u>Chaetotaxy.</u> Pubescence anterior to M_1 scattered and short; tubercles about one-half as long as the microtrichia they support. Medial cluster

4-10, rarely containing one or two strong setae as does that of *mutica*. Radial cluster 9-13. Specimens of *obliqua* showing enlarged setae in medial cluster may be distinguished from *mutica* by their much less dense pubescence on the discal cell, the absence of any appreciable number of microtrichia on the medial fork, and by their greater size.

Venation. Venation normal.

Remarks. Hind margin deeply indented, jugum often broadly rounded. Length, 15-17 mm.; width, 6-6.5 mm. Plate IV, fig. 2.

Saperda calcarata Say

Coloration. Ground color typically light chestnut brown, though dark brown specimens occur. In lighter specimens the entire jugum devoid of pigment; in darker wings a considerable part of this area transparent. Veins dark brown, yellowed at their bases. Hind margin with two transparent areas, one at the tip of M_4 + Cu and the other at tip of 2nd A_3 + 3rd A_1. These areas usually extend and merge, giving the entire hind margin a hazy, indistinct appearance characteristic of the typical specimen.

Venation. Venation normal.

Chaetotaxy. Pubescence anterior to M_1 short, sparse. Medials, 4-9; radials, 10-17.

Remarks. Hind margin strongly and equally indented, apex rather pointed. Wing widest at a point posterior to tip of 3rd A. Length 22-26 mm.; width, 7.5-.0 mm. Plate III, figs. 5, 6. Easily recognized by its large size and transparent hind margin.

Sanerda crelata Newman

Coloration. Ground color light brown, presenting a rather faded appearance. Basal transparent area of jugum extending down 2nd A and 3rd A nearly to hind margin; basal fourth of discal cell transparent. Pattern of radial cell region sharply defined, much darker than ground color. Veins Cu and R light yellowish brown, never darker than ground color of discal cell.

Venation. Venation normal.

Chaetotaxy. Pubescence irregular, sparse in the M_1 region; setae on the hind margin basal to 2nd A long and closely crowded. Medial cluster, 3-7; radials, 7-13.

Remarks. Hind margin deeply and regularly indented at the tips of M_4, Cu and 2nd A_3 + 3rd A_1. Length 15.5-19 mm.; width, 5.5-7.5 mm. Plate IV, figs. 3, 4b.

Sanerda candida Fabricius

Coloration. Ground color typically dark brown, though light brown and smoky black wings occur. Entire jugum often transparent and usually lighter than vannus. Pattern well defined; radial cell nearly always heavily pigmented, often nearly black and dark enough to obscure completely the adjoining veins. Veins dark brown, Cu sometimes yellowish for nearly its entire length. Subcosta dark; R_3 represented by a sharply pigmented line.

Venation. Venation normal.

Chaetotaxy. Pubescence near M_1 scattered. Setae on hind margin long and irregularly spaced. Medial cluster 4-9; radial cluster, 6-12.

Remarks. Hind margin irregularly curved, the indentations unequal. Wing somewhat lanceolate in appearance, often as wide at jugum as at vannus. Length, 12-19.5 mm.; width, 4.5-7.5 mm. Plate III, fig. 6; plate IV, fig. 4a.

This wing shows the greatest variation of any species of either genus considered in this study. Typical specimens are recognized easily by their sharp pattern, dark radial cell, and transparent jugum; but atypical specimens have been found which do not show marked development of these characters, and they are extremely difficult to distinguish from a well marked wing of cretata or tridentata. In the key, the more typical forms, because of their light pubescence in the M_1 region, will key out with cretata, but specimens having dense pubescence in this area will be carried, by virtue of their generally dark vein pigment, to tridentata.

Saperda lateralis Fabricius

Coloration. Ground color chestnut brown, rarely yellowish; apex usually darker than discal cell and vannus. Pattern not so well defined as is that of candida; never dark enough to obscure veins. Veins R and Cu dark brown, their bases distinctly yellow.

Venation. Venation normal.

Chaetotaxy. Area at tip of M_1 densely pubescent; rarely a narrow, glabrous band present. Marginal setae varying in length and irregularly spaced. Medial cluster, 1-7; radial cluster, 4-16.

Remarks. Wing elongate, parallel; indentations equal and slight. A distinct indentation appears in some specimens at tip of M_1; apex bluntly pointed. Length 8-12.5 mm.; width, 3-4.5 mm.

Saperda populnea Linnaeus and Saperda concolor LeConte

No satisfactory means of separating the wings of these two species has been found. They agree in all characters given in the key, and in the following general description:

Coloration. Ground color light brown, uniform except for basal two-thirds of jugum; pattern distinct.

Venation. Venation normal.

Chaetotaxy. Pubescence anterior to M_1 short; uniformly and closely distributed. Medial cluster, 6-12; radials, 10-25. Setae often present on all veins of the radial cell. Marginal setae sparse and irregular.

Remarks. Hind margin never deeply indented; tip of wing bluntly pointed. Length, 7-10.5 mm.; width, 2.5-4 mm.

In general it may be noted, to furnish some means of distinguishing the wings of the two species, that the Radius, radial cell, and fork of populnea are somewhat blacker than are the corresponding veins of concolor, and the ground color of concolor is a lighter and more uniform brown than is that of populnea. The vannus of concolor is slightly expanded, and the wing of concolor is therefore a little the wider of the two.

Saperda tridentata Olivier

Coloration. Ground color dark brown. Pattern distinct; jugum concolorous with vannus except near base of wing.

Venation. Radius often shorter than that of other species, placing radial cell at the center of the front margin.

<u>Chaetotaxy</u>. Microtrichia anterior to M_1 long and closely crowded, typical of this division of the genus. Marginal setae dense, varying in length. Medial cluster 2-6; radial cluster, 15-20.
<u>Remarks</u>. Entire hind margin expanded, the indentations subequal and dividing the margin into three nearly equal parts. Apex bluntly pointed. Length, 9-13 mm.; width, 3.5-5 mm.

<u>Saperda puncticollis</u> Say

<u>Coloration</u>. Ground color a uniform light brown, pattern indistinct. Tip of wing distal to $M_4 + Cu$ somewhat darker than vannus and jugum. Veins R and Cu dark brown, distinctly yellow at their bases. 2nd A darkly pigmented.
<u>Venation</u>. Junction of R and $R_s + r$ prolonged distally, giving the tip of the radial cell a fingerlike projection.
<u>Chaetotaxy</u>. Area at tip of M_1 regularly and densely pubescent, a narrow, glabrous, marginal line appearing in some specimens. Marginal setae short and closely crowded from base of jugum to extreme apex of wing. Medial cluster, 4-7; radial cluster, 5-6.
<u>Remarks</u>. Hind margin only slightly sinuate at 2nd A_3 + 3rd A_1; deeply indented at $M_4 + Cu$. Wing widest at radial cell. Length, 7.5-9 mm.; width, 3-3.5 mm.

The prolongation of R noted above occurs in several other species and is not constant in any. It seems inadvisable, therefore, to consider the prolongation in <u>puncticollis</u> as being of more than secondary importance.

Saperda discoidea Fabricius

Coloration. Ground color light brown; tip of wing, especially that region anterior to M_1, considerably darker than discal cell, jugum, and vannus. Pattern well defined, though often only slightly darker than the darkest ground color. Veins R, Cu, and 2nd A_2 typically light yellowish brown, their extreme bases yellow. Radius rarely dark brown, yellowed only at base. Anterior half of jugum nearly transparent.

Venation. Venation normal.

Chaetotaxy. Apex regularly and densely pubescent; microtrichia extending to hind margin at M_1. Marginal setae closely crowded on apex, vannus, and jugum. Medial cluster, 4-6; radials, 5-13.

Remarks. Wing rather elongate; marginal indentations well defined, equal. Length, 10-15 mm.; width, 3.5-6 mm.

Saperda vestita Say

Coloration. Ground color uniform yellowish brown, occasionally dark brown. Discal cell never entirely transparent or unicolorous; as dark as vannus and apex. Jugum transparent only along 3rd A and 4th A. Discal cell and vannus transparent in a small area at their bases. Color pattern distinct, though often not darker than darkest ground color. Basal fourth of R yellow, the remainder dark brown. Cubitus uniformly yellowish brown.

Venation. Venation normal.

Chaetotaxy. Pubescence of apex dense, becoming somewhat more sparse posterior to M_1. Marginal setae close, varying greatly in length on the vannus. Medial cluster, 4-11; radial cluster, 7-18.

Remarks. Hind margin regularly and deeply indented, outline of both jugum and vannus only slightly convex. Wing widest at jugum; in some specimens costal and hind margins nearly parallel. Length, 15.5-20 mm.; width, 5-7.5mm. Plate IV, fig. 5.

Closely resembles the preceding species, but may be distinguished by characters given in the key and by its more yellow veins.

Saperda imitans Felt and Joutel

Coloration. Ground color varying from light to dark brown, slightly darker at apex. Discal cell, jugum, and vannus each transparent in a small area at its base. Pattern distinct, radial cell dark brown, its pigment sometimes obscuring R. Radius and Cu dark brown, only slightly yellowed at their bases.

Venation. Venation normal.

Chaetotaxy. Pubescence dense on apex; a narrow, glabrous band sometimes occurring on hind margin. Marginal setae closely crowded, uniform in length. Medial cluster, 2-5; radials, 5-13.

Remarks. Hind margin only slightly sinuate at tip of 2nd A_3 + 3rd A_1, diverging from costal margin steadily and smoothly as far as the indentation at M_4 + Cu; thence converging upon the costal margin to form, without further expansion, a rather acute apex. Costal margin somewhat arcuate at tip of radial cell, producing a slightly reflexed wing tip. Length, 9-11 mm.; width, 3.5-4 mm.

DISCUSSION OF PHYLOGENETIC RELATIONSHIPS

The Wings of Silpha Species

According to Forbes, the wings of the Silphidae as a whole form, with those of the Staphylinidae, a single isolated group and are not closely related to any other family. If this be so, one should be doubly sure of finding in the wings of Silpha characters and structures completely different from those formed by Saperda. Such a condition proves to be the case, not only as regards the over-all venational and color plan of the two groups of wings, but also in such smaller details as the structure of the microtrichia and the actual morphology of the veins themselves. Examples are numerous: the preservation of the anal arculus is distinct in Silpha; the diversification and specialization of microtrichia in the calcarata group of Saperdae; the broad, splayed-out veins of Silpha all attest the wide separation of the two genera.

If it is true, then, that sufficient variation has taken place in the wings of Silpha to permit identification of species by means of the wings alone, and if it is assumed that such variation is a result of evolutionary tendencies at a subgeneric level, then it should be possible, by examination of the varying characters, to develop a tentative evolutionary tree to show the degree of specialization among the wings of the various species. Such a tree is presented in plate V.

At the base of this tree one could reconstruct a hypothetical Silpha wing, having the following characters:

Coloration. Ground color uniformly light brown, covering entire wing. Veins light brown, fading to yellow at their bases.

Venation. Probably as in the present species, with stigma the size and shape of that of *discicollis*. Costa distinct for its entire length; r-m present; 1st A continuous.

Chaetotaxy. Densely pubescent, the microtrichia arising from the surface of the wing rather than from tubercles. Hind margin setiferous.

From such a generalized form specializations occurred, sometimes in parallel. Pattern became more definite and distinct; ground color became darker in some species, lighter in others; microtrichia and marginal setae became reduced, both in size and in number, and tubercles appeared at their bases.

It is not to be expected that these modifications and others should all take place at the same rate, or should correspond exactly to the development of the insect as a whole. However, considering only the wings, and the apparent relative importance and degree of their different specializations, the following hypothetical arrangement of species is suggested:

Silpha discicollis and *surinamensis* are obviously distinct from all other species and obviously closely related. Both have lost all ground color; both lack the anal cluster——a condition not found again until the most specialized forms are reached; both have relatively long and dense pubescence. Of the two, *surinamensis* is believed to be the more specialized, showing a reduction in the number of marginal setae and having the stigma reduced in size and taking a more definite shape. Specialization is by no means one-sided, however. *Silpha discicollis* exhibits the beginning of pattern in the pigmentation of Radius and stigma; a complete loss of r-m (which is present in 50% of the wings of surinamensis); and a striking modification of the course of 1st A, the diagnostic character of the species. Therefore the two wings are placed at approximately the same level of specialization, on a branch by themselves.

In considering the reduction of the pubescence and marginal setae, the development of pigmentation of the veins, and the secondary reduction of ground color, with its varying distribution and resultant patterns, americana appears to be the least specialized of the remaining species. Ground color is dark, and although it is beginning to fade at its base, it still remains darker and more evenly distributed than in any other species. The wing of americana is densely pubescent and moderately setiferous, little reduction having taken place. It is more specialized in venation than elsewhere, all veins showing strongly and distinctly. However, since costa shows in the higher species a tendency to weaken and be lost at its apex, its strong development in americana must be regarded as a primitive character. Stigma shows little specialization, and in summarizing it may be said that any attempt to derive americana from any other wing meets with so many difficulties and so few successes that it is believed a justifiable conclusion is reached in calling it the most generalized of the eight color-bearing wings.

Silpha quadripunctata resembles americana rather closely. Ground color is still dark, but the transparent streak which began to appear in americana between R_2 and M_1 has become more pronounced, and much of the jugum has been cleared entirely of color. Costa has disappeared at its apex as a distinct vein; R has shortened, though stigma still shows little modification. Marginal setae are still numerous and pubescence is dense, often obliterating the narrow glabrous band usually present along the hind margin.

In placing the wing of lapponica, one is faced with a dilemma. Superficially, this wing appears more highly specialized than is implied by the position given it on the americana-quadripunctata branch. It shows greater reduction in ground color than do the wings of the other two species; it shows considerable pigmentation along the main veins; and it has the most highly modified stigma of the entire genus. Silpha noveboracensis and inaequalis could conceivably be derived from it. Yet the reduction in ground color has taken place as an over-all weakening and fading, rather than producing definite colored and transparent areas; pubescence is still dense and uniform; and the number of marginal setae is much more suggestive of americana than of any of the four remaining species.

In the wing of trituberculata ground color reaches a high state of specialization. The basal half and the tip of the wing are entirely transparent, and the colored portion is sharply truncate basally. Pigmentation is not highly developed in the veins. Marginal setae are still numerous ---in fact, more so than in the americana group. Because of its primitive marginal setae and lack of vein pigmentation it cannot logically be derived from the americana branch; because of its unique ground color, no other wing, with the possible exception of that of bituberosa, could be derived from it. It is therefore placed on a separate branch, intermediate between americana and bituberosa.

Silpha bituberosa also presents a high degree of specialization in its ground color, but it is not considered closely related to trituberculata since the specialization in the two appears to be of an entirely different type. In trituberculata the tendency has been to concentrate pigment into a single, well defined area. On the other hand, bituberosa has specialized by reduction of ground color in several different regions, producing not only a well defined transparent area basally, but also streaks and spots in the apical portion of the wing, a condition which does not obtain in trituberculata. Also, marginal setae are less dense in bituberosa than are those of trituberculata. In short, bituberosa and trituberculata may be regarded as two well developed but aberrant wings, neither derived directly from lower forms nor giving rise to higher ones, but branching from the main stem separately and individually.

Three species remain to be fitted into the tree---ramosa, inaequalis, and noveboracensis. All three are obviously close, combining reduced ground color, sharp and distinct vein pattern, and reduction of microtrichia in a considerable degree of balance.

The two wings of Silpha noveboracensis and inaequalis are the most closely related of the three. They are difficult to separate even by use of the key, and have so many characters in common that it is impossible to say one is more advanced than the other. The wing of noveboracensis has fewer marginal setae than has that of inaequalis, but the latter species shows somewhat greater specialization of vein pattern and sharpness of ground color.

Having given noveboracensis and inaequalis a close and equal standing on the tree, the only remaining problem is that of deciding whether ramosa properly belongs above or below them. This decision is not an easy one, since in many ways the wing of *ramosa* is highly developed. It is here considered more primitive, however, since more of the marginal setae have been retained; ground color is no better defined than is the case in the other two species; and vein pattern, though distinct, is less so than is that of *inaequalis*.

A comparison of the tree of wings with one which might be constructed from Horn's key to adults reveals both similarities and discrepancies. *Silpha discicollis* and *quadripunctata* are not keyed by Horn, and hence cannot be directly compared with the wing phylogenetic scheme. Neither *S. opaca* nor *S. truncata* was included in the present paper, since specimens of these species were not available. Eight species remain, therefore, which are common to Horn's key and to the present study, and these afford an opportunity to attempt a correlation of the phylogeny of the wings with that of the complete adults.

It should be pointed out that Horn does not make a phylogenetic study of *Silpha spp.* Such a study can be deduced to some extent, however, from an examination of his key.

Horn separates *surinamensis* immediately, by means of its large, prominent eyes and a sexual character of the femora, and notes that the species approaches in many ways *Necrophorus*. The wing of *surinamensis*, together with that of *discicollis*, is separated with equal ease, though both differ considerably from a wing of *Necrophorus orbicollis* (Say). In both trees *surinamensis* is placed in a primitive position.

At the end of the first line of characters Horn places *lapponica* and tritubercululata, these species having in common a broadly emarginate labrum, elytra sinuate at tip and costate, and thorax emarginate at middle of base. They are finally separated by the presence or absence of tubercles on the elytral costae. This close relationship does not agree with the evidence of the wings; it is difficult to visualize the wing of tritubercululata as being close to that of lapponica, for reasons already given.

Silpha inaequalis and noveboracensis are next keyed out close together and require more characters for their separation than do any other two species. With this the wings are in complete agreement; they are considered the most specialized of the entire group, and of the entire group they are the two most dificult to separate from each other.

The position of americana in Horn's key indicates it to be the most primitive of the species the wings of which show ground color, with somewhat less specialization than lapponica, though on a different branch. The morphology and color of the wing readily agree in placing it in a primitive position, but the characters of the wing entitle it to be placed in a closer relationship to lapponica than Horn's key allows.

Horn would place ramosa at the end of the americana branch, considering it a highly specialized Silpha. The wing is undoubtedly highly specialized, and could possibly be derived from americana with loss of ground color and modification of the stigma——all wings except discicollis and surinamensis could be derived from americana if one desired——but to assume this origin wound give it a closer relationship to lapponica than the great difference in their stigmata would appear to justify. It would ignore also the closer relationship of *ramosa* to *noveboracensis* and *inaequalis*, which, in turn, are not closely related to *americana*, either in Horn's key or by wing structure.

Silpha bituberosa, according to Horn's key, is a comparatively primitive form, not closely related to any of the other species except *opaca*, which it "greatly resembles." Its wing also is recognized as being divergent from the others, its distinctive streaks of transparent areas making it unique in the genus. For reasons already given, it is here placed above all but the most specialized forms——as regards ground color alone it is perhaps the most specialized. Horn would have placed it *slightly* above *americana*, and still on a separate branch of the main stem.

Reviewing briefly the results of the above discussion, it is found that the relationships of four of the eight wings here compared with those of the adults agree closely with those expressed in Horn's key; three could be made to agree, with a different evaluation of the characters used, and one definitely disagrees with the phylogeny of the adults.

The Wings of Saperda Species

In the following discussion of the wing relationships of *Saperda* the same general criteria of specialization will be used as were applied to *Silpha*: i. e. coloration and chaetotaxy. Venation, which was useful in the stigmata of *Silpha*, is of no value in *Saperda*. As in the study of *Silpha*, certain characters were selected which could be readily defined, and which seemed to show modification away from more simplified types. A tree was constructed on the basis of these characters (plate VI). Characters less easily defined, such as degree of pattern clarity and density of ground color, were also given due consideration. The four principal characters chosen, and their distribution among the wings of Saperda, are shown in Table 4.

Table 4.
Specialization in the Wings of Saperda

	Setae of Medial Cluster Enlarged	Arculus Lighter than Cu	Indentation at tip of M_1	Glabrous Area at tip of M_1
mutica	+	+	+	+
hornii	−	+	0	+
fayi	−	0	+	+
cretata	+	−	−	+
obliqua	0	−	−	+
lateralis	0	−	+	−
candida	0	0	−	0
tridentata	−	−	+	−
calcarata	−	−	−	+
puncticollis	−	−	−	+
vestita	0	−	0	−
discoidea	−	0	0	−
populnea	−	−	−	−
concolor	−	−	−	−
imitans	−	−	−	−

Key: + Character present in all wings observed.
0 Character present in some of the wings observed.
− Character not present in any wings observed.

All of the characters mentioned in Table 4 have appeared in the key or have been considered elsewhere except that of the marginal indentation at the tip of M_1. This indentation is a rather variable character throughout the entire genus, occurring in the species indicated, and rather prominent in a few cases. It is caused by an expansion of the hind margin between the tips of M_4+ Cu and M_1.

The wings of Saperda, as already noted, fall into two groups with regard to the structure of the predominant microtrichia in the M_1 region. Giving this character equal value in each group results in a two-branched tree, having on the "tuberculate" branch populnea, concolor, hornii, calcarata, obliqua, and mutica. The relationships of these wings will be considered first.

The wings of populnea and concolor obviously belong close together, wherever they may be placed. The failure to find a single character adequate for their separation in the key testifies to their close relationship, and a glance at Table 4 confirms the fact that they are less specialized than are any of the remaining species of the tuberculate group.

Of the remaining four wings, mutica is the most highly developed. In addition to possessing all the specializations noted in the Table, it has sharp, well defined areas of pattern and ground color, veins are strong and well demarked, and no adventitious branching occurs. It has carried out the reduction of the tuberculate microtrichia until little more than the tubercles remain.

Closest to mutica is hornii, with almost equally well developed pattern and ground color. The shape of the hornii wing somewhat resembles that of calcarata, marginal indentations tending to be lost in both, and the jugum broadly expanded. On the basis of color alone, *hornii* most nearly resembles *mutica*, having much less yellow in ground color and veins than do the two remaining species.

Saperda obliqua and *calcarata* are distinguished from the preceding species in having their ground color and veins a lighter, more yellowish brown. Some variation occurs, but the darkest wing of *calcarata* is far lighter than is a wing of *hornii* or *mutica*. The two (*obliqua* and *calcarata*) appear so close that there is little basis for placing one above the other; *calcarata's* transparent hind margin, which is unique in the genus, may perhaps entitle it to a higher place than does the tendency for *obliqua* to have enlarged setae in the medial cluster, a character shared with one or two other species.

Turning to the remaining non-tuberculate species, we find at the foot of the Table, showing the least specialization of the characters listed, the wings of *discoidea*, *vestita*, and *imitans*. The wings of *discoidea* and *vestita* are very close, having many characters in common in the key, and not being easy to separate. For that reason they are placed together, and since both show a slight variation in the direction of the characters in the table, they are placed above *imitans*, which does not show this variation.

Saperda puncticollis is believed to be the lowest of the six remaining wings, its only major specialization being the loss of microtrichia in the M_1 region. It alone has lost the marginal indentation at 2nd A_3 + 3rd A_1, retained by all other wings to some extent at least. Its lack of other specializations, however, deprives it of a higher place.

The wings of *lateralis* and *tridentata* form another similar pair.

They show considerable consistency in the development of the expansion of the hind margin between $M_4 + Cu$ and M_1, and agreement in general coloration and shape. A few wings of lateralis show some enlargement of the setae of the medial cluster, a point in favor of giving that wing a slightly higher position than that of tridentata.

The wings of favi, crotata, and candida remain to be fitted into the tree. Of the three, favi appears to be the most specialized, having a well developed glabrous area at M_1 and a distinct indentation at the tip of that vein. Some variation in the color of the veins in the basal region of the wing is apparent, though not in all specimens seen. Ground color is clear and distinct, varying almost not at all among the specimens studied. In addition, the characteristic setae on the costal margin contribute to the opinion that favi is the most highly specialized of the non-tuberculate wings.

Sanarda crotata is also a rather highly specialized wing, though definitely less so than is favi. Ground color and pattern are well demarked, ground color varying more than in favi, however. It is not placed on the lateralis-tridentata branch because of its lack of any sign of an indentation at M_1; it is not placed more closely to favi for the same reason.

The wing of S. candida, as already noted, is extremely variable. The great majority of candida wings seen have lost the microtrichia in the region of M_1, and when this is the case their sharp pattern and usually distinct ground color align them closely with crotata. This seems to be the most logical place for this wing, though atypical specimens occur. It certainly resembles no other wing so closely in color and pattern.

Having arranged the wings in a phylogenetic tree as their similarities appear to place them, the correlation of this arrangement with the established relationships of the genus remains to be considered. Since Felt and Joutel present a complete phylogenetic tree of the genus, and make a study of the relationships of the species, it is possible to compare the present study with such relationships much more closely than was the case with *Silpha*.

These authorities note the natural grouping found when the American species are separated on the basis of unicolorous or annulated antennae. Antennae are annulated in *obliqua*, *mutica*, *hornii*, *populnea*, and *concolor*. It seems significant that with only one addition (*calcarata*) these species are also the ones having modified, bifid microtrichia.

The statement is made by Felt and Joutel that the American species have specialized along several different lines, and that any arrangement of species in a systematic list merely represents the degree of removal from an ancestral type. Evidence of the wings is at least partly in accord with this hypothesis, if the fundamental two-branched plan of the tree of wings is valid.

The columns of Table 5 show a single systematic list after Felt and Joutel, and a similar single list adapted from plate VI of the present study.

Table 5.
Comparison of Systematic
Lists of Species of *Saperda*

Entire Adults (Felt & Joutel)	Wings Only
concolor	*concolor*
populnea	*populnea*
puncticollis	*imitans*
fayi	*vestita*
lateralis	*discoidea*
imitans	*puncticollis*
vestita	*tridentata*
discoidea	*lateralis*
cretata	*candida*
tridentata	*cretata*
calcarata	*fayi*
candida	*obliqua*
hornii	*calcarata*
mutica	*hornii*
obliqua	*mutica*

It is hardly to be expected that the wing should in all cases follow the specialization of other parts of the body, yet Table 5 discloses a few similarities. The close relationship of *mutica* and *hornii*; *populnea* and *concolor*; and *vestita*, *discoidea*, and *imitans* is further emphasized. In all, six of the fifteen species are placed two places, or less, apart in the two lists; eight fall three places apart; and only *S. fayi* shows a wide discrepancy between the specialization of the wing and the development of the insect as a whole. So much is apparent at once, merely from a superficial observation of the two lists.

Statistical Treatment

Statistical analysis of the two lists of *Saperda spp.*, using the methods of rank correlation outlined by Kendall (9) and Hotelling and

Pabst (8) reveals a coefficient of correlation, ρ, equal to $+0.7714$. This coefficient may be corrected (Kendall (9)) to $x = +0.7685$ to take into account the small value of n ($n = 15$). The values of t, computed from both ρ and x, are 4.366 and 4.326 respectively. Both are statistically significant at a probability level of 0.01. It appears, therefore, that in *Saperda* a positive correlation exists between the sequence of species based on morphological structures in general and a sequence based upon examination of the hind wings alone.

In concluding, it may be said that of the 23 species with which comparison of the wing with adult structures was possible complete or close agreement was found in four *Silphas* and six *Saperdas*. Three *Silphas* and eight *Saperdas* showed considerable agreement, and one *Silpha* and one *Saperda* exhibited a definite disagreement. In defense of the disagreements no further reasons can be offered at the present time, beyond the discussion already given in the pages dealing with the construction of the trees. The characters chosen at that time to represent specialization were not the only ones available; others could probably be found which would give a higher degree of correlation, but whether they would be as significant from an evolutionary standpoint as the ones employed is open to question. To the best knowledge of the writer, no attempt has previously been made to conduct a similar study of subgeneric relationships, and only considerable time and study among many different genera can produce the ultimate in a dependable evolutionary theory as applied to species variation in the wings of Coleoptera.

CONCLUSIONS

1. Close examination of the hind wings of two genera of Coleoptera has been found to yield, in a great majority of cases, characters sufficiently constant to permit species determination in the two genera.

2. Characters found to be constant in one genus usually showed the same degree of constancy in the other.

3. Categories of characters, in order of decreasing importance, were found to be: coloration, chaetotaxy, and venation.

4. Specialization of given characters in the wing tended to follow specialization of other parts of the body, and in *Sanenia* showed a statistically significant positive correlation with the specialization of the insect.

5. The wings of the comparatively primitive genus *Silpha* show greater diversification of characters, and are more easily separated, than the wings of the more specialized and, on the whole, more highly developed species of *Sanenia*.

SUMMARY

The wings of two genera of Coleoptera, Silpha and Saperda, were examined for constant and valid differences between the species. A series of from three to twenty-two wings of 15 North American Saperdas and from three to nineteen of 10 North American species of Silpha was used. Keys were formulated making use of the characters found. Variation sufficiently constant for species determination was found in all except two species of Saperda, the characters used consisting for the most part of coloration and chaetotaxy.

Phylogenetic trees showing relationships and degrees of specialization of the wings are presented and compared statistically with the established phylogeny of the genera as determined by the best authorities available. It was found that the wings tend, in general, to follow the specialization of the insect, though a few exceptions are noted.

ACKNOWLEDGEMENTS

The preparation of the material contained in this discussion has extended over a period of several years, and has been carried on under rather varied conditions. In addition to the several private collectors from whom material was borrowed, thanks are due the curators of the insect collections at Massachusetts State College, Virginia Polytechnic Institute, and Harvard University, without whose cooperation this study could not have been attempted. To Dr. Charles P. Alexander, of Massachusetts State College, under whom the idea originated, and to Dr. James McD. Grayson, of Virginia Polytechnic Institute, under whom the work was developed and completed, grateful acknowledgement for criticism and encouragement is made. Dr. H. G. Crecilius, of the University of New Hampshire (then Captain, A.U.S.) made available for nearly two years the facilities of the Station Hospital Laboratory, Camp Edwards, Massachusetts, at which a large part of the work was done. Mr. F. G. Werner, of Harvard, identified several of the specimens of *Silpha*. The writer is indebted also to Mr. S. N. Freedman, of Virginia Polytechnic Institute, for photographic duplication of plates.

APPENDIX A

Illustrations

Plate I Details of *Silpha spp.*

Fig. 1 Venation.

Fig. 2 Setal Clusters

Ac, Anal cluster; Hc, Humeral cluster; Poc, Postarcular cluster; Prc, Prearcular cluster; Scc, Subcostal cluster.

Fig. 3 *Silpha surinamensis.* 1st Anal vein.

Fig. 4 *Silpha discicollis.* 1st Anal vein.

Fig. 5 *Silpha trituberculata.*

Fig. 6 *Silpha bituberosa.* Apex.

Plate I

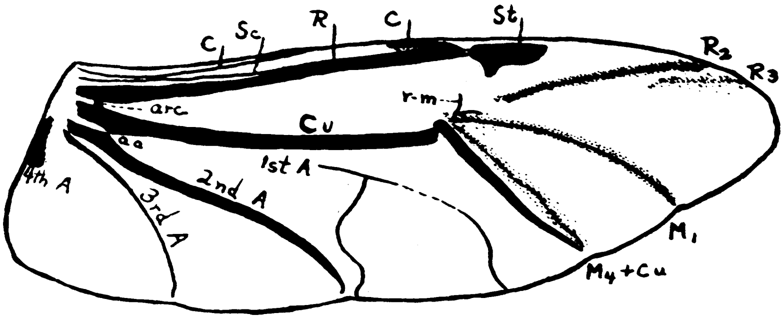


Fig. 1

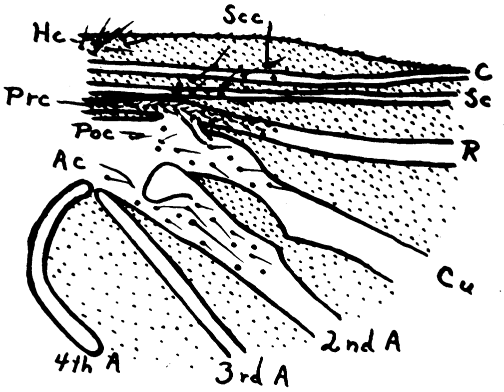


Fig. 2

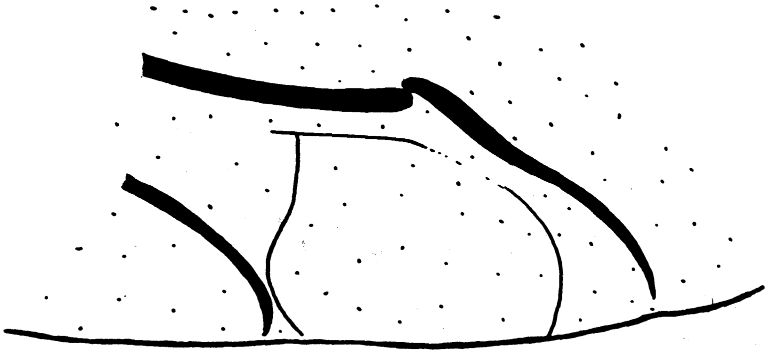


Fig. 3

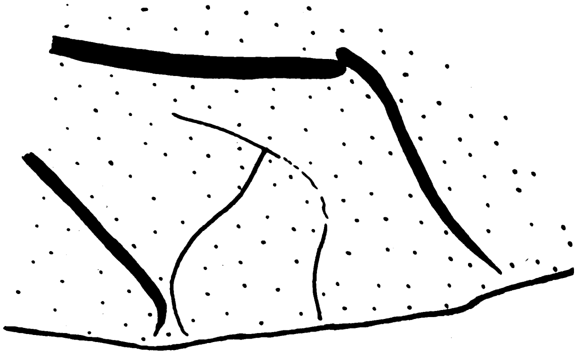


Fig. 4

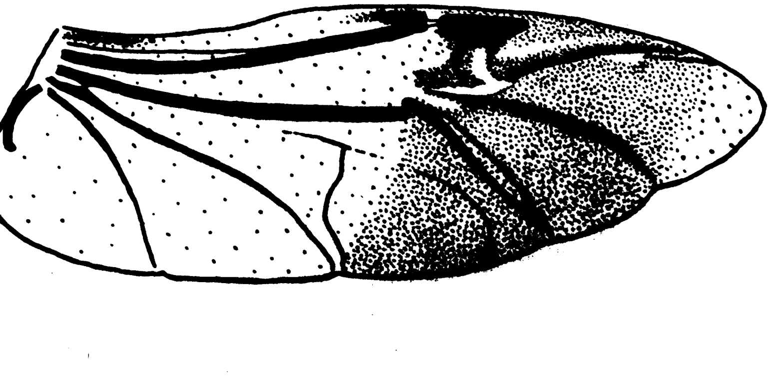


Fig. 5

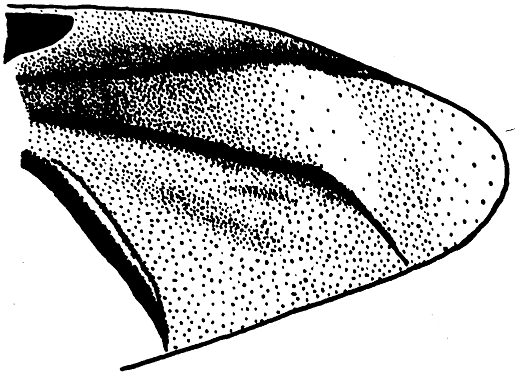


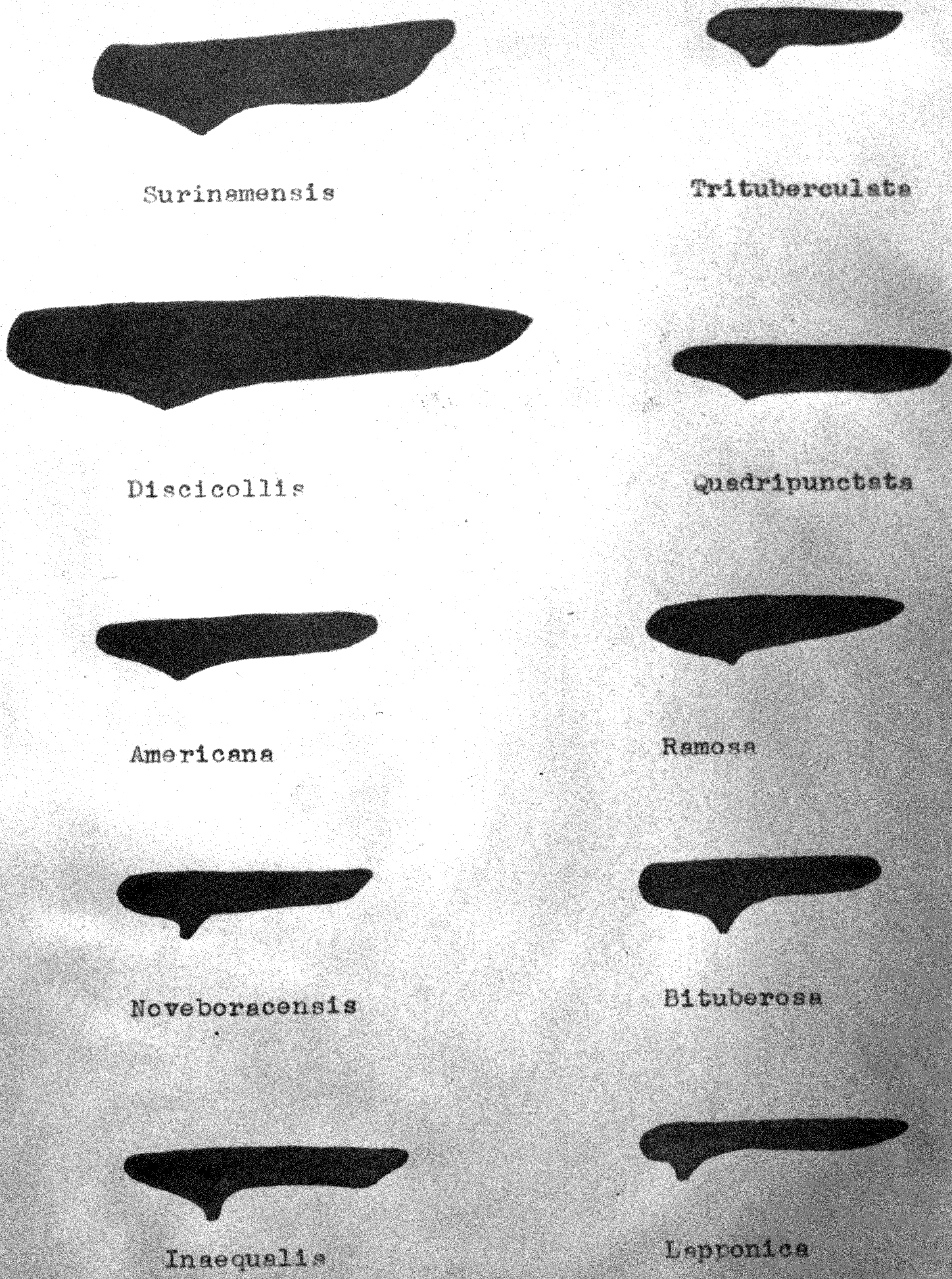
Fig. 6

Details of <u>Silpha</u> spp.

Plate II Stigmata of _Silpha spp._

(Drawn to uniform scale)

Plate II



Stigmata of *Silpha* spp.

Plate III Details of *Saperda spp.*

Fig. 1 *Saperda sp.*
Fig. 2 *Saperda mutica.* Mc, Medial cluster.
Fig. 3 *Saperda sp.* Venation and areas of the wing. Dc, Discal cell; Ju, Jugum; Vn, Vannus.
Fig. 4 *Saperda concolor.* Mc, Medial cluster.
Fig. 5 a. *Saperda mutica.* Hind margin.
        b. *Saperda calcarata.* Hind margin.
Fig. 6 a. *Saperda calcarata.* Microtrichium.
        b. *Saperda candida.* Microtrichium.

Plate III

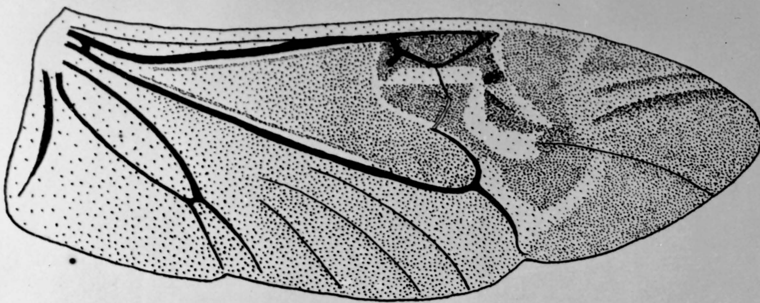


Fig. 1

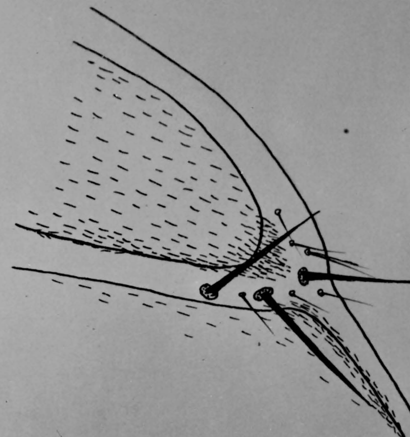


Fig. 2

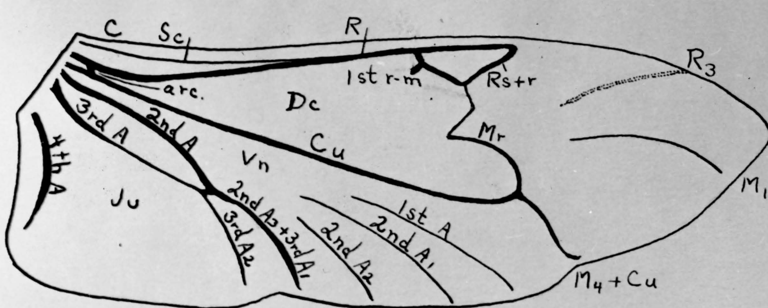


Fig. 3

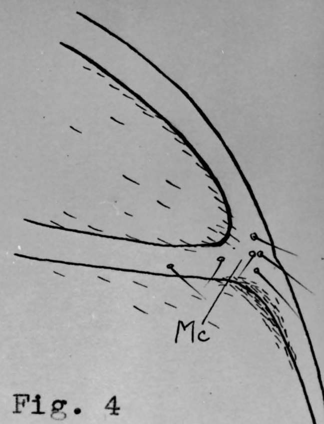
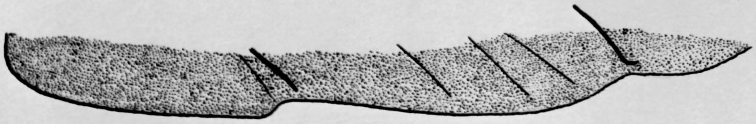
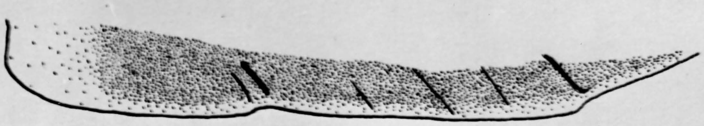


Fig. 4



a



b

Fig. 5

a b

Fig. 6

Details of <u>Saperda</u> spp.

Plate IV Details of *Saperda spp.*

Fig. 1 *Saperda hornii.* Arculus and related veins.
Fig. 2 *Saperda obliqua.* Arculus and related veins.
Fig. 3 *Saperda cretata.* Apex.
Fig. 4 a. *Saperda candida.* Hind margin.
b. *Saperda cretata.* Hind margin.
Fig. 5 *Saperda vestita.* Apex.
Fig. 6 *Saperda fayi.* Adventitious cluster. Rcl, Radial cluster; al, alveolus.

Plate IV

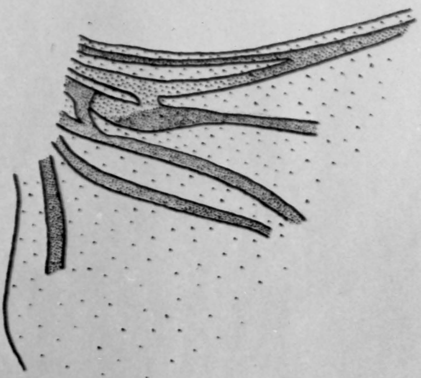


Fig. 1

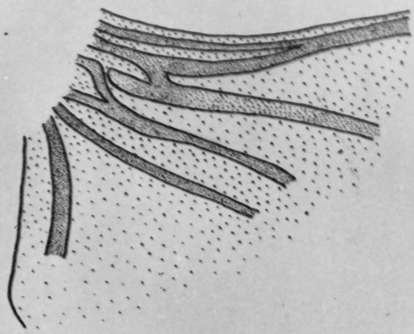


Fig. 2

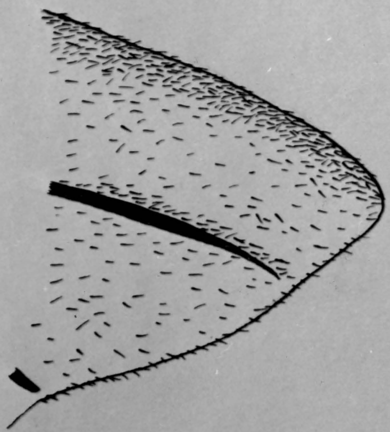


Fig. 3

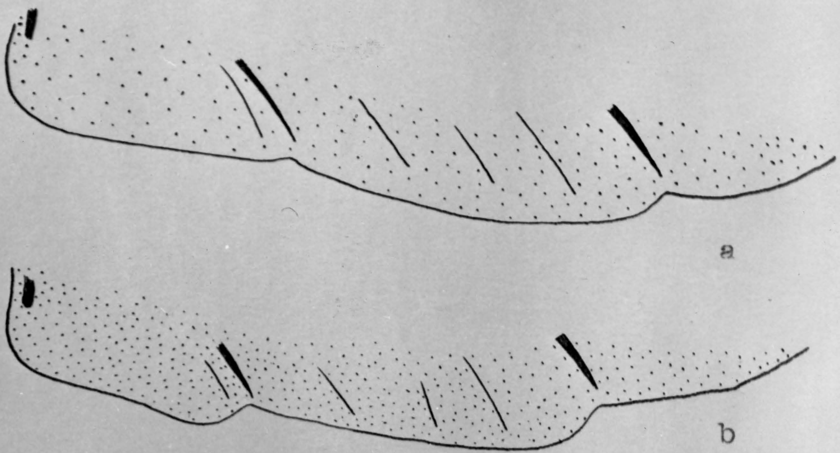


Fig. 4

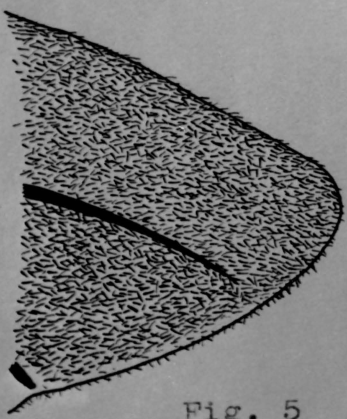


Fig. 5

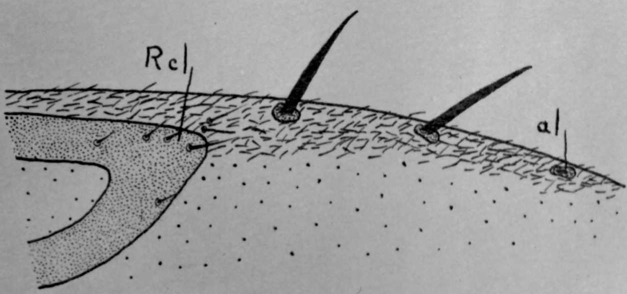
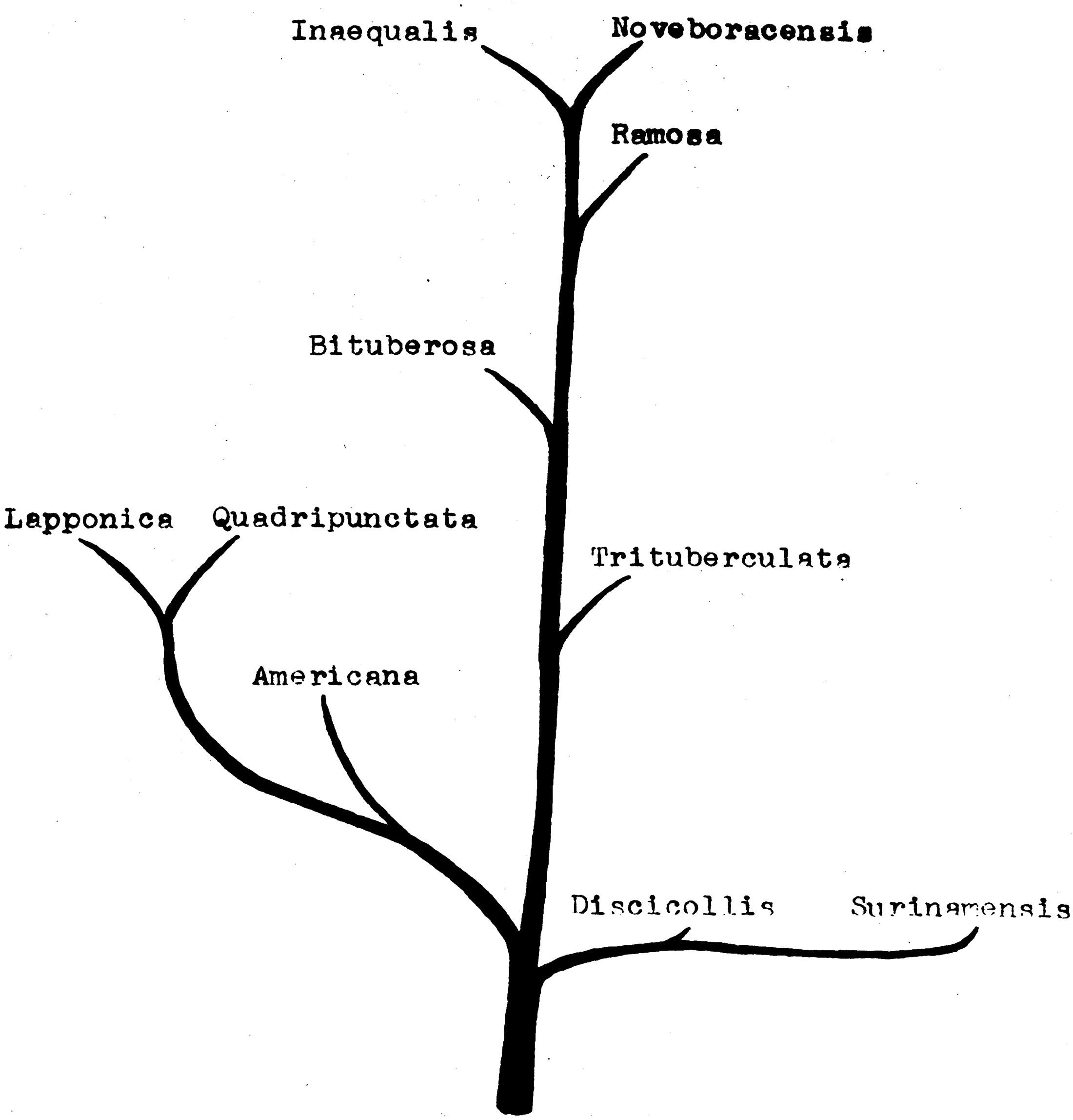


Fig. 6

Details of <u>Saperda</u> spp.

Plate V Phylogeny of Wings of _Silpha_.

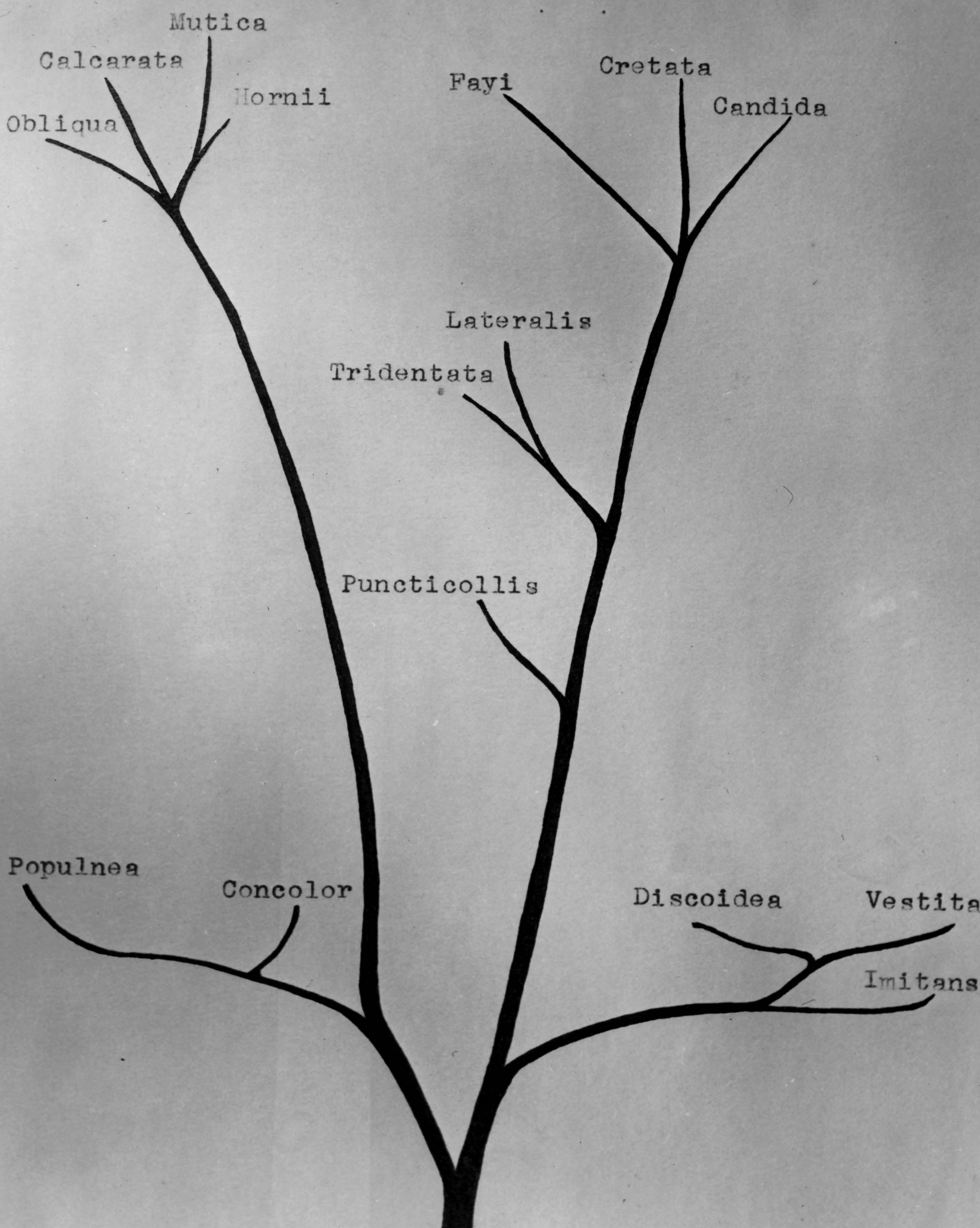
Plate V



Phylogeny of the Wings of
Silpha

Plate VI Phylogeny of Wings of *Saperda*.

Plate VI



Phylogeny of the Wings of

Saperda

APPENDIX B

Literature Cited

1. Comstock, J. H.

1918. The Wings of Insects.

2. Felt, E. P. and Joutel, L. H.

1904. Monograph of the Genus *Saperda*. N. Y. State Mus. Bul. 74.

3. Forbes, W. T. M.

1922. The Wing Venation of the Coleoptera. Ann. Ent. Soc. Am. 15:328-352.

4. Forbes, W. T. M.

1926. The Wing Folding Patterns in the Coleoptera. Jour. N.Y. Ent. Soc. 34:42-68, 34:92-139.

5. Good, H. G.

1925. Wing Venation of the Buprestidae. Ann. Ent. Soc. Am. 18:251-276.

6. Graham, S. A.

1922. A Study of the Wing Venation of the Coleoptera. Ann. Ent. Soc. Am. 15:191-200.

7. Horn, G. H.

1880. Synopsis of the Silphidae of the United States with Reference to Genera of Other Countries. Trans. Am. Ent. Soc. 8:219-322.

8. Hotelling, H. and Pabst, M. R.

1936. Rank Correlation and Tests of Significance Involving No Assumptions of Normality. Ann. Math. Stat. 7:29-46.

9. Kendall, M. G.

1945. The Advanced Theory of Statistics. Vol. I, 389-401.

10. King, E. W.

1943. A Taxonomic Distinction Between _Cyllene robiniae_ (Forst.) and _Cyllene caryae_ Gahan. Am. Midl. Nat. 29:180-182.

11. LeConte, J. L.

1853. Synopsis of the Silphales of North America. Proc. Phil. Acad. Nat. Sci. 6:274-287.

12. Leng, C. W.

1920. Catalogue of the Coleoptera of America North of Mexico.

13. McIndoo, N. E.

1931. Tropisms and Sense Organs in Coleoptera. Smithsonian Misc. Coll. Vol. 82 No. 18:45-53.

14. Needham, J. G.

1935. Some Basic Principles of Insect Wing Venation. Jour. N. Y. Ent. Soc. 43:113-129.

15. Saalas, U.

1936. Uber des Flugelgeader und die Phylogenetische Entwicklung der Cerambyciden. Annales Zoologicae-Botanicae Fennicae Vanamo 4:1-198.

16. Snodgrass, R. E.

1935. Principles of Insect Morphology. pp. 55-57; 225-228.

17. Swaine, J. M. and Hopping, R.

1928. The Lepturini of America North of Mexico. Nat. Mus. Can. Bul. 52:6-7.

18. Woodworth, C. W.

1906. The Wing Veins of Insects. Univ. of Cal. Pub. Tech. Bul. 1:1-152.