CATALOGUE

OF THE

COLEOPTERA

OF

AMERICA, NORTH OF MEXICO

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1920

Printed by
The Cosmos Press
Cambridge, Mass.
U. S. A.

DEDICATED TO

SAMUEL HENSHAW

IN GRATEFUL RECOGNITION OF THE SERVICE TO COLEOPTERISTS OF THAT LIST OF THE COLEOPTERA WHICH FOR THIRTY-FIVE YEARS HAS BEEN THE INDISPENSABLE AND ACCURATE GUIDE FOR ALL STUDENTS OF THE NORTH AMERICAN SPECIES

PREFACE

The aim of this catalogue is to enumerate systematically all the species of Coleoptera described prior to January 1, 1919, which occur in America, north of Mexico, Greenland included; with consecutive numbers, synonyms, citation of original description, and an indication of distribution. An effort has been made to arrange the species in genera, tribes, families, superfamilies and series, in accordance with the most recent works on classification; an explanation of the difficulty of doing so in a satisfactory manner follows this preface. No attempt has been made to determine the validity of the numerous specific names proposed by recent authors. Numbered names indicate species described and unquestioned in print. A letter, a, b, etc., following the numeral indicates variety, subspecies, race, etc. Names proposed by one author and disputed by another, are usually unnumbered, but are sometimes treated as varieties. Synonyms are always unnumbered, but the reader must guard against regarding unnumbered names as being invariably synonyms, for they often represent forms which, to their authors, seemed worthy of a name.

The names of authors are usually abbreviated to the first three or four letters of their names; the few cases which are differently treated are explained below in the list of signs and abbreviations used. Authors' names are usually in parenthesis if the species was originally described in a different genus; the correct placing of the parenthesis involved reference to many books and is not entirely complete.

The citations are indicated by figures following the author's name; the first two are the final figures of the year in which the description was published; the remainder, separated by a hyphen, give the page on which the description occurs. In conjunction with the chronological list of each author's papers at the end of the book, the citation is thus given in the most condensed form possible.

The distribution is indicated by the usual geographical abbreviations (explained below) for the localities given in original descriptions and in various faunal lists. Intermediate localities have usually been omitted to save space, but particular care has been taken to include references to the extremities of the area covered, e. g., Newfoundland, Alaska,

N. W. Wyom.	Northwest Wyoming	s. str.	sensu strictu, in a restricted sense
n. m.	nomen mutatum, name changed (when preoccupied)	s. g.	subgenus
		Sask.	Saskatchewan
n. sp.	new species	Schffr.	Schaeffer
Neb. Nebr.	Nebraska	Schp.	Schaupp.
Nev.	Nevada	Shas.	Shasta
Newn.	Newman	Sib.	Siberia
Nfld.	Newfoundland	Sier.	Sierra
No. N. Y.	Northern N. Y.	So. Ariz.	Southern Arizona
No. Ill.	Northern Illinois	So. Cal.	Southern California
N. Y.	New York	So. Fla.	Southern Florida
O.	Ohio	So. St.	Southern States
O. Sz.	Otto Schwarz	Sz.	E. A. Schwarz
Okla.	Oklahoma	Tenn.	Tennessee
Ont.	Ontario	Tex.	Texas
Or. or Oreg.	Oregon	Tul.	Tulare
Pa.	Pennsylvania	Tuol.	Tuolumne
Pac. St.	Pacific States	U. S.	United States
Plac.	Placer	Ut.	Utah
Plum.	Plumas	Va.	Virginia
Q. Char. Is.	Queen Charlotte Island	Vanc.	Vancouver
Que.	Quebec	Vt.	Vermont
R. I.	Rhode Island	W. Can.	Western Canada
Russ. Am.	Russian America	W. H.	Walther Horn
S. Am.	South America	W. I.	West Indies
S. C.	South Carolina	W. Kan.	Western Kansas
S. D.	South Dakota	W. St.	Western States
S. F.	San Francisco	W. Va.	West Virginia
S. I.	Staten Island, N. Y.	Wash.	Washington
S. St.	South States	Wis.	Wisconsin
S. W. Utah	Southwest Utah	Wy.	Wyoming

EXPLANATION OF SEQUENCE OF FAMILIES

American students of Coleoptera have been accustomed for 35 years to the Leconte system of classification, first proposed by Dr. Leconte in 1861,[1] and completed by him and Dr. Horn in 1883.[2] This system was followed in the Henshaw Check List in 1885, in Smith's "List of the Insects of New Jersey," in Blatchley's "Beetles of Indiana" and in many other books and papers; no doubt a great many collections, public and private, are also arranged in accordance with its sequence of families, tribes and genera.

Meanwhile the Leconte system has been under investigation here and in Europe and each investigator has proposed some alleged improvement. Some of these improvements have been accepted as such by subsequent authors, some have been the subject of more or less dispute. All, as far as a great part of American literature indicates, have been practically disregarded here, where Dr. Leconte's system has apparently been treated by many coleopterists as a finality, to be serenely followed despite all criticism.

Whether this course, undoubtedly convenient, should be continued in this Check List, or some more recent system should be adopted as the basis of its arrangement, has caused me to compare carefully the changes proposed by Sharp, Lameere, Kolbe, Ganglbauer, Gahan, Verhoeff and Sharp and Muir. Unfortunately such comparison discloses a lack of agreement on many points between these critics of Leconte. If, therefore, any departure from Leconte's system be made, it must be after study of the conflicting arguments that have been brought forward and by personal decision as to their respective merits.

Since these arguments relate principally to questions of phylogeny, necessarily a matter of theory and deduction, though larval studies also play an important part, I have found such decision difficult to reach and present the results that follow with much fear that many errors are included, but with the hope that they may be useful in making better known the work of recent investigators of the classification.

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[1] Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution by John L. Leconte, M. D., Part 1. Washington: May, 1861–March, 1862.

[2] Classification of the Coleoptera of North America. Prepared for the Smithsonian Institution by John L. Leconte and George H. Horn. Washington, 1883.

As a preliminary matter it may be well to recall that the classification of the Coleoptera has been frequently altered. In our own country the following catalogues have appeared:

F. V. Melsheimer	1806
F. E. Melsheimer	1853
J. L. Leconte	1863
G. R. Crotch	1873 and E. P. Austin, Supplement, 1880.
Samuel Henshaw	1885 and Snpplement, 1895.

There is no agreement in the sequence of families in these American catalogues, nor do they agree with those published abroad, which also differ among themselves. The reason is that each is based upon a different stage in the ever-changing system of classification.

Systems formerly in Use

The earliest system employing binomial nomenclature is of course that of Linné's, ed. X, 1758. In that work, the beetles (with a few insects no longer considered beetles) are divided into three groups, according to the form of the antennæ, "clavatis," "filiformibus" and "setaceis."

Many other attempts (among which Latreille's recognition of the different forms of the outer maxillary lobe, by which he separated what he called beetles with six palpi from those with four palpi, is noteworthy) led up to the system developed by Latreille, Erichson, Lacordaire, Duval and other great coleopterists. This system was in use when Dr. Leconte began his studies; it had then long held sway and has profoundly influenced him and all the writers on Coleoptera even to this day. It attempts to classify beetles primarily by the number of their tarsal joints, thus:

PENTAMERA	— beetles with all the tarsi 5-jointed.
TETRAMERA	— " " " " " 4 "
TRIMERA	— " " " " " 3 "
HETEROMERA	— " " front and middle tarsi 5-jointed, hind tarsi 4-jointed.

The existence of minute joints, difficult to see but actually present, necessitated the use of terms like pseudotetramera and cryptotetramera. Such a classification, unless qualified by many exceptions, leads to the most unnatural aggregations and is now practically discarded, except that Heteromera are retained by many modern authors as a natural series.[1] I believe that it is an unfortunate retention,

[1] The families (or part of them) usually included in Heteromera may truly constitute a natural series, but, if so, it cannot be safely defined by the heteromerous tarsi.

though Dr. Gahan describes the suggestion that they are not really a natural series as "heresy,"[1] for, if the definition were strictly applied, the series would include *Hydroporus* among water beetles, many Silphids and Staphylinids, and many Clavicorns, as well as the Tenebrionid-like beetles, for which it was intended. Even in that restricted sense, the heteromerous tarsi do not afford a good definition, as may be noted in comparing Tetratomini and Triphyllini, formerly far apart, now united by Casey,[2] or *Ababa* and *Othnius*, considered allies by that author, though *Ababa* was later shown to be a Clerid by Schaeffer.[3] Heteromerous tarsi are in fact found in so many groups that the character cannot safely be used to define a primary division or to found a natural series. Nevertheless the reader will note as the more recent systems are explained how their authors have clung to the tarsal system and especially to the heteromerous division.

Leconte System

The great merit of the Leconte system is the primary use of many other characters drawn from the sutures, palpi, abdominal segments and antennæ, guided throughout by Dr. Leconte's wonderful instinct, which led him so nearly right that few changes in his system, out of the many that have been proposed, meet with general approval. He was, however, bound to be influenced by his early studies and the ideas thereby derived from his illustrious predecessors, such influence, as it seems to me, showing in his divisions Isomera and Heteromera, based upon the formerly used tarsal characters. He divided beetles into:

I. COLEOPTERA GENUINA:	— double gular suture and flexible palpi.
1. ISOMERA:	— all the tarsi of same number of joints.
a. ADEPHAGA	— first visible abdominal segment divided.
b. CLAVICORNIA	— clavate antennæ.
c. SERRICORNIA	— serrate antennæ.
d. LAMELLICORNIA	— lamellate antennæ.
e. PHYTOPHAGA	— 4-jointed tarsi
2. HETEROMERA	— heteromerous tarsi.
II. RHYNCHOPHORA	— single gular suture and rigid palpi.

This is the system in general use in America. The objections that have been urged against it are that the tarsal character can only be used with exceptions, that Clavicornia and Serricornia merge one into the

[1] The Entomologist, December, 1911, p. 395.
[2] Journ. N. Y. Ent. Soc. VIII, 1900, p. 167.
[3] Journ. N. Y. Ent. Soc. XXV, 1917, p. 133.

other by transitional forms, that Lamellicornia deserve more exalted rank and Rhynchophora less, that Phytophaga and Rhynchophora are closely related and should not be separated by Heteromera, and that Adephaga are more entitled to sub-ordinal rank than any other division. While these objections may all be valid, no one has yet offered a better system in the form of a complete classification. The improvements suggested and substantially approved include two series:

PALPICORNIA for Hydrophilidæ, etc., with palpi longer than antennæ.
STAPHYLINOIDEA for a series of families mostly with short elytra and with three or more dorsal abdominal segments corneous.

Except for a change in the position of the Phalacridæ, these series do not alter materially the sequence of families as arranged by Leconte, they only supply names for groups of families in his series Clavicornia. Other series that have been proposed have not met with such substantial approval and will be discussed later. Clear cut definitions for them are more or less difficult to find.

Sharp System

Dr. Sharp's system [1] was published 16 years after Leconte's and much that had been developed in the interval, especially in larval studies is admirably treated and illustrated by him. His great knowledge of the Coleoptera of the whole world and his knowledge of the entire class of Insecta make his opinions worthy of the highest respect. His classification is:

LAMELLICORNIA — 5-jointed tarsi — antennæ lamellate.
ADEPHAGA — 5-jointed tarsi — maxillæ with outer lobe palpiform.
POLYMORPHA — tarsi variable — antennæ serrate or clavate.
HETEROMERA — tarsi heteromerous.
PHYTOPHAGA — tarsi 4-jointed.
RHYNCHOPHORA — head with a beak, gular suture single, palpi usually not evident.

Here the isolation of the Lamellicornia is better shown, the Clavicornia and Serricornia are consolidated into a series embracing in Sharp's words "a large number of forms still unclassified," though "a large part of them belong to four great families (Staphylinidæ, Buprestidæ, Elateridæ, Malacodermidæ) which are easily recognizable." Such was the state of the classification in 1909 (or 1899, if the date of the first edition is used) with tarsal characters still prominent.

Neither Leconte's nor Sharp's classification professes to be phylo-

[1] Cambridge Natural History, VI, 1909. Insects, by David Sharp, M. A., M. B., F. R. S.

genetic; the position assigned Lamellicornia by Sharp does not mean that he considered them lowest in the phylogenetic scale, but simply so distinct from other beetles as to require a special place, while the position given them by Leconte was avowedly simply a matter of convenience.

Phylogenetic Systems

The phylogenetic systems seek to arrange the families and series so that the more primitive beetles shall precede the more derivative; in such systems certain characters are assumed to indicate a stage in the progressive modification of the Coleoptera, rather than a relationship.

Taking the tarsi as an example, a primitive beetle is assumed to have had tarsi composed of five equal, elongate, unmodified joints, as in a generalized sort of insect. Tarsi in which by fusion some of the five joints are shortened, or modified, might have been derived from the simple 5-jointed tarsi; further progressive modification might have reduced the number on one leg to four, producing the heteromerous condition; still further modification might have produced the 4-jointed tarsus, or even three, or two, or one. All such modified tarsi would indicate a greater or less degree of derivation or specialization.

The same theory may be and has been applied to many parts, external and internal, of the body and its appendages. Sometimes the modification, perhaps under the influence of special environment, has been apparently rapid in certain directions, while in others it has stood nearly stationary. In such cases it may be possible to build up series of families showing progressive modifications in various directions, but each united as a series by the possession in common of those characters which have been scarcely modified. But the results may, and indeed have, varied greatly, according to the value attached to the various characters as indices of phylogenetic rank.

The first serious attempt to do this is by Auguste Lameere, the great Belgian coleopterist, in 1900[1]). His first results were corrected in 1903[2]) and give the following classification, based primarily on the venation of the hind wings:

CARABIFORMIA — hind wings with cross-veins connecting longitudinal veins.
STAPHYLINIFORMIA — hind wings without cross-veins connecting longitudinal veins
CANTHARIFORMIA — hind wings with longitudinal veins hooked or recurrent.

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[1] Notes pour la classification des Coleoptères (Ann. Soc. Ent. Belg. XLIV, 1900).
[2] Nouvelles Notes pour la classification des Coleoptères (Ann. Soc. Ent. Belg. XLVII, 1903).

The Canthariformia were divided into following series; defined only by the list of families included.

TERIDILIA
MALACODERMATA
STERNOXIA
MACRODACTYLIA
BRACHYMERA
PALPICORNIA
CLAVICORNIA
PHYTOPHAGA
HETEROMERA
LAMELLICORNIA

Lameere's Carabiformia is equivalent to the Adephaga of other authors and it is noteworthy that he considers the genus *Omophron*, as did Kolbe in 1880, as a sub-family leading from Carabidæ to Haliplidæ, in which I am glad to follow him. Of the groups he separated in Canthariformia, many, sometimes in a modified form, have met with much approval. Kolbe for instance, adopts Malacodermata, Palpicornia and Sternoxia; Gahan also considers Malacodermata a natural group and he says that Teridilia, composed of Lymexylidæ, Lyctidæ, Ptinidæ, Anobiidæ and Bostrichidæ would be a fairly natural one. Dr. Gahan's general attitude, however, is in his language "finding serious difficulties in accepting the groups proposed either by Lameere or by Kolbe" and published in 1911[1]), after much *pro* and *con* had been written, fairly reflects the conservative opinion of Lameere's work.

But if not entirely acceptable, Lameere's work certainly stirred up other authors. The most voluminous was Ludwig Ganglbauer, custos in Hof-Museum in Vienna, and author of the unfinished "Käfer von Mitteleuropa." His system, unfortunately never entirely worked out, appeared in its most complete form in 1903[2] and classified beetles much as was done by Leconte, but raising the rank of Adephaga, separating Palpicornia and Staphylinoidea as series, and consolidating Serricornia and Clavicornia to form series Diversicornia, also Phytophaga and Rhynchophora, in one series Phytophaga. The result gives:

Sub-order	ADEPHAGA
"	POLYPHAGA
Series	Palpicornia
"	Staphylinoidea
"	Diversicornia
"	Heteromera
"	Phytophaga
"	Lamellicornia

[1] On some recent attempts to classify the Coleoptera in accordance with their Phylogeny (The Entomologist, XLIV, 1911, pp. 121–351).
[2] Systematisch-Koleopterologische Studien (Münch. Kol. Zeitschr. I, 1903, pp. 271–319).

As in Lameere's system the highest rank is assigned to Lamellicornia; principally, it seems to me, on account of the high degree of concentration of the ganglia of the nervous system. I cannot share this view for reasons that will be given later, but it may be here stated that Dr. Gahan in a cautious way commends the Ganglbauer system and ends his masterly review in the "Entomologist" thus: "I think that his classification may well stand for the present as the one best devised to express our knowledge of the phylogeny of the Coleoptera."

Ganglbauer's system is also substantially approved by Anton Handlirsch,[1]) who in 1430 pages and 70 plates reviews the accumulated knowledge of fossil insects and deduces from the study thereof, and the study of various systems of classifications of living insects, a phylogenetic classification of the latter. For the purpose of this paper, pp. 1271–1280 and "stammbaum" VII, in which the families of Coleoptera are treated, are of the greatest interest, and as the results I have reached do not entirely agree with those therein set forth, it seems proper to preface an account of them by pointing out that Handlirsch admits that he is not a coleopterist (p. 1276) and that his reference to verbal communications from Ganglbauer, both authors being attached to the Hof-Museum in Vienna, may indicate that to some extent the one was influenced by the other.

Handlirsch considers the Coleoptera as being derived from Protoblattoidea previous to Triassic times, rejecting the alleged Coleopterous fossils of earlier epochs as being very doubtfully beetles at all; during the Triassic epoch he conceives that from an extinct protocoleopterous fauna two suborders arose, *viz.*: Protoadephaga and Protopolyphaga. Triassic fossil remains consist of elytra only, which cannot with certainty be ascribed to any existing families. During the succeeding Liassic epoch the Protoadephaga began to divide into the Adephagous families as now known; the more numerous fossil remains (pl. XLI), showing sometimes head and thorax as well as elytra, permit of the family being recognized by general appearance, though legs, antennæ and other appendages are missing. During the Lias also the Protopolyphaga began to divide into something approaching their present divisions; among the Lias fossils resemblances to our present Elateridæ are not uncommon, the peculiar prosternal process being plainly seen in some; while the blattoid form of thorax found in other fossils is very suggestive of Malacodermata like our Lampyridæ. But Handlirsch expressly disputes the reference of Trias or Lias fossils to existing fami-

[1] Die Fossilen Insekten und die Phylogenie der Rezenten Formen, Leipzig, 1906–1908.

lies, except in Adephagous forms, his theory being that as the Protocoleopteron arose from Protoblattoidea prior to the Triassic, and the Protoadephagon during Triassic, so did the Protopolyphagon arise and divide during Liassic.

In the Jurassic fossils, plate 45, more progress was made; among the Adephaga, water beetles like *Dytiscus*, and Carabids like *Calosoma*, are plainly seen with their characteristic legs; but among the Polyphaga it is still hard to place the species in existing families. The Cretaceous fossils are so few and imperfect that nothing can be said of them; but in the Tertiary fossils from Oeningen in Baden, and from Florissant in Colorado, the extraordinary numbers that have been found and their comparatively complete preservation have permitted of referring them not only to living families, but even genera in those families. Of the existing families very nearly all are now known among Tertiary fossils. Finally, in Quaternary fossils, in peat, and in interglacial deposits, it becomes a question as to their difference from living species.

To me it seems strange that Handlirsch, after establishing by fossil evidence the appearance of the Serricorn series, Sternoxia and Malacodermata, before any other polyphagous series, should in his "stammbaum" place Sternoxia after the Clavicornia. In his catalogue of Tertiary fossils, p. 743, he places them before the Clavicornia, and more correctly in my view.

As intimated above, he was possibly influenced by Ganglbauer and considerations of internal structures to which both authors attach great importance. At any rate his final conclusions are very much like Ganglbauer's and are based upon the conception of the sub-order Adephaga, having first become divided from other Coleoptera, which later became successively broken up into series as follows: Staphyliniformia, Palpicornia, Malacodermata, Clavicornia, Brachymera, Serricornia (=Dascilloidea), Sternoxia, Teredilia, Heteromera, Phytophaga, Rhynchophora, Lamellicornia, of which the last named were the last to be evolved from the protopolyphagon. It is in the division of Ganglbauer's Diversicornia into at least ten series that the greatest difference between the two authors appears; Dr. Sharp, in a letter, insists upon even many more lines of descent, and Dr. Gahan, as already stated, finds serious difficulty in accepting the groups proposed by Kolbe and Lameere. All recently expressed opinions, in short, tend towards the recognition of more numerous groups.

H. J. Kolbe, a German author of high standing, has on the contrary attacked the Ganglbauer system and has proposed one that is quite different, based on the theory that parts of the body proper, rather than its appendages, truly show the progressive modifications of the Coleoptera. His early work [1] was considerably altered in 1908 [2] and as altered gives the following system:

ADEPHAGA
HETEROPHAGA (= POLYPHAGA Ganglbauer.)

HAPLOGASTRA Sternites of 2d and 3d abdominal segments separate, their pleuræ separated by a suture.

including: Staphylinoidea, Lamellicornia.

SYMPHYOGASTRA Sternites of 2d and 3d abdominal segments connate, no trace of suture between their pleuræ.

including: Cupesidæ, Malacodermata, Trichodermata, Palpicornia, Dascilloidea, Sternoxia, Bostrichoidea, Heteromera, Clavicornia, Phytophaga, Rhynchophora.

This system seems to have had some influence upon Kuhnt, in preparing the "Illustrierte Bestimmungstabellen"[3] and upon Dr. Pierce, but was never fully worked out by Kolbe himself, though his earlier "Natürliches System der carnivoren Coleoptera" (D. E. Z. 1880, pp. 258–280) superficially covers Adephaga. As counteracting the possibly extreme views of Ganglbauer regarding Lamellicornia and Rhynchophora, Kolbe's work is valuable; and in corroboration of his estimate of the highest rank for Rhynchophora, I would here quote Dr. Sharp's sentence, "we should be inclined to place such forms as Calandrides among the most perfect of insects."

Systems based on Genitalia, etc.

An entirely different point of view is that taken by Sharp and Muir who have devoted considerable time to a comparative study of the genitalia.[4] The heterogeneous character of the Heteromera, which have appeared intact in every system so far, is brought out by their work; Cistelidæ, Lagriidæ and Monommidæ are found to resemble

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[1] Vergleichend-morphologische Untersuchungen an Coleopteren nebst Grundlagen zu einem System und zur Systematik derselben (Arch. f. Naturg 1901, pp. 89–150).
[2] Mein System der Coleopteren (Zeitschr. fur wissenschaftliche Insektenbiologie, IV, 1908, 116–400).
[3] Illustrierte Bestimmungs Tabellen der Käfer Deutschlands, Stuttgart, 1912. (This work has 10,000 illustrations, including larvae.)
[4] The comparative anatomy of the male genital tube in Coleoptera (Trans. Ent. Soc. Lond. 1912, pp. 477–639, and 1918, pp. 223–229).

Tenebrionidæ in the form of the genitalia, but all the other families heretofore called Heteromera more nearly resemble Cucujidæ in the form of genitalia than Tenebrionidæ. They suggest the arrangement of the Coleoptera in eight series, thus:

BYRRHOIDEA	— most of Leconte's Serricornia.
CARABOIDEA	— Adephaga.
CUCUJOIDEA	— all not included elsewhere.
STAPHYLINOIDEA	— Staphyliniformia.
MALACODERMOIDEA	— Malacodermata.
TENEBRIONOIDEA	— Cistelidæ, Lagriidæ, and Tenebrionidæ.
SCARABAEOIDEA	— Lamellicornia.
PHYTOPHAGOIDEA	— Phytophaga and Rhynchophora combined.

but they give no definitions other than those drawn from the genitalia and admit that their work is unfinished and subject to revision, especially as to division of the series Cucujoidea. It is noteworthy that they found two types of genitalia in the family Colydiidæ, and that the more primitive of the conditions of the coleopterous genital tube, so far as existing forms are concerned, occurred in the Byrrhoidea, contradicting to this extent the phylogeny presented above.

I have been greatly impressed by the results of this work by Sharp and Muir and regret that it has not yet been completed. Its recognition of Caraboidea, Staphylinoidea, Malacodermoidea, Tenebrionoidea, Scarabæoidea and Phytophagoidea, as six great series, each having characters in common, while each at the same time shows a definite different direction in which modification has progressed, seems to be final corroboration of results obtained by previous authors from studies of adult and larval characters. Its severance of Tenebrionoidea from the heterogeneous assemblage heretofore called Heteromera is the step needed to correct the old error inherited from Latreille. While I have been so far unable to correlate their series Byrrhoidea and Cucujoidea with any series based on external characters, I feel that these divisions of theirs may nevertheless be indications in the right direction, but obscured at present by the fact, recognized by Sharp and Muir also, that a number of series are possibly combined in these two groups.

Another worker with genitalia is Verhoeff [1] who studied also the number of abdominal segments, but in both subjects for a few families only. The accuracy of his observations and the value of his deduc-

[1] Vergleichende Untersuchungen über die Abdominal segmente und die copulations organe der mannlichen Coleoptera (D. E. Z. 1893, pp. 113–170); and weiblichen Coleoptera (D. E. Z. 1893, pp. 209–260).

tions have been strongly attacked in Germany by Julius Weise [1] and Otto Schwarz,[2] and have received scant attention elsewhere. In this connection the excellent drawing of the extruded genitalia of *Brachyacantha* by Grossbeck [3] should not be overlooked. The most striking feature of Verhoeff's contribution seems to me his recognition of the isolated position occupied by the Coccinellidæ, for which he made a sub-order ELEUTHERESIPHONA, based upon the genitalia, larval characters and life history. The subordinal rank of the family is not conceded by any other author, as far as I know, but its separation as a series from the other clavicorns, may be the outcome.

Pierce [4] has revived the separation of the family Stylopidæ as an order, STREPSIPTERA, and has recently repeated the arguments in favor of this course.[5] This is questionable, as they seem to lead quite readily from a series composed of Mordellidæ, Rhipiphoridæ and Meloidæ, and connected, judging from larval characters, through the Mordellidæ with Lymexylidæ. That they should have become highly specialized would naturally follow from their parasitic habits.

A similar separation was proposed for the parasitic Platypsyllidæ by Westwood, who called them ACREIOPTERA, but has long since been discarded.

LARVAL CHARACTERS

There has been much written about the larvæ of Coleoptera, especially by the Danish and French authors, but there is no complete classification based on larval characters. The larvæ of the primitive families are either campodeaform, with elongate bodies, long legs, and anal cerci, or blattoid, broader in outline, with expanded sides. In the Adephaga, the legs terminate usually in two claws and according to some authors, are composed of one more joint than in Polyphaga, but there are exceptions to the dual claw, and further studies of Adephagous larvæ may show other exceptions. In some primitive Polyphaga the larvæ are also campodeaform, but with only one claw. In Staphyliniformia, the blattoid form often occurs and it is also seen in *Psephenus;* it becomes therefore difficult to say which is the more primitive of the two forms

[1] D. E. Z. 1894, pp. 155–157 also, D. E. Z. 1894, pp. 177–188; 1895, pp. 65–78.
[2] D. E. Z. 1894, pp. 153–155; 1895, pp. 27–36.
[3] Bull. Am. Mus. Nat. Hist. XXX, 1911, p. 284.
[4] A monographic revision of Strepsiptera (Bull. U. S. Nat. Mus. No. 66, 1909, pp. 1–232.)
[5] The comparative morphology of the order Strepsiptera (Proc. U. S. Nat. Mus. LIV, 1918, pp. 391–501.)

of larvæ, campodeaform or blattoid; if, indeed, there is any phylogenetic significance in such forms. There are, moreover, a number of larval forms that are apparently very peculiar, as in Dermestidæ and Coccinellidæ; and many of the Polyphagous larvæ exhibit modifications in various directions.

In the decidedly derivative series the larvæ apparently show uniform progressive modification in a definite direction. The larvæ of Lamellicornia are eruciform, fat, curled grubs, thickened at anal extremity, but still with legs. The larvæ of the Phytophaga are also eruciform, sometimes with, sometimes without, legs; in Bruchidæ the young larvæ have legs that are lost in the later moults. The larvæ of the Rhynchophora (except Brentidæ) are always curled, legless grubs. There seems thus to be a progressive development from the active larvæ of the Adephaga, through the Polyphagous and Lamellicorn forms of larvæ, that reaches its climax in the slothful seed-eating larvæ of Rhynchophora. Packard has traced an interesting parallel between this development and the life history of hypermetamorphic beetles as stated by Riley [1] and others. If one compares Riley's figure of the first larva (or triungulin) with the campodeaform larva of Adephaga, and his figure of the last larval stage with the eruciform larva of Rhynchophora, a striking resemblance will certainly be detected. The history of the development of Coleopterous larvæ seems to be repeated in the various moults.

But when one considers the legless larvæ of the Buprestidæ and Eucnemidæ, groups that retain many characteristics we have called primitive, the active larvæ of many Coccinellidæ, a group that in many respects seems highly derivative, one is forced to consider the gradual loss of larval legs as possibly the result of atrophy, rather than as an indication of phylogenetic rank. The references made by Handlirsch to the blattoid form of larva as characteristically primitive are still more disconcerting, for such forms are rare in the Adephaga (*Cychrus* is an example and it is certainly far from the most primitive of Adephaga) though his fossil evidence strongly favors their early origin.

It seems too early in the study of Coleopterous larvæ to attempt to draw any definite conclusions therefrom, except as a corroboration of those drawn from the study of adults. Mr. Schwarz has given long study to the subject; and his present feeling, as I gathered from a recent conversation with him, is not very different from that I have just expressed. Dr. Böving's results and those of Dr. F. C. Craighead,

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[1] On the Larval Characters, etc. (Trans. Ac. Sci. St. Louis, III, 1877, pp. 544–562).

based upon long study and extensive material, may however, when published, afford an independent basis for classification.

Until that time comes we have no system of classification, as already stated, based on larval characters; but alleged resemblances in the larvæ have frequently been used to support relationships based primarily on adult characters; and if such resemblances are, at least in part, cases of convergence, even such may be hazardous.

It may be added that McGillivray's key to Coleopterous larvæ,[1] though excellent for the period in which it was prepared, now requires considerable modification.

I have now given an account of the principal changes that have been proposed in the Leconte system. But it is a bare sketch of their salient points. A complete synopsis and argument may be found in Dr. Gahan's paper from which I have already quoted. This should be studied by every one interested in the subject of family classification. It is, however, a critical paper and points out the weak points in other systems without constructing a new one. The treatment of the Coleoptera by Brues and Melander,[2] incorporates many of the ideas which I have endeavored to repeat, but gives no clue to the sequence in which the families should be arranged. So that we are left to choose between the rival continental authors, but with the guidance of Dr. Gahan's impartial criticism and of Sharp and Muir's work on genitalia.

System adopted for Check List.

In this way, balancing one argument against another, I am led to believe that a division of the Coleoptera into two sub-orders is established; and that possibly the sub-division of the sub-order Polyphaga into several series, approaching the rank of sub-orders, is at present the best course to pursue. The definition of some of these series, and consequently the inclusion or exclusion of certain families, remains doubtful; but for many purposes such definition is practically accomplished by the families included. The two sub-orders would be separated as follows:

Outer lobe of maxillæ palpiform; first visible ventral segment divided; hind wings with cross-veins; pleural sutures of prothorax present; antennæ never serrate, clavate or lamelate; tarsi 5-jointed (except in the genus *Hydroporus*); larvæ generally campodeaform, with legs, tarsus with one or two claws, sometimes blattoid........................ADEPHAGA.

[1] New York State Museum Bulletin 68, 1903, pp. 288–294.
[2] Key to the Families of North American Insects, 1915.

Outer lobe of maxillæ not palpiform; first visible ventral segment not divided (except Rhysodidae); hind wings without cross-veins (except Lymexylon, Rhysodidæ and Cupesidæ); pleural sutures of prothorax absent (except Cupesidæ); antennæ and tarsi variable; larvæ variable, tarsus and claw fused (except in *Rhysodes, Cupes* and *Micromalthus*) . . POLYPHAGA.

The families Rhysodidæ and Cupesidæ have been variously assigned to both sub-orders as above defined, since they possess some of the characters of each. It is conceivable that they represent the modified descendants of families that existed prior to the separation of Adephaga and Polyphaga; if so, they should in a phylogenetic arrangement precede both, as being more primitive. It is certain that their position has been greatly disputed, but the recent discovery of their larvæ convinces me that they are not Adephaga.

The Polyphaga would be separated into seven series as follows:

Palpi flexible; gular sutures double . . . . 1.
Palpi rigid or concealed; gular sutures single . . . . 2.

1. Hind wings with simple, straight veins; abdomen with at least three corneous segments dorsally, and exposed more or less by the short elytra; antennæ variable, but never lamellate; tarsi variable; larvæ campodeaform, or blattoid, always with legs. BRACHELYTRA or STAPHYLINIFORMIA.
   Hind wings with veins in part connected by hooks, or recurrent veins; abdomen with at most two corneous segments dorsally, usually completely covered by the elytra; antennæ and tarsi variable; larvæ variable . . . . 3.
3. Antennæ never lamellate; tarsi variable . . . . 4.
   Antennæ always lamellate; tarsi 5-jointed . . . . 5.
4. Palpi never longer than antennæ, tarsi variable . . . . 6.
   Palpi often longer than antennæ, tarsi usually 5-jointed . . . . 7.
6. Antennæ variable, usually filiform, serrate or modifications of those forms, never lamellate or suddenly clubbed; body in the more primitive families elongate, not strongly chitinized; tarsi 5-jointed or heteromerous; larvæ sometimes remarkably differentiated, with legs (except in Buprestidæ and some Eucnemidæ) that are usually short. POLYFORMIA.
   Antennæ usually clavate, though variable and sometimes only thickened externally; tarsi variable, including heteromerous, 4 and 3-jointed; body strongly chitinized; larvæ with legs, never blattoid . . . . CLAVICORNIA.
   Antennæ variable, usually serrate, or with outer joints wider, sometimes pectinate or flabellate; tarsi always 4-jointed . . . . 8.
7. Antennæ clavate, body strongly chitinized; larvæ campodeaform with legs. PALPICORNIA.
5. Antennæ lamellate; body usually strongly chitinized; pleuræ of 2d and 3d abdominal segments separated by the suture between their sternites; larvæ eruciform, with legs. LAMELLICORNIA.
8. Palpi with last joint triangular in primitive families, but becoming small in the more derivative families; tarsi always 4-jointed; larvæ usually eruciform, sometimes without legs . . . . PHYTOPHAGA.
2. Antennæ variable, even lamellate in one genus, head frequently with a beak; abdomen usually covered by elytra; tarsi 4-jointed, except in three genera, *Tomicus, Dryophthorus* and *Platypus*, larvæ eruciform, usually without legs (except in Brentidæ?). RHYNCHOPHORA.

The family Brentidæ appears to form an exception to the larval character in Rhynchophora, if the descriptions are correct. It is also exceptional in the form of its beak and in certain other respects. It is possible that it, like Rhysodidæ and Cupesidæ, belongs to an old proto-coleopterous family.

DISCUSSION OF SYSTEM ADOPTED.

As to the isolation of the Adephaga there is no dispute; all authors are in agreement on that point and every character, whether drawn from the venation, the external or internal structure, the genitalia, or the larval characters, support it. The case is different, however, with the other groups. The separation of the Rhynchophora was proposed by Leconte and urged in special papers on the subject;[1] it has been endorsed by Sharp and, to a less degree, by Kolbe; it has been opposed by Lameere, Ganglbauer and Gahan on phylogenetic grounds because they think the Rhynchophora are plainly derived from the Phytophaga, or the two from a common source; it has also been opposed by Muir because the genitalia are of the same type as those of the Phytophaga, and in our country by Pierce.[2] Numerically the opposition would rule, but the following reasons support Leconte's view.

There can be little question that the Rhynchophora are the most specialized of all beetles, remarkably distinct by the characters discovered by Leconte, as well as by their legless larvæ and the great development of the snout. As I shall show presently, they seem to be the most recent also of all beetles. That the links connecting them with their ancestors, admittedly the Phytophaga (in part at least), have survived is a result of their recent origin and no argument against their isolation if their characters otherwise warrant it. Had all the links survived, the isolation of the Adephaga might be no greater than that of the Rhynchophora. After trying to give due weight to the arguments to the contrary, I can find nothing to balance the strong characters of rigid palpi and single gular suture originally developed by Leconte and repeated in the Rhynchophora of N. E. America,[3] and I am still disposed to follow Dr. Leconte in isolating Rhynchophora, but as a series, not a sub-order, for reasons given below.

The isolation of the Lamellicornia has also been recognized since the days of Burmeister.[4] They appear as a series in every system, no element has ever been added or subtracted, there are no other beetles

[1] Amer. Naturalist, VIII, 1874, pp. 385–396 and 452–470.
[2] Studies of Weevils, etc. (Proc. U. S. Nat. Mus. LI, 1916, pp. 461–473).
[3] Rhynchophora or Weevils of North Eastern America, Blatchley & Leng, Indianapolis, 1916.
[4] Handbuch der Entomologie, III, 1842.

that have the lamellate antennae or anything approaching them, except perhaps a few Scolytids. Dr. Sharp's course in treating them first, before even the Adephaga, is perhaps a consequence of their isolation being prominent in his thoughts. Dr. Leconte also considered but rejected the same course. The final disposition of this question must be left for the future; I am unwilling to add another sub-order, though I can see many reasons in favor of doing so; such reasons, however, are part of those that prevent me treating Rhynchophora as a sub-order.

The isolation of the Staphyliniformia by recent authors seems to be based on very strong grounds. In degree it may be less complete than that of Rhynchophora and Lamellicornia, for there are forms like *Sphaerites* that have been placed in Polyformia. But there must be such differences in degree of isolation of series, families, tribes, genera and species, for we can never expect an absolute equality in that respect.

The isolation of Phytophaga is even less complete; many authors unite them with Rhynchophora, others see a remote connection with some families of Polyformia. It is difficult indeed to frame a definition for them based on adult characters alone. Still the term has long been used and is perfectly understood as one admirably covering Cerambycidæ, Chrysomelidæ and Bruchidæ as a series of plant-eating families.

Still more difficult to define as a whole are the numerous smaller series here grouped under the names Polyformia, Palpicornia and Clavicornia. They are in fact what remains after separating the larger and more strongly characterized series. They include some series like Malacodermata and Sternoxia that though smaller in number of species involved are very distinct; the distinctions, however, occur in structures that have not been used in making primary divisions, and are perhaps in that sense of less importance. The Rhynchophora seem to me very nearly of the subordinal importance that Leconte gave them; those included above seem nearest to them in degree of important difference. I have reduced the Rhynchophora somewhat unwillingly because I feel that their isolation is less than that of Adephaga, but I cannot still further reduce them by elevating more, even of the best defined series in Polyformia, to equivalent rank.

Progressive Modification of Various Structures

Before discussing the sequence in which the series as defined above should be arranged, I would like to state the general conditions under which the order has become specialized in different directions and the general character of the specialization in a few important structures. As it seems to me the primitive habit of the Coleoptera must have been feeding upon a variety of decaying substances, animal and vegetable indifferently, and the first Coleoptera, newly derived from some even more primitive insect, must have been but poorly adapted to their work. It has been shown by Sandor Gorka [1] that the digestive system of such as still feed upon decaying substances is of the simplest form. The habit of feeding principally on animal matter, which characterizes the Adephaga, is accompanied in the larvæ as well as in the adults by adaptations of structure that in classification justify making of them a sub-order. The adaptation extends to the digestive system, which is highly specialized. The habit of feeding largely upon living vegetable tissue which characterizes the more specialized Phytophaga and nearly all the Rhynchophora is also accompanied by adaptations of structure, though in an entirely different direction. These adaptations extend, as in the Adephaga, to the digestive system and to the larvæ; and in the Rhynchophora, whose food is largely derived from the most recent developments of the vegetable kingdom, have reached a degree of specialization that justifies treating that group as the highest development of the sub-order Polyphaga, even if its comparatively recent origin permits of tracing its descent and forbids treating it as a sub-order.

The primitive beetles from which the two sub-orders have been derived are of course extinct, and their characters must be deduced from the theory just suggested. Being derived from some more primitive generalized insect form and being the progenitors of the existing forms, their structures must have been those common to both, but in degree of adaptation exactly the opposite of that found in the most specialized of existing forms. I have already pointed out that the tarsi of the primitive beetle must have been composed of five equal, unmodified joints and that tarsi of a less number of joints, or with joints adapted to swimming or digging, must be regarded as derivatives from the primitive form. Since, according to Dollo's Law,[2] a part once lost or reduced to a vestigial condition cannot be regained in progressive modification, a 3-jointed tarsus must be a derivative in comparison with a 4-jointed tarsus, not *vice versa*, and such tarsal appendages as lobes and onychium must be primitive indications, for they are lacking in highly specialized beetles, but present in many more primitive insects.

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[1] Allgemeine Zeitschrift fur Entomologie about 1913.

[2] See "A History of Land Mammals in the Western Hemisphere," New York, 1913, p. 656 The author, Wm. Berryman Scott, discussing the so-called law of irreversibility in evolution, decides that while it is perhaps not universally exemplified, deviations are certainly exceptional.

For similar reasons primitive elytra would be elongate, pubescent, and imperfectly adapted to the other parts of the body, because in the highly specialized beetles of each sub-order, they are short, glabrous, and very perfectly adapted to the parts they adjoin.

The hind wings in the primitive beetle should be efficient in flight, with veins similar to those of a generalized insect, *i. e.*, joined by cross-veins, if the studies of Comstock and Needham are accepted.

The abdominal segments would be the largest number known in existing forms, *viz*: eight.

The antennæ would be composed of eleven, similar, unmodified joints, pubescent, not geniculate.

The palpi would be composed of four, similar, unmodified joints; the triangular and securiform modification of the last joint are a specialization in one direction, often seen in Polyphaga; the gradual loss of flexibility and prominence, which attains its maximum in Rhynchophora, is apparently a specialization in an opposite direction, or atrophy from disuse.

The occurrence of ocelli is rare in beetles and is a primitive character, because ocelli are present in lower orders and lacking in the higher Coleoptera. In Cicindelidæ they are present in the larva only.

The presence of certain sutures, *viz*: the double gular suture, the propleural suture and the suture between the 2d and 3d abdominal pleuræ is a primitive character, because the general progressive modification from an elongate, loosely organized creature to a short, compact insect, with all its parts closely co-adapted, could only be accomplished by a fusion of parts that would obliterate such sutures.

The occurrence of some appendages to the legs, *viz*: membranous appendages to the claws, membranous lobes beneath the tarsi, the onychium (or arolium) and paronychium between the claws (treated by some authors as representing the pulvillus of lower orders) and the more or less distinct trochantin, is also an indication of primitive character; such appendages are never found in highly specialized beetles. The trochanter also in the exaggerated form found in some Carabidæ and Lampyridæ is a primitive character, being greatly reduced in specialized beetles.

In certain families, like Staphylinidæ, the effect of this modification of the general form is also seen in the character of the coxæ and their cavities, the broad and prominent coxæ being the primitive forms, often accompanied by an unusual development of the trochanter. The open coxal cavity, appertaining to a loosely organized beetle, is more primitive than the closed cavity.

Now while the Adephaga, with their acquired habit of eating flesh and its accompanying modifications of structure, are plainly derivatives of the primitive beetles that preceded them, it seems as if they might be the first great offshoot and, having preserved more of the primitive characters than the other sub-orders, were entitled to the first place, even though some other beetle may have better preserved one or more different primitive characters.

Tabular Comparison

In tabular form, using P for primitive, D for derivative and P D, counted as ½ D, where both primitive and derivative forms occur in the series, the sub-orders and series would stand as follows in respect to each character I have considered above:

	Elytra	*Wings*	*Tarsi*	*Abdomen*	*Antennae*	*Palpi*	*Lobes*	*Onychium*	*Ocelli*	*Pp. Suture*	*Gul. Sut.*	*Larva*	*Total*
ADEPHAGA	D	P	P	P	P	P	D	PD	D	P	P	P	= 3½D
POLYPHAGA:													
Palpicornia	D	D	PD	PD	PD	D	D	D	D	D	P	P	= 8½D
Staphyliniformia	D	PD	PD	PD	PD	PD	D	D	PD	D	P	P	= 7 D
POLYFORMIA:													
Cantharoidea	PD	D	P	P	PD	D	D	D	D	D	P	P	= 7 D*
Cupesoidea	D	P	P	D	P	D	D	D	D	P	P	D	= 7 D*
Teredilia	PD	D	P	P	P .	D	D	D	D	D	D	P	= 6½D
Mordelloidea	PD	D	D	PD	PD	D	D	P	D	D	P	P	= 6½D
Sternoxia	PD	D	P	PD	D	D	P	D	D	D	P	P	= 7½D
Macrodactylia	D	D	P	PD	D	D	D	D	PD	D	P	P	= 8 D
Dascilloidea	PD	D	P	D	D	D	D	D	D	D	P	P	= 9½D
Brachymera	D	D	P	D	D	D	PD	D	D	D	P	P	= 8½D
Clavicornia	D	D	PD	D	D	D	D	D	PD	D	P	PD	= 9½D
Coccinellidæ	D	D	D	PD	D	D	D	D	D	D	P	D	= 10½D
Tenebrionoidea	D	D	D	D	D	D	PD	D	D	D	P	PD	= 10 D
Bostrichoidea	D	D	PD	D	PD	D	D	D	D	D	P	D	= 10 D
LAMELLICORNIA	D	D	P	PD	D	D	D	PD	D	D	P	D	= 9 D**
Phytophaga	D	D	D	PD	D	D	D	D	D	D	P	PD	= 10 D
RHYNCHOPHORA	D	D	D	D	D	D	D	D	D	D	D	D	= 12 D

* In these series the broad coxæ and prominent trochanters are additional primitive characters.

** Somewhat higher rank than indicated must be assigned on account of nervous system.

The minor series that have been proposed are introduced under Polyformia, though I am not yet prepared to define or accept them all; the names are for the most part taken from Lameere. The totals show plainly the primitive character of Adephaga, the intermediate character of most of the Polyphaga, with the highly derivative character of the Rhynchophora. They apparently support also Lameere's first thought that Teredilia were very primitive beetles, and Verhoeff's claim for a relatively exalted place for Coccinellidæ; but I am unwilling to entirely subvert Leconte's sequence of families on such theoretical grounds, especially as the totals run so close that any small error would affect the result. I think, however, that this table shows that Leconte's serricorn families are more primitive than his clavicorn families so definitely that there remains no doubt his sequence should be reversed in that section of his work.

If Lamellicornia are compared, their formula would correspond neither with the highest rank that Ganglbauer gave them nor the lowly position assigned by Kolbe, but an intermediate place such as they occupy in the Leconte system. Ganglbauer has maintained, and is apparently supported therein by Dr. Gahan, that they are the most highly specialized of all beetles, in the antennæ, in the high degree of concentration of the nerve ganglia, and in the social instincts displayed by their highest tribe. He is opposed by Kolbe, who cites their 5-jointed tarsi and abdominal structure as strikingly primitive characters, and he might have included the frequent occurrence of the onychium. It appears also by Ganglbauer's own statements that the nerve ganglia are highly concentrated in the Rhynchophora also and he appears to have overlooked the occurrence of lamellate antennæ in certain Scolytids. I have therefore no hesitation in adopting approximately as far as Lamellicornia are concerned the results of the formulas given above, especially since they only corroborate those reached by Leconte and coincide with the sequence for the principal families to which we are accustomed.

The internal structures have also been studied and confirm more or less the results obtained from the study of the external structures. I know these data only from Dr. Gahan's paper, already quoted, in which he reviews the work of Escherich,[1] Emery,[2] Dufour[3] and Bordas[4] on sexual organs, ovaries and testes, Brauer[5] and Wheeler[6] on the Malpighian vessels, and Blanchard,[7] Brandt[8] and other anatomists on the nervous system. Korshelt and Heider[9] are also quoted as the latest review of these internal structures.

The phylogenetic deductions from the studies of internal structures by various authors are not entirely in accord, but taken as a whole confirm the primitive character assigned to the Adephaga. Their bearing upon the rank to be assigned to Lamellicornia is to elevate that

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[1] Zeitschr. fur Wissensch. Zool. LVII, 1894, pp. 620–641.
[2] Biol. Central. Bl. V, 1885, p. 652.
[3] Ann. Soc. Nat. VI, 1825.
[4] Ann Sc. Nat. Zool. et Pal. 8 ser. XI, 1900, pp. 283–448.
[5] Verh. zool. bot. Ges. Wien. XIX, 1869.
[6] Psyche, VI, 1893.
[7] Ann. Sc. Nat. 3 ser. Zool. V. 1846, pp. 273–279.
[8] Hor. Soc. Ent. Ross. XIV, 1878.
[9] Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere, Jena, 1902.

series above that which it would take from a comparison of external characters alone. This is one of the considerations that lead me to place it where I do. Special discussion of Palpicornia and some smaller groups will be found below.

An Alternative View of Phylogeny

I have thus far presented the phylogeny as developed by continental authors with but little interpolation of individual opinion. To complete the account of the bearing of their hypotheses upon the classification it seems necessary to point out that they are only fairly supported by part of the known facts and so contradicted by some others that it would be extremely injudicious to subvert an established classification on such theoretical grounds, though some modifications based thereon may be acceptable.

To my mind, the assumption implied in the phylogeny thus far presented, that of all the families of the protocoleoptera of pretriassic times, none have survived except those that were succeeded by Adephaga and Polyphaga (as defined by phylogenetic authors), is unwarranted. I can conceive of the great groups of flesh-eating Adephaga and plant-eating Phytophaga arising under favorable environment; and of other similar groups responding by increase in genera and species to various environments produced by geological changes, but I must maintain that the utter extinction of all the families of protocoleoptera that existed prior to the origin of such groups is improbable and that it is far more likely that some of the present small families, especially those of disconnected distribution, represent remnants of families that existed prior to the origin of the Adephaga.

The consequences of the false assumption may be seen in the failure of the phylogenetic scheme to coincide with the results obtained from study of genitalia, from study of larvæ, especially the blattoid forms, from study of digestive system, and other internal parts, all of which have been mentioned above. The remedy may lie in separating from the mass called Polyphaga all the small families with primitive characters in the adult and larva, and treating them phylogenetically as more primitive than Adephaga. It is not, however, my purpose to propose a new system of phylogeny, but rather in this paragraph to point out the defects of that already presented as a reason for not following any phylogenetic theory in arranging the sequence of families beyond the point at which it is in approximate accord with a sequence otherwise established.

I cannot refrain from inserting a few words on environmental adaptation. I have already alluded to the three-fold division of the Coleoptera indicated by the digestive system. This is in a measure confirmed by the modifications of the palpi. In papers read before the New York Entomological Society some years ago, but still unpublished, I tried to show that while the chief environmental factor for plants might be moisture, for beetles it was certainly food; and profound structural modifications were correlated therewith. This is naturally nowhere more marked than in the mouth parts and especially in the palpi. Assuming, as I feel compelled to do, the habit of feeding (possibly in very moist, swampy localities) on decaying matter, vegetable and animal indifferently, as the primitive habit of beetles, it is found to be associated with the simplest form of digestive apparatus and with mouth parts of varied form, but extreme in no direction.

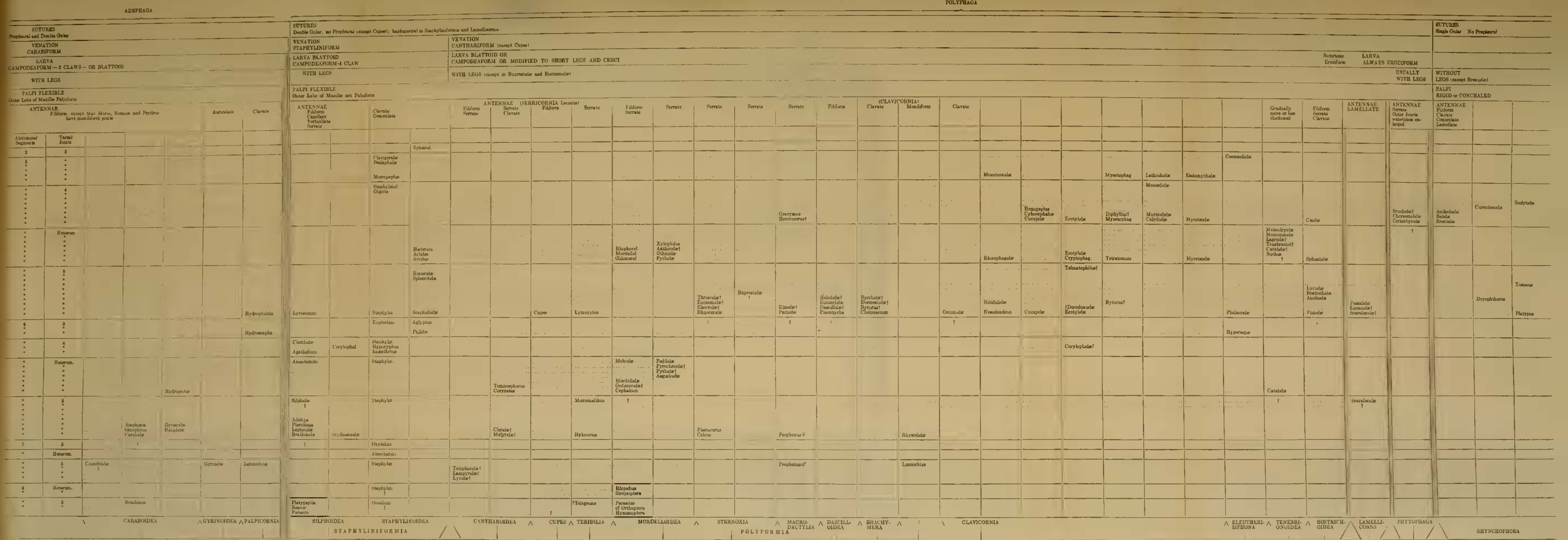
It is noteworthy also that among such forms the blattoid larva is also most frequently found. The habit of feeding on animal matter is associated with a more complex digestive system and with the equivalent of six palpi. The habit of feeding on living vegetable tissue is associated with an equally complex, but different digestive system, and a gradual atrophy of palpi, practically complete in the highly derivative Rhynchophora.

It may still be true that the extinction of the most primitive of polyphagous families leaves the Adephaga possessed now of the greatest aggregate of primitive characters (as indicated on p. 21), but if such be the case, it does not necessarily imply an origin for them antecedent to that of all Polyphaga. While, therefore, I place Adephaga first, my doing so is more because Leconte did so than because I believe they are more primitive than every family of Polyphaga; and while I have arranged the families of Polyphaga in accordance with the phylogenetic table on p. 21, including with them Rhysodidæ and Cupesidæ, it is not my intention to conceal the heterogeneous character of the assemblage. It seems better, however, to retain existing errors if such there be, rather than to risk introducing new ones on no better basis than disputable phylogeny.

Explanation of Chart

Having thus established with a fair degree of certainty the sequence in which the series should be placed, I will now endeavor to exhibit the position, in the series, in which the families and some of their most

CHART ILLUSTRATING PHYLOGENETIC RANK OF FAMILIES OF COLEOPTERA



† indicates additional primitive characters.

peculiar tribes should be placed, if the more primitive are to precede the more derivative. On the accompanying chart vertical lines indicate separations based respectively on the sutures, the venation, the larva, the palpi and the antennæ, the left hand columns being the most primitive; horizontal lines indicate separations based on the number of abdominal segments and number of tarsal joints, the most primitive being at the bottom of the sheet. A dagger indicates the primitive characters of tarsal lobes, onychium, ocelli, soft, pubescent, elytra ill adapted to the body, or trochantin visible. All the characters used in the tabular presentation are thus included; and the sequence of the series is substantially the same as I there employed.

I think it will be seen at a glance that in a general way the sequence of the families proceeds quite regularly from the lower left hand corner of the chart to the upper right hand corner, that is, from the most primitive in respect of the twelve important characters used to the most derivative. In certain cases, however, a primitive series, Staphyliniformia for example, runs higher in abdominal or tarsal development than the more derivative series that follow. If one used those characters only a false idea of the position of the series would result; and I believe Verhoeff's conception of Coccinellidæ as a sub-order is an actual example of such a result. I have tried to incorporate in this chart all the characters that have been used to obtain a balanced result. In many of the series, a single or a few genera are placed below the bulk of the families on account of their possessing more primitive abdominal or tarsal characters. This appears to indicate the survival in that series of some of the more primitive forms, forms that in most of the series have become extinct. While such cannot be entirely disregarded, I think it would be a mistake to class the series according to these survivals alone. Some extraordinary forms are tentatively placed. Parasitic insects are regarded as a result of degradation, rather than as a primitive indication. If *Telegeusis* is correctly placed in Teredilia, it may be necessary, as Lameere did, to place that series first of the Polyphaga, but its affinities are still disputed.

I should like to be able to discuss the considerations that have caused me to put each family in the position assigned in the series and continue the same treatment for each tribe in the family, but that is not now practicable. I will, however, briefly review each series, giving the Adephaga and Staphyliniformia the most space. For the purpose of bringing the terminology into harmony with that of other orders of insects, I have, at the suggestion of Dr. J. Chester Bradley, used words ending in oidea except for sub-orders.

ADEPHAGA

As defined by Leconte, the families included are, Cicindelidæ, Carabidæ, Haliplidæ, Amphizoidæ, Dytiscidæ and Gyrinidæ. Omophronidæ may be separated from Carabidæ as suggested by Kolbe and Lameere and Rhysodidæ has been added by many. As indicated above I believe, however, that Rhysodidæ is one of the nearly extinct branches of the primitive Coleoptera that originated while they still possessed hind wings with cross-veins, divided first abdominal segment, and propleural suture, characters that are shared by Adephaga. I have expressed by a query the reply of Mr. Schwarz to a direct question as to its position "We do not even know how to spell its name;" but, in default of a surely better place, I have left them as Leconte did, near the beginning of the Clavicorns.

Two series are indicated in Adephaga as follows:

Eyes two, soles of tarsi beneath as usual, antennæ filiform . . . . . CARABOIDEA.
Eyes four, soles of tarsi lateral; antennæ auriculate . . . . GYRINOIDEA.

The second series consists of one strongly isolated family; the first series may be divided into six families as on p. XXX of Leconte's classification, with Omophronidæ separated from Carabidæ by the character given on p. 6 "prosternum prolonged and dilated, entirely concealing the mesosternum." The larva of *Omophron* is aquatic and the family seems intermediate between Carabidæ and Haliplidæ. There may be still other families incorrectly included with the Carabidæ which are an assemblage of somewhat heterogeneous character. While the antennæ are usually filiform, three genera have them moniliform; while the larvæ are usually compodeaform, there are some exceptions and these are correlated with exceptional adult characters. Their classification has been worked over by Latreille, Bonelli, Dejean, Schaum, Erichson, Schioedte, Lacordaire, Leconte, and owes its present form to G. H. Horn. I am sorry that Lameere finds the last, in which I know the author took great pride, "detestable"; and it certainly is far from according with views based on phylogeny, which would bring *Elaphrus* nearer to Cicindelidæ, and *Brachinus*, with its pubescent elytra poorly adapted to the body and 8-segmented abdomen, both primitive characters, near the first; with the tribes like Pterostichini and Bembidiini, in which the glabrous elytra have developed the internal plica, near the end. The palpi also indicate a highly derivative position for Carabini and Bembidiini; while the Lebiini, by their truncate elytra, bright colors, and arboreal habits seem to constitute an isolated group, perhaps even higher in rank.

The abdomen has always six or more segments in Adephaga, seven in Cicindelidæ ♂ and in Gyrinidæ, eight in the genus *Brachinus*. The tarsi are 5-jointed throughout, but in *Hydroporus* the front and middle tarsi are apparently 4-jointed, the fourth joint being either actually wanting or concealed by the deeply lobed third joint. Ocelli are wanting in the adults, but very perfect in the larvæ of Cicindelidæ. In the Carabidæ a striking peculiarity is the development of tactile setæ. These are wanting in the genus *Oodes* and the aquatic Adephaga; also in the subfamily Pseudomorphinae, which is also remarkable for its short legs and rigid tarsi. Still another large group is characterized by fossorial legs, by which it aids its underground operations, and by pedunculate thorax. The position of *Amphizoa* is a matter of doubt; but I have not attempted to make any changes in the place at present assigned to it or other divisions. The sequence follows American precedents because there is no other at present available.

POLYPHAGA

The number of families in this sub-order is so great that it will be most convenient to consider the divisions. I use the terms that have been suggested by Lameere principallv, adding Mordelloidea for the remainder of the old series Heteromera, after separating Tenebrionoidea.

PALPICORNIA or HYDROPHILOIDEA

The great length of the palpi, exceeding that of the antennæ in the most derivative forms, but far less developed in the primitive sub-families, gives this series its name. In Dr. Leconte's system the principal families included follow the Adephaga, and I have made no alteration. The campodeaform larva of the Hydrophilidæ seems to support Dr. Leconte's view. The phylogeny has been carefully studied by d'Orchymont;[1] he arranges the sub-families in the following order, *viz*: Hydræninæ, Limnebiinæ and Spercheinæ (not American) as the more primitive, and Helophorinæ, Epimetopinæ, Hydrochinæ, Sphæridiinæ, Hydrophilinæ, as the more derivative; and agrees with Handlirsch and

[1] Ann. Soc. Ent. Fr. LXXXV, 1916, pp. 91–106; and 235–240.

Peyerimhoff that they should follow Staphyliniformia. He admits, however, some doubt pending further study of the more primitive Silphidæ, wherefor the theoretical reason seems an insufficient basis for a change in the sequence to which we are accustomed. The sub-family Hydroscaphinæ has been added by Dr. Böving [1] as closely allied to Limnebiinæ; the larvæ of both are very similar to those of such Staphy linidæ as *Tachinus* and *Tachyporus*. The sum of all the characters, (see table on p. 21) seems to me to indicate a higher rank phylogenetically than is conceded by any of the authors named, but this may result from attaching too much importance to the acquired characters due to aquatic environment in most of the sub-families; and on the whole it seems best to continue to place, as did Dr. Leconte, this series immediately after the Adephaga. As I had some trouble in finding the reference, it may be added that Handlirsch (p. 1277) announces that Ganglbauer had verbally agreed to the separation of Palpicornia as a series.

BRACHELYTRA or STAPHYLINIFORMIA or STAPHYLINOIDEA

This division possesses, according to Ganglbauer and Lameere, the most simple form of wing venation, without either cross-veins or hook-veins, but if I correctly apprehend Comstock and Needham's theory of tracheation, while apparently simple, it is not primitive, but a derivative from the more primitive form with cross-veins. By omitting Phalacridæ it comprises all the families in Leconte's system from VII to XIX that follow Hydrophilidæ. These families all have more or less short elytra, and at least three dorsal abdominal segments corneous. They have a distinctive type of genitalia. The larvæ of many at least are campodeaform and greatly resemble Adephagous larvæ except that they have only one claw. Everything therefore indicates that they should precede other Polyphaga; the comparatively large number of derivative characters shown in the table results from including the more derivative forms of this very large group and would be somewhat reduced if cognizance were taken of their primitive coxæ and trochanters.

I have followed Ganglbauer's treatment in the "Käfer von Mitteleuropa" almost exactly. Readers of Leconte's classification will note that it embodies also most of his ideas. The Leptinidæ, with 11-jointed, filiform antennæ, *Pteroloma*, with the same antennæ and Carabid-like

[1] Notes on the Larva of Hydroscapha (Proc. Ent. Soc. Wash. XVI, 1914, pp. 169–74.)

form, and especially *Brathinus*, with both these characters and ocelli to boot, seem to me more primitive than the Scydmaenidæ and Silphidæ, with clavate antennæ, often 10- or 9-jointed, that Ganglbauer puts first. Also the method of counting the number of abdominal segments has been questioned by Verhoeff, and if erroneous, as he thinks, would remove the last reason for putting Staphylinidæ before Silphidæ. In reference to *Brathinus*, Casey[1] has urged its being placed in Omaliini on account of its having the ocelli characteristic of that tribe of Staphylinidæ, but it lacks so many of the other characters that I have placed it as a family (following Leconte's earlier idea) near Leptinidæ and primitive Silphids like *Pteroloma*. For these few changes in Ganglbauer's treatment I am responsible.

The following table shows the diversity of abdominal, tarsal and antennal structure in the Staphyliniformia which have led to the changes that have been made in Leconte's system:

Abd.	*Tarsi*	*Antennæ: Filiform*	*Clavate*	*Capitate*	*Verticillate*	*Capillary*	*Moniliform*	*Geniculate or simple*
3	3		*Sphæridius* 11					
5	3			*Microp.* 9				
5	3		*Pselaph.* 2–11				*Pselaph.* 11	
5	4							Oligota 10
5	Het							*Hister* 11
5	5	Lyrosomini 11	Colones 11	*Sphæriles* 11		*Scaphid* 11		"
6	3		Aglyptus 11		*Ptilidæ* 11			Euplectini 11
6	4		Clamb. 9–11					Euaesthetus 11
6	4		Agathidium 11					Hypocyptus 10
6	4			*Coryloph* 11				
6	Het		Anisot. 10–11					
6	5		"			*Habroceri* 11		Megalops 10
6	5	Adelops 11	Choleva 11					
6	5	Pteroloma 11	Silpha 10–11					
6	5	Leptinus 11	*Scydm.* 11					
6	5	*Brathinus* 11						
7	3							Oxytelini 11
7	5							Staphylin 11
7 to 8	Het		*Antennæ Fringed*					Aleoch. 10–11
8	5		*Platypsylla* 10					Omaliini 11

It must be evident from this table how little value for separating series the number of tarsal joints has, for every combination from eight abdominal segments with five tarsal joints, the most primitive known in existing beetles, up to three abdominal segments with three tarsal joints, nearly the most derivative known is included. The number of antennal

[1] In letters, and Ann. N. Y. Acad. Sci. IX, 1897, p. 354.

joints is shown after every name and runs from eleven to two, the latter in the Pselaphids that live with ants. A great variety of forms of antennæ is also indicated and might even be extended, for in one genus of Silphidæ (*Captotrichus*) the antennæ are serrate, and there are variations in the number of joints forming the club and in the compactness of the club that are not indicated.

There are also special characters belonging to many of the groups that are not indicated, as the ocelli of *Brathinus* and Omaliini, the fringed wings of Ptilidæ, the parasitic break-down of many characters in Platypsyllidæ, etc.

The peculiar larval characters of Corylophidæ,[1] Histeridæ, Scaphidiidæ are also omitted; but as an indication of isolation, either in adult or larval characters, I have italicized certain names. Omitting them, the remainder appear to compose two series, Silphoidea and Staphylinoidea, to which the more isolated families are for the present attached as aberrant branches. Handlirsch considered the Histeridæ as an early offshoot from Staphylinoidea; it may be necessary to separate them at least as another series.

MALACODERMATA or CANTHAROIDEA

The Lampyridæ of Leconte, divided into Lycidæ, Lampyridæ, Telephoridæ, Phengodidæ and Drilidæ by more recent authors, possess very primitive characters in their 7-segmented abdomen, 5-jointed tarsi, and broad elytra, not co-adapted to the body, and also pubescent in the more primitive forms. The coxæ and trochanters are of the exaggerated form seen only in primitive beetles, and they have also the soft texture of generalized insects. Brauer's Law might also be invoked to support the primitive character of the Malacodermata in view of the larviform females of some species. With them may be associated the families of Kolbe's series Trichodermata [2] where the texture becomes firmer, the abdominal segments six, and the tarsi even reach the heteromerous condition in *Temnopsophus* and *Corynetes*. The heteromerous tarsi of Othniidæ are therefore no reason why it also should not be included.[1] The antennæ exhibit a wide modification as in the preceding division, being filiform in the lowest forms, serrate in the bulk of the

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[1] Since this introduction was written Mr. Schwarz has advised placing Othnius near Pythidæ; the position assigned to Corylophidæ is also seriously questionable.

[2] Handlirsch (p. 1277) inclines to tracing a different line of descent for Trichodermata on account of difference in number of Malpighian vessels.

series and finally clubbed in the most derivative forms. Their modifications in this series illustrate the difficulty of applying Leconte's Serricorn and Clavicorn divisions, for both forms are found in this as in the preceding series.

The larvæ are imperfectly known, but apparently carnivorous, the more primitive families on or in the ground, the higher families in trees, *Corynetes* in hams, etc.

ARCHOSTEMATA or CUPESOIDEA

The first name has been proposed by Kolbe for the small family Cupesidæ, which includes the genus *Cupes* in North America and the genus *Omma* in Australia. They have been placed in Adephaga on account of their cross-veined wings and propleural sutures, but lack the divided first ventral segment. Their 5-segmented abdomen forbids considering them as of equal primitive rank with Adephaga, but their 5-jointed tarsi and filiform antennæ are certainly primitive. Until recently the larva was unknown, but the work of Snyder [1] finally clears up that mystery. To me, in view of the larva greatly resembling primitive Polyphaga like Teredilia, they seem to be the modified survivors of an old polyphagous series, properly placed by Kolbe by themselves, but as indicated by Leconte, near his Serricornia.

TEREDILIA or LYMEXYLOIDEA

The genus *Hylocoetus*, which with *Lymexylon*, composes this small series, seems in many of its characters, extremely like the most primitive beetles. Six ventral segments, five tarsal joints, soft integuments, elongate form, badly adapted, pubescent elytra, are all primitive characters. It has, however, serrate antennæ, large, stout palpi and no ocelli or onychium, and must be a derivative. *Atractocerus*, an exotic form, has short elytra like the Staphylinidæ. Handlirsch dissents totally with Lameere as to Teredilia. *Telegeusis* has been included, on account of a verbal communication regarding its genitalia, but as a family, Telegeusidæ, on account of its otherwise divergent characters. Micromalthidæ are also included, though some of my friends prefer to attach them to preceding series.

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[1] Record of the Rearing of Cupes concolor (Proc. Ent. Soc. Wash. XV, 1913, pp. 30–31).

MORDELLOIDEA

It is with great hesitation that I propose the interpolation at this point of a series composed of those families possessing heteromerous tarsi and comparatively soft integuments. If, however, the elongate body, 6-segmented abdomen, elytra poorly co-adapted to the body and pubescent, claws with appendage, have any phylogenetic meaning their combination in Cephaloidæ must indicate that family as one of the most primitive ones, while the larvæ of Mordellidæ and Oedemeridæ seem to tell a similar story. I have already mentioned the conclusion of Sharp and Muir from study of genitalia, *viz*: that such families must be separated from the Tenebrionidæ; and I can see no better place for them than one following (on account of their more derivative tarsi) the other soft beetles. The publication of Dr. Böving's larval studies may, however, supply more information. In some of the families here included the modification of some structures seems to have been very great, as in the overlapping elytra of *Meloe* for example; and these modifications, like others that have been noticed, are correlated with parasitic habits. An extraordinary multiplicity of specific differences also, as usual, mark some of the higher genera, like *Anthicus;* but in spite of such difficulties I hope this union of families into a series or possibly two series if Meloidæ requires greater separation may prove correct.

STERNOXIA or ELATEROIDEA

This series seems to have met with considerable approval. I had at first separated Buprestidæ on account of their distinctive larval characters, but the *Rhaeboscelis* larva discovered by Weiss and Nicolay is intermediate and perhaps Cebrionidæ should also be withdrawn for similar reason. The prolongation of the prosternum seems, however, to warrant keeping the series intact.

MACRODACTYLIA or DRYOPOIDEA

This series seems to be naturally defined by the extraordinary development of the claws. Its elements are not greatly disputed, but forms like *Placonycha* can only be placed with certainty by knowing the larva.

DASCILLOIDEA

Closely connected with Macrodactylia through the larval resemblance of *Psephenus* and *Placonycha*, the component parts of Leconte's family Dascillidæ seem to indicate several modified survivals of an ancient group, from which possibly the Phytophaga may have also originated. Their aquatic habits seem like an inheritance from primitive ancestors, but they have acquired a higher degree of specialization than many other of Leconte's Serricorns. Some of the genera now included in Dascillidæ may have to be removed therefrom when the larvæ are better known.

BYRRHOIDEA

Byrrhidæ and Dermestidæ are here drawn together with Byturidæ as an offshoot, apparently by its lobed tarsi of most primitive character. Taken collectively, they seem to have preserved more primitive characters than most of Leconte's clavicorn series and should therefore precede the more derivative Clavicornia.

BOSTRICHOIDEA

Leconte's family Ptinidæ, divided into several sub-families by him that have since been raised to families, constitutes the bulk of this series, with Sphindidæ and Cisidæ added though the Sphindidæ may also be related to the next series. The antennæ in the primitive forms are filiform, but rapidly become clavate; this series, like the last, refuses to be classified by the antennal characters.

CLAVICORNIA or CUCUJOIDEA

This series is copied from Ganglbauer, but with Byrrhoidea and Coccinellidæ removed. Some of my friends advocate including Byturus on account of its close relation to Mycetophagidæ. It is still very heterogeneous and requires more study. It seems to me to unite, without a sufficient bond, the remnants of several ancient groups; but no one has yet succeeded in detecting their characteristics. Handlirsch separates the family Cucujidæ as a separate series.

COCCINELLOIDEA

It is with the hope that Verhoeff is partly right in claiming a special place for this family that I have separated them. The phytophagous-like larva of *Hyperaspis* as described by Böving,[1] the extraordinary larvæ of the other genera, seem to justify this course, as well as the adult characters. Handlirsch (p. 1277) suggests their having become separated from Clavicornia at a very early period.

TENEBRIONOIDEA

This series restricted to Cistelidæ, Monommidæ, Lagriidæ, Tenebrionidæ and part of the Melandryidæ, seems fairly consistent, all having the margins of the ventral segments semi-membranous. Like the Clavicornia, the differences in the larvæ seem to indicate more than one origin if their descent could be completely traced. The position here assigned to Tenebrionoidea is relatively high among the series as the result of adopting Sharp and Muir's views as to the significance of the characters they found in the genitalia. If the differences between the genitalia of Mordelloidea and Tenebrionoidea should prove to be only progressive modifications of a single type, as is possible, the position of Tenebrionoidea might be altered, to follow that of Mordelloidea, Cephaloidæ and Oedemeridæ forming a connecting link. Larval resemblances when worked out, may determine this point.

LAMELLICORNIA or SCARABÆOIDEA

Have been discussed above. Handlirsch is singularly silent as to the rank of this series, possibly from disagreement with Ganglbauer. Troginæ may probably require elevation to family rank, as indicated in conspectus on page 38.

PHYTOPHAGA or CERAMBYCOIDEA

Here there seems to have been a modification of the palpi from an enlarged last joint to a partial atrophy, quite the reverse of that observed in previous series and possibly the result of their plant-eating

[1] A Generic Synopsis of Coccinellid Larvæ, etc. (Proc. U. S. Nat. Mus. LI, 1917, pp. 621–650).

habits. They have been commonly divided into Cerambycidæ, Bruchidæ and Chrysomelidæ, but the last division should probably be much subdivided, in harmony with the habits and character of the larvæ. Handlirsch (p. 1279) says there have been at least three lines of descent.

RHYNCHOPHORA

Have been lately discussed in the "Rhynchophora of N. E. America." I have only to add a reference to Dr. Sharp's studies [1] by which *Ithycerus* is shown to belong to the family Belidæ; and Dr. Pierce's recent studies,[2] with which I cannot agree in some points, especially in the transfer of Scolytidæ from Rhynchophora to Phytophaga on the basis of tarsal characters, which have been discussed at length above. The characters developed by Leconte, the rigid palpi and the single gular suture, seem to me to exceed in importance both tarsal and beak characters. The union of Phytophaga and Rhynchophora into a single series has frequently been proposed, but there are weighty reasons against doing so; I am free to say that one of the results of my study has been to discourage all such forced unions and to seek the true lines of descent by isolating aberrant forms. It is quite likely that the resemblance of *Choragus* to the Cryptocephalini, of other Anthribids to the Bruchidæ and of certain Cossonids to Clavicornia, indicates more than one line of ancestry for the Rhynchophora; it may also be urged that the resemblance between certain Scolytids and the Bostrichidæ is the result of convergence following similar habits.

CONCLUSION

Such matters, however, are outside the domain of the present essay. My object has been to study the phylogeny of the Coleoptera sufficiently to arrange the families as they exist at the present time, substantially in accordance with their relative degree of derivation from the primitive beetles. And even if it could be conclusively shown that Rhynchophora were descended entirely from Phytophaga, and they in turn from Dascilloidea, which I do not believe, it would not justify a corresponding arrangement of the catalogue. So far from being conclusively shown are such speculations regarding the origin of Rhynchophora, and the

[1] Journ. N. Y. Ent. Soc. 1918, pp. 215–218.
[2] Proc. U. S. N. M. LI, 1916, pp. 461–464.

haplogastral resemblance of Staphylinidæ and Lamellicornia urged by Kolbe, that authors are not even agreed upon the origin of the order Coleoptera. While the study of phylogeny is of absorbing interest, carrying us back far beyond historical or even glacial times, for Lyell[1] speaks, perhaps in error, of beetles in the Carboniferous Epoch, it may never, from the scarcity of early fossil insects, have enough facts to prove or disprove some of the extreme views that have been advanced. Disregarding them the phylogenetic consideration of the modifications of beetle structure, as given by Lameere, Ganglbauer and Kolbe and analyzed by Gahan, seems to warrant the few changes in the Leconte classification that I have adopted.

My final conclusion is, that bearing in mind the speculative character of the phylogeny of the Coleoptera, and the failure of any theory thus far advanced to reconcile all the facts of larval, adult and fossil studies, it would be premature to base any radical changes in Leconte's classification thereon. The division of the order by recognition of the Adephaga as a sub-order seems to have become established since Dr. Leconte's time; but the inclusion in Adephaga of Rhysodidæ and Cupesidæ on the basis of venation and propleural sutures is forbidden by every other character we have considered. The division of the remainder of the Coleoptera into more series than Leconte contemplated seems also to be justified; and the arrangement of these series in such sequence as their phylogenetic rank suggests seems, though still somewhat open to argument, better than one based on the assumed importance of tarsi, antennæ or any other separate structure, or even partial combination of structures. Acting upon these ideas I have altered the place assigned by Dr. Leconte to the heteromerous series and reversed the relative position of his serricorn and clavicorn families, because I believe the latter are plainly the more derivative. Some minor changes, as in family names and division of families, have been made to harmonize our list with recent European research, but these do not affect the main principles of the classification. The net result is given below in a conspectus of families.

In closing these remarks, intended to explain as well as I can the reasons for making some changes that seemed unavoidable, I wish to express my appreciation of the kindness of some friends, especially Wm. T. Davis and Andrew J. Mutchler, who have frequently discussed the matters involved, and E. A. Schwarz and Herbert S. Barber, whose criticism of my first results, and communication of unpublished larval

[1] Elements of Geology, 1868, p. 494.

studies, were of prime assistance. The criticisms of Dr. Joseph Bequaert and Mr. Charles Schaeffer, while my remarks were under discussion at meetings of the New York Entomological Society, also saved me from some errors. Finally, Dr. Frank E. Lutz has been good enough to read the Mss. from the standpoint of general biology and evolution, and Dr. Adam Böving has, with great generosity, told me of some results of his deep studies of the larvæ of Coleoptera, in advance of his own publication thereof, thereby enabling me to indicate some, at least, of the points of difference.

CONSPECTUS OF FAMILIES OF COLEOPTERA

Following Leconte Classification, modified to accord with recent phylogenetic studies, and embodying changes in family names required by priority:

Sub-order **ADEPHAGA**

Caraboidea: 1. Cicindelidæ, 2. Carabidæ, 3. Amphizoidæ, 4. Omophronidæ, 5. Haliplidæ, 6. Dytiscidæ.

Gyrinoidea: 7. Gyrinidæ.

Sub-order **POLYPHAGA**

Hydrophiloidea: (= *Palpicornia*) 8. Hydrophilidæ (including *Hydroscaphinæ*).

(*STAPHYLINIFORMIA* or *BRACHELYTRA* auct.).

Silphoidea: 9. Platypsyllidæ (= *Acreioptera* Westw.), 10. Brathinidæ, 11. Leptinidæ, 12. Silphidæ, 13. Clambidæ, 14. Scydmaenidæ, 15. Orthoperidæ? (= *Corylophidæ*).

Staphylinoidea: 16. Staphylinidæ, 17. Pselaphidæ, 18. Clavigeridæ, 19. Ptilidæ? (= *Trichopterygidæ*), 20. Scaphidiidæ, 21. Sphaeritidæ, 22. Sphaeriidæ, 23. Histeridæ?

(*POLYFORMIA* auct.) (*SERRICORNIA* in part).

Cantharoidea: 24. Lycidæ, 25. Lampyridæ, 26. Phengodidæ, 27. Cantharidæ, 28. Melyridæ (= *Malachiidæ*), 29. Cleridæ, 30. Corynetidæ.

Lymexyloidea: ? = (*Teredilia*) 31. Telegeusidæ? 32. Lymexylidæ, 33. Micromalthidæ?

Cupesoidea (= *Archostemata*) 34. Cupesidæ.

Mordelloidea: ? 35. Cephaloidæ? 36. Oedemeridæ? 37. Mordellidæ, 38. Rhipiphoridæ, 39. Meloidæ? 40. Eurystethidæ (= *Aegialitidæ*), 41. Othniidæ, 42. Pythidæ, 43. Pyrochroidæ, 44. Pedilidæ, 45. Anthicidæ, 46. Euglenidæ (= *Xylophilidæ*).

Elateroidea: (= *Sternoxia*) 47. Cerophytidæ, 48. Cebrionidæ, 49. Plastoceridæ, 50. Rhipiceridæ, 51. Elateridæ, 52. Eucnemidæ, 53. Throscidæ (or *Trixagidæ*), 54. Buprestidæ.

Dryopoidea: 55. Psephenidæ? 56. Dryopidæ (= *Parnidæ*), 57. Elmidæ, 58. Heteroceridæ, 59. Georyssidæ.

Dascilloidea: 60. Dascillidæ, 61, Eucinetidæ, 62. Helodidæ (or *Cyphonidæ*).

Byrrhoidea: 63. Chelonaridæ, 64. Dermestidæ, 65. Byrrhidæ, 66. Nosodendridæ.

(*CLAVICORNIA* auct.).

Rhysodoidea: ? 67. Rhysodidæ?

Cucujoidea: 68. Ostomidæ? (= *Trogositidæ*, *Temnochilidæ*), 69. Nitidulidæ, 70. Rhizophagidæ, 71. Monotomidæ, 72. Cucujidæ, 73. Erotylidæ, 74. Derodontidæ? 75. Cryptophagidæ, 76. Byturidæ, 77. Mycetophagidæ, 78. Colydiidæ, 79. Murmidiidæ, 80. Monoedidæ (= *Adimeridæ*), 81. Lathridiidæ, 82. Mycetæidæ, 83. Endomychidæ, 84. Phalacridæ, 85. Coccinellidæ (= *Eleutherosiphona*).

Tenebrionoidea: ? 86. Alleculidæ (= *Cistelidæ*), 87. Tenebrionidæ, 88. Lagriidæ, 89. Monommidæ, 90. Melandryidæ?

Bostrichoidea: 91. Ptinidæ, 92. Anobiidæ, 93. Bostrichidæ, 94. Lyctidæ, 95. Sphindidæ? 96. Cisidæ.

(*LAMELLICORNIA* auct.).

Scarabæoidea: 97. Scarabæidæ, 98. Trogidæ, 97. Lucanidæ, 100. Passalidæ.

(*PHYTOPHAGA* auct.).

Cerambycoidea: 101. Cerambycidæ, 102. Chrysomelidæ, 103. Mylabridæ (= *Bruchidæ*).

(*RHYNCHOPHORA* auct.).

Brentoidea: 104. Brentidæ.

Curculionoidea: 105. Belidæ (*Ithycerus*), 106. Platystomidæ (= *Anthribidæ*), 107. Curculionidæ.

Scolytoidea: 108. Platypidæ, 109. Scolytidæ.

The family Stylopidæ (of previous lists) is here regarded as an order, Strepsiptera, and is treated in an appendix.

Certain changes were made in this conspectus after Mr. E. A. Schwarz had read the galley proof, whereby the position of Othniidæ and Byturidæ was altered and Trogidæ was raised to family rank. The serial numbering had however, been completed so that it was not practicable to make corresponding changes therein. The position of other families has also been criticized as well as the composition of the Mordelloidea and Tenebrionoidea; such comments by Mr. Schwarz, Dr. Böving and other friends are indicated by ? after the name. The conspectus thus shows some of the uncertainties that still remain in the classification of Coleoptera as well as the progress that has been made.

Stilbus Seid.
10828. pallidus Csy. 93–127 R.I. Mass. N.Y.
29. apicalis (Melsh.) 46–102 N.Y.-So.Cal. Ind. Ct.
consimilis Marsh. ‡ nec Melsh. Fla. L.Sup.
30. shastanicus Csy. 16–58 Cal.
31. probatus Csy. 16–59 Ia. N.Y. Man.
32. nanulus Csy. 93–131 Tex.-So.Cal.
33. limbatus Csy. 16–59 Fla.
34. ludibundus Csy. 16–60 N.Y.?
35. floridanus Csy. 93–129 Fla.
36. finitimus Csy. 16–61 Ia. N.Y.
37. obscurus Csy. 93–130 Ia. Ill. Minn.
38. sphæriculus Csy. 16–61 R.I.
39. fidelis Csy. 16–62 Fla.
40. prudens Csy. 16–62 Fla.
41. obtusus (Lec.) 56–17 So.Cal.
42. apertus Csy. 16–63 So.Cal.
43. notabilis Fall 01–230 So.Cal.
44. nitidus (Melsh.) 46–102 L.I. Fla. Tex. Ind. L.Sup.
45. convergens Csy. 93–134 Fla.
46. trisetosus Csy. 16–64 Va.
47. ludovicianus Csy. 16–65 La.
48. aquatilis (Lec.) 56–17 So.Cal.
49. thoracicus Csy. 16–66 N.Y.
50. attenuatus Csy. 93–135 Tex.

Stilbus Seid.
10851. quadrisetosus Csy. 16–66 Mich. L.I.
52. ochraceus Csy. 16–67 Cal.
53. belfragei Csy. 16–67 Tex.
54. modestus Csy. 93–133 Tex.
55. pusillus (Lec.) 56–17 D.C. Fla.
56. abbreviatus Csy. 16–68 Fla.
57. galvestonicus Csy. 16–69 Tex.
58. subalutaceus Csy. 93–133 N.J.
59. angustus Csy. 16–70 Va.

Leptostilbus Csy. 16–71
10860. rutilans Csy. 16–72 Tex.
61. concinnus Csy. 16–72 Miss.
62. elongatulus (Csy.) 93–136 Fla.

Litochrus Er. 45–108
10863. pulchellus Lec. 56–17 Fla. Tex.
64. crucigerus Csy. 93–138 Fla.
65. immaculatus Csy. 93–139 N.J. S.C. Fla.
66. aterrimus Csy. 93–140 Fla.

Erythrolitus Csy. 16–85
10867. rubens (Lec.) 56–16 N.C. Fla. Ind.

Litochropus Csy. 93–140
10868. scalptus Csy. 93–141 N.C. D.C.
69. clavicornis Csy. 16–86 Tex.

Ochrolitus Sharp 89–256
10870. tristriatus Csy. 93–142 Fla.

COCCINELLIDÆ

Mulsant 51, 53, 66; Crotch 73, 74; Leconte 80; Casey 99, 08; Leng 03, 08, 11; Johnson 10

COCCINELLINÆ

Hyperaspini

Hyperaspis Chev. 35–459
(*Oxynychus* Lec. 50–238)
(*Cleothera* Muls. 51–541)
10871. bolteri Lec. 80–186 Ill. Ind.
72. octonotata Csy. 99–121 Ariz.
73. montanica Csy. 99–122 Mont.
74. lateralis Muls. 51–657 Mex.& So.Cal.
pinguis Csy. 99–122 Ariz.
omissa Csy. 99–122 Ariz.
lævipennis Csy. 99–122 Cal.
a. flammula Nun. 11–72 Mont. Colo.
75. wellmani Nun. 11–73 Nev.
76. idæ Nun. 12–430 Cal.
77. bigeminata (Rand.) 38–32 Tex. Mass. Fla. Ind.
guexi Muls. 51–687 [L.Sup.
78. hæmatosticta Fall 07–222 N.Mex.
79. signata (Oliv.) 08–1047 Fla.Ga.Ill.Pa. Ind.
binotata (Say) 25–302 Ind.Fla.Conn.
normata (Say) 25–302 [L.Sup.
affinis Rand., 38–50 Mass. L.Sup.
leucopsis Melsh. 46–179
80. proba (Say) 25–503 Fla. Pa. Ill. Ind. Conn.
81. rotunda Csy. 99–123 Tex.
82. gemma Csy. 99–123 Tex.
83. fastidiosa Csy. 08–414 Cal.
84. conspirens Csy. 08–414 Ariz.
85. sexverrucata (Fab.) 01–383 Mex. & Ariz.
medialis Csy. 99–123 Tex.

Hyperaspis Chev.
10886. æmulator Csy. 08–413 Ariz.
87. triangulum Csy. 99–123 Ariz.
88. regalis Csy. 99–124 Fla.
89. imperialis Csy. 08–415 Mex. & U.S.?
90. inedita Muls. 51–684 N.C.
91. bicentralis Csy. 99–124 Tex.
92. globula Csy. 99–124 Tex.
93. centralis Muls. 51–685 Mex.
wickhami Csy. 99–124 Tex.
94. oculifera Csy. 08–415 Ariz.
95. osculans Lec. 80–187 Cal. Ariz.
96. pleuralis Csy. 99–125 Tex.
97. significans Csy. 08–416 Ut.
98. concurrens Csy. 08–416 Ut.
99. aterrima Csy. 08–416 Ut.
10900. tæniata Lec. 52–134 So.Cal. Ariz.
01. excelsa Fall 01–232 So.Cal.
02. lengi Schfr. 05–144 Tex.
03. nevadica Csy. 99–125 Nev.
04. psyche Csy. 99–125 Cal.
05. dissoluta Cr. 73–379 L.Sup. So.Cal.
06. colorodana Csy. 08–417 Colo. [Ind.
07. trifurcata Schfr. 05–143 Tex.
08. fimbriolata Melsh. 46–180 Kan. L.Sup. Fla. Ind. Pa.
rufomarginata Muls. 51–661 Tex. Colo. So.Cal. Fla. Ariz. Conn.
09. limbalis Csy. 99–126 Cal.

Hyperaspis Chev.
10910. protensa Csy. 08–417 Ariz.
11. cincta Lec. 58–89 Cal.
12. nupta Csy. 99–126 Cal.
13. inflexa Csy. 99–126 Dak.
14. serena Csy. 08–417 Pa.
15. elliptica Csy. 99–126 Cal.
angustula Csy. 99–127 Cal.
16. postica Lec. 80–188 Cal.
17. nunenmacheri Csy. 08–417 Cal.
18. oculaticauda Csy. 99–127 Cal.
19. effeta Csy. 99–127 Cal.
20. subdepressa Csy. 99–127 Cal.
21. disconotata Muls. 51–653 L.Sup.
22. troglodytes (Muls.) 53–219
discreta Lec. 80–187 Mass.
23. lugubris (Rand.) 38–52 Ill. Mass. (Ariz.?)
venustula Muls. 51–671
jucunda || Lec. 52–134
lecontei Cr. 74–233 Ill.
24. quadrioculata (Mots.) 45–383 Cal.
elegans Gorh. 94–199 nec Muls.
25. notatula Csy. 99–121 Nev.
26. horni Cr. 73–381 Cal.
27. spiculinota Fall 01–232 So.Cal.
28. fidelis Csy. 08–418 Cal.
29. bensonica Csy. 08–418 Ariz.
30. undulata (Say) 24–92 Ind. Pa. Can. Vt. Mass. Ariz. (So.Cal.?) Ill. Pa. L.Sup. Conn.
elegans Muls. 51–658
maculifera Melsh. 47–179
a. guttifera Weise 95–128
31. octavia Csy. 08–419 Miss.
32. paludicola Sz. 78–362 Fla.
33. filiola Csy. 08–419 Ariz.
34. annexa Lec. 52–133 So.Cal. Kan.
35. revocans Csy. 08–419 Ut. [Ill.
36. quadrivittata Lec. 52–133 Ariz. Colo.
37. tetraneura Csy. 08–420 Colo. [Ind.
38. mœrens (Lec.) 50–238 L.Sup.
consimilis Lec. 52–134 L.Sup.
39. simulans Csy. 99–128 Ariz.
40. falli Nun. 12–450 Nev.
41. weisei Schfr. 08–126 Tex.
kunzei ‡ Schfr. 05–145 nec Muls.
42. levrati (Muls.) 51–613 Mex. & Ariz.
43. metator Csy. 08–413 Tex.
44. nigrosuturalis Blatch. 18–420 Fla.
45. cruenta Lec. 80–187 Tex.
46. lewisi Cr. 73–380 U.S.
47. tædata Lec. 80–187 Fla.
48. gemina Lec. 80–188 Ga. Tex.
49. pratensis Lec. 52–134 Ind. Mo. Kan.
50. punctata Lec. 80–188 Tex. [N.J.
51. tristis Lec. 80–188 Colo. So.Cal.
— ?floridana Muls. 51–1040 Fla.
— subsignata Cr. 74–226 Mex. Tex.
— festiva Muls. 51–659 Brazil (N.Am.?)

Helesius Csy. 99–129
10952. nubilans Csy. 99–129 Tex.
53. nigripennis (Lec.) 79–453 Colo.

Hyperaspidius Cr. 73–382
10954. vittigera (Lec.) 52–133 Mex. Kan. Dak.
trimaculatus Cr. 73–382 nec L. So.Cal. Ariz.
55. oblongus Csy. 08–421 Tex.
trimaculatus Csy. 99–130 nec. L.
56. pallescens Csy. 08–420 Ariz.
57. comparatus Csy. 99–130 Cal.
58. ingenitus Csy. 99–131 N.Mex.
59. insignis Csy. 99–131 Colo.
60. arcuatus (Lec.) 52–133 So.Cal.
61. militaris (Lec.) 52–133 S.C. Fla
62. transfugatus Csy. 99–131 Mass.
63. conspiratus Csy. 99–131 Cal.
64. wolcotti (Nun.) 11–73 Ind.
65. ploribunda (Nun.) 11–74 Nev.

Brachyacantha Chev. 42–704
10966. bistripustulata (Fab.) 01–383 Tex.
a. decora Csy. 99–119 Tex.
b. minor Leng 11–298 Tex.
67. dentipes (Fab.) 01–381 E.N.Am. Fla.
a. socialis Csy. 99–119 Kan.
b. separata Leng 11–301 Va.
68. subfasciata Muls. 51–527 Ariz. Tex.
69. quadrillum Lec. 58–89 Tex.
70. blaisdelli Nun. 09–132 Nev. Cal.
71. tau Lec. 59–28 Neb. Mont.
72. ursina (Fab.) 87–61 E.N.Am. Ind.
stellata Csy. 99–117 Ill. Mo. Ky. Ind.
a. congruens Csy. 99–117 N.C. Ga.
b. utcella Csy. 08–413 Ut.
c. sonorana Csy. 08–412 Ariz. N.Mex.
73. testudo Csy. 99–118 Tex.
74. felina (Fab.) 75–87 E.N.Am.
a. decempustulata Melsh. 47–179 Pa. Ind. Fla.
75. bolli Cr. 73–379 Tex. La.
76. arizonica Schfr. 08–125 Ariz.
77. indubitabilis Cr. 73–379 E. N.Am.
78. fenyesi Leng 11–316 Colo.
79. quadripunctata Melsh. 47–178 E.N.Am. Ind.
basalis Melsh. 47–179 Fla. [Fla.
diversa Muls. 51–538
a. confusa Muls. 51–537 E. N.Am.
b. flavifrons Muls. 51–531 E. N.Am. Fla.
80. floridensis Blatch. 16–93 Fla.
81. albifrons (Say) 24–94 Neb. Colo.
82. illustris Csy. 99–118 Colo. [Mont.
83. pacifica Csy. 99–119 Cal.
84. lengi Nun. 12–449 Cal.
85. querceti Sz. 78–362 Fla.
86. lepida Muls. 51–523 Tex.
— erythrocephala (Fab.) 87–61 Not N.Am.

Thalassa Muls. 51–511
10987. montezumæ Muls. 51–512 La. Ariz. Mex.

MICROWEISEINI

Microweisea Ckll. 03-38
(*Smilia* || Weise 91-285)
(*Pentilia* ‡ Lec. 78-400)
(*Pseudoweisea* Sz. 04-118)
(*Epismilia* || Ckll. 00-606)
10988. marginata (Lec.) 78-400 Mich. N.Y.
89. misella (Lec.) 78-400 Ct. Fla. Can.-
Tex. Ind.
90. atronitens (Csy.) 99-135 Cal.

Microweisea Ckll.
reversa Fall 01-231 So.Cal.
10991. minuta (Csy.) 99-135 Tex.
92. planiceps (Csy.) 99-135 Cal.
93. coccidivora (Ashm.) 80-10 Fla.
94. ovalis Lec. 78-400 Fla. (So.Cal.?)
felschei Weise 91-288 Fla.
95. suturalis Sz. 04-118 So.Cal.

CRANOPHORINI

Nipus Csy. 99-132
10996. biplagiatus Csy. 99-133 So.Cal.

Nipus Csy.
10997. niger Csy. 99-133 Cal.

SCYMNINI

Stethorus Weise 85-22
10998. punctum (Lec.) 52-114 E. N.Am. Ind.
99. picipes Csy. 99-136 Cal. [L.Sup.
11000. brevis Csy. 99-136 Cal.
01. utilis (Horn) 95-107 Fla.
02. atomus Csy. 99-136 Tex.

Didion Csy. 99-137
11003. longulum Csy. 99-137 Cal.
04. parviceps Csy. 99-137 Cal.

Selvadius Csy. 99-137
11005. rectus Csy. 99-138 Ariz.

Scymnus Kug. 94-547
(*Pullus* Muls. 51-976)
(*Diomus* Muls. 51-951)
(*Scymnobius* Csy. 99-139)
11006. flavescens Csy. 99-139 Colo.
07. pallens Lec. 52-137 Ariz. Cal.
So.Cal.
08. mimus Fall 01-234 So.Cal.
09. nugator Csy. 99-140 Colo.
10. semiruber Horn 95-102 Fla. Tex.
11. creperus Muls. 51-985 N.C. Tex.
astutus Muls. 51-986 [Ariz.
a. fraternus Lec. 52-138 M.St. Ind. Fla.
Conn. L.Sup.
texanus Csy. 99-141 Tex.
12. brullei Muls. 51-984 Fla.
13. hæmorrhous Lec. 52-138 Ariz.? Fla.
Ind. N.Y.
dentipes Fall 01-234 ♂ Mass.
a. divisus Csy. 99-140 Kan.
b. laurenticus Csy. 99-140 Can.
c. subæneus Csy. 99-141 Tex.
14. postpictus Csy. 99-141 Wy.
15. rubricauda Csy. 99-141 Kan. Ind.
16. chromopyga Csy. 99-141 Pa.
17. canterius Csy. 99-142 R.I.
18. cervicalis Muls. 51-984 Fla. So. St.
Can.-Mo.
19. kansanus Csy. 99-142 Kan. [So.Cal.
20. marginicollis Mann. 43-313 Cal. So.Cal.
californicus Boh. 59-207 [Ariz.
21. consobrinus Lec. 52-139 L.Sup.
22. iowensis Csy. 99-143 Ia.
23. natchezianus Csy. 99-143 Miss.
24. caudalis Lec. 50-238 Ala.-Colo. Ind.
25. medionotans Csy. 99-143 Tex.
26. kinzeli Csy. 99-143 Fla.
27. socer Lec. 52-139 Ga.

Scymnus Kug.
11028. collaris Melsh. 47-180 Ind. Fla. Conn.
subtropicus Csy. 99-143 Tex.
29. horni Gorh. 97-229 Ariz.
30. cockerelli Csy. 99-144 N.Mex.
31. uteanus Csy. 99-144 Ut.
32. rhesus Csy. 99-144 Ind.
33. fastigiatus Muls. 51-986 Ind.
chatchas Muls. 51-986
34. indutus Csy. 99-145 Pa.
puncticollis Horn 95-102 nec Lec.
35. puncticollis Lec. 52-139 Ind. Conn.
36. agricola Csy. 99-145 R.I.
37. innocens Csy. 99-145 N.C.
38. solidus Csy. 99-145 Cal.
39. desertorum Csy. 99-145 Nev.
40. apacheanus Csy. 99-146 Ariz.
41. monticola Csy. 99-146 Colo.
42. aridus Csy. 99-146 Ut.
subsimilis Csy. 99-150 Ut.
43. luctuosus Csy. 99-146 Cal.
44. humboldti Csy. 99-146 Cal.
45. sonomæ Csy. 99-147 Cal.
46. gilæ Csy. 99-147 Ariz.
47. decipiens Csy. 99-147 Ut.
48. garlandicus Csy. 99-147 Colo.
49. blaisdelli Csy. 99-147 Cal.
50. advena Csy. 99-147 Cal.
51. extricatus Csy. 99-148 Cal.
52. ardelio Horn 95-105 Ariz. Fla. Tex.-
B.C. So.Cal.
53. jacobianus Csy. 99-148 Cal.
54. jacinto Csy. 99-148 Cal.
55. tenebrosus Muls. 51-989 Atl. St. Ind.
56. compar Csy. 99-148 Ind. [Conn
57. infans Csy. 99-149 Ariz.
58. weidti Csy. 99-149 Ut.
59. abbreviatus Lec. 52-140 L.Sup.
60. lacustris Lec. 52-140 L.Sup. Ariz.?
renoicus Csy. 99-149 Nev.
a. nigrivestis Muls. 51-990 La.
61. tahoensis Csy. 99-150 Cal.
62. mormon Csy. 99-150 Ut.
63. saginatus Csy. 99-150 Cal.
64. strenuus Csy. 99-150 Cal.
65. mendocino Csy. 99-151 Cal.
66. stygicus Csy. 99-151 Cal.
67. tenuivestris Csy. 99-151 Cal.
calaveras Csy. 99-150 Cal.
68. papago Csy. 99-151 Ariz.
69. flebilis Horn 95-100 Ariz. So.Cal.
70. nubes Csy. 99-151 Ariz.

Scymnus Kug.
11071. cinctus Lec. 52–137 La.-So.Cal.
72. lecontei Cr. 74–261 Cal. [Ariz.
suturalis || Lec. 52–138
73. sarpedon Csy. 99–152 Cal.
74. pacificus Cr. 73–77 Cal. So.Cal.
75. strabus Horn 95–100 N.Mex.
76. coniferarum Cr. 73–77 Colo.-So.Cal.
77. punctatus Melsh. 47–180 Can.-Tex.
78. occiduus Csy. 99–153 Nev. [Man.
79. nanus Lec. 52–140 Mich. Fla.
So.Cal. Ariz.
80. circumspectus Horn 95–96 Tenn. La.
81. opaculus Horn 95–96 Colo.
82. americanus Muls. 51–965 N.E. Am. Ind.
L.Sup. Conn.
83. caurinus Horn 95–97 Cal.-Wash.
84. innocuus Csy. 99–154 Nev.
85. rusticus Csy. 99–154 Ind.
86. aluticollis Csy. 99–154 Cal.
87. difficilis Csy. 99–154 Cal.
88. phelpsi Cr. 73–77 No. Cal.-B.C.
89. nebulosus Lec. 52–137 So.Cal.
90. megacephalus Fall 01–233 So.Cal.
91. bivulnerus Horn 95–92 Fla.
92. bisignatus Horn 95–92 Cal.
93. flavifrons Melsh. 47–181 Can.-Ga.-Ind.
Fla.
a. bioculatus Muls. 51–960 N.J.-Ga. Fla.
guttiger Muls. 51–965
marginellus Muls. 51–965
94. ornatus Lec. 52–135 L.Sup. Mass.
95. sanguinifer Csy. 99–155 Mass.
96. naviculatus Csy. 99–155 Colo.
97. amabilis Lec. 52–135 La.
98. guttulatus Lec. 52–136 So.Cal.
99. bijugus Fall 09–162 L.Cal.
11100. scitus Csy. 99–156 Cal.
01. suavis Csy. 99–156 Cal.
02. coloradensis Horn 95–94 Colo.

Scymnus Kug.
11103. sordidus Horn 95–93 So.Cal.
04. intrusus Horn 95–92 Fla. Md. Tex.
05. inops Csy. 99–156 Fla. [Ind.
06. oculatus Blatch. 17–140 Fla.
07. balteatus Lec. 78–399 Fla.
08. bigemmeus Horn 95–88 Fla.
09. tædatus Fall 01–233 So.Cal.
10. dichrous Muls. 51–951 N. Am.?
11. quadritæniatus Lec. 78–400 Fla.-La.
12. myrmidon Muls. 51–954 Pa. Md. Fla.
13. adulans Csy. 99–157 N.C.
14. liebecki Horn 95–89 N.J. Ind.
15. terminatus Say 35–203 Fla. N.E. Am.
femoralis Lec. 52–136 Pa. [Ind.
a. brunnescens Csy. 99–158 Tex.
16. partitus Csy. 99–158 Tex. Ind.
17. houstoni Csy. 99–158 Tex.
18. xanthaspis Muls. 51–952 Ga. Fla. Tex.
19. appalacheus Csy. 99–158 N.C.
20. stigma Csy. 99–158 Fla.
21. dulcis Csy. 99–159 Kan.
22. æger Csy. 99–159 Mich. Ill. Fla.
23. debilis Lec. 52–137 Cal.
24. pusio Csy. 99–159 Fla.
25. redtenbacheri Muls. 46-240 Greenland
— ?icteratus Muls. 51–969 N.Am.?
— ?cyanescens Muls. 51–993 N.Am.?
— ?atramentarius Boh. 58–207 Cal.??
— ?infuscatus Boh. 58–209 Cal.??
— ?arcuatus Rossi 92–88 Eur. & N.Am.?

Cephaloscymnus Cr. 73–382
11126. zimmermanni Cr. 73–382 Md. D.C. S.C
Ind.
27. occidentalis Horn 95–111 So.Cal. Ariz.

Cryptolæmus Muls. 50–140
11128. montrouzieri Muls. 53–140 †Cal.

NOVIINI

Rodolia Muls. 51–902
(*Vedalia* ‡ auct.)
11129. cardinalis (Muls.) 51–906 †Cal. Fla.

Novius Muls. 51–942
11130. kœbelei (Olliff) Coq. 93–24 †Cal.

Anovia Csy. 08–408
11131. virginalis (Wickh.) 05–166 Ut. Tex.

Exoplectra Chev. 42–545
11132. subænescens Gorh. 95–214 Mex. & Ariz.

RHIZOBIINI

Lindorus Csy. 99–162
11133. lophantæ (Blaisd.) 92–51 †Cal. So.Cal.
toowoombæ (Blackb.) 92–254

Rhizobius Steph. 32–396
(*Rhyzobius* ‡ auct.)
11134. ventralis (Er.) 42–239 †Cal.
35. debilis Blackb. 88–201 †Cal.

SCYMNILLINI

Zagloba Csy. 99–113
11136. ornata (Horn) 95–111 Cal.
37. laticollis Csy. 99–114 Cal.
38. orbipennis Csy. 99–114 Cal.
39. bicolor Csy. 99–114 Fla.

Zagloba Csy.
11140. hystrix Csy. 99–114 Tex.

Scymnillus Horn 95–110
11141. aterrimus Horn 95–110 No. Cal. Or.
42. cochisiensis Nun. 12–451 Ariz. [So.Cal.

OENEINI

Delphastus Csy. 99–111
(*Cryptognatha* Cr. nec Muls.)
(*Oeneis* Lec. nec Muls.)
11143. pusillus (Lec.) 52–135 N.Y. Fla. Tex.
Ind. So.Cal.
Conn.

Delphastus Csy.
puncticollis (Lec.) 52–135 So. St.
11144. sonoricus Csy. 99–112 So.Cal. Ariz.
45. catalinæ (Horn) 95–83 So.Cal.
46. pallidus (Lec.) 78–400 Fla.

† Introduced.

COCCIDULINI

Coccidula Kug. 98–421
11147. lepida Lec. 52–132 Can.-Pa. Ind. Conn.

Coccidula Kug.
11148. occidentalis Horn 95–114 Wy.-Vanc.
49. suturalis Weise 95–132 Ohio

PSYLLOBORINI

Psyllobora Chev. 42–606
11150. viginti-maculata (Say) 24–96 R.I.-Wis. Ind.
obsoleta Csy. 99–101 Ia.
a. parvinotata Csy. 99–101 Fla.
b. pallidicola Blatch. 14–66 Fla.
c. renifer Csy. 99–102 Tex.
d. tædata Lec. 57–70 Pac. Coast, So.Cal. Ariz.

Psyllobora Chev.
borealis Csy. 99–102 Idaho
separata Csy. 99–102 Cal.
deficiens Csy. 99–102 Cal.
11151. nana Muls. 51–181 Fla.
52. kœbelei Nun. 11–71 Ariz.
53. plagiata Schffr. 08–125 Ariz.

COCCINELLINI

Anisosticta Chev. 35–456
11154. bitriangularis Say 24–269 No.U.S.& Can.
multiguttata Rand. 38–51 Mass.
?novemdecim-punctata L. 58–366 Eur.
strigata ‡ auct. nec Thunb. Eur. L.Sup.
dohrniana Joh. nec Muls. Eur. [Conn.
a. irregularis Weise 85–14 Or.

Næmia Muls. 51–30
11155. seriata (Melsh.) 47–177 Conn.-Fla.
a. litigiosa Muls. 51–31 So.Cal.-So. Am.

Macronæmia Csy. 99–76
(*Micronæmia* Weise 05–218)
11156. episcopalis (Kby.) 37–228 No. St. & Can. Cal. Kan. Wy. Colo.

Ceratomegilla Cr. 73–365
(*Megilla* || Muls. 51–24)
11157. ulkei Cr. 73–365 H.B.T.
58. fuscilabris (Muls.) 66–22 U.S. & Can. Ind. So.Cal.
maculata auct. nec DeG. [Ariz.
strenua (Csy.) 99–76 Tex.
a. floridana (Leng) 03–38 Fla. La.
b. decepta (Blatch.) 14–65 Fla.

(*Paranæmia* Csy. 99–76)
59. vittigera (Mann.) 43–312 So.Cal. Kan. Mex.
a. similis (Csy.) 99–76 Colo. Ariz.

Adonia Muls. 51–37
11160. variegata (Goeze) 77–246 Eur. & N.S.?
constellata (Laich.) 81–121
mutabilis (Scriba) 90–183

Eriopis Muls. 51–6
11161. connexa (Germ.) 24–621 S.Am. & U.S.? Cal.? Vanc.? Tex.

Hippodamia Dej. 36–456
I
11162. tredecim-punctata (L.) 65–336 H.B.T.-Cal. Ind. Alas. Sib. Atl.St. Ut. N.Dak. Minn.
tibialis (Say) 24–94
signata (Fald.) 32–398

Hippodamia Dej.
II
11163. parenthesis (Say) 24–93 No. St. Cal. Ind. Ariz. Mass. Md. Dak. Ut. Colo.
lituricollis Fitch 61–853 N.Y.
confluenta Fitch 61–853 N.Y.
insulata Fitch 61–853 N.Y.
nimia Fitch 61–853 N.Y.
tridentifrons Fitch 61–853 N.Y.
permacrifrons Fitch 61–853 N.Y.
triangularis Fitch 61–853 N.Y.
albomaculata Fitch 61–853 N.Y.
linearis Fitch 61–853 N.Y.
approximata Fitch 61–853 N.Y.
discopunctata Fitch 61–853 N.Y.
connata Fitch 61–853 N.Y.
a. tridens Kby. 37–229 N.W.St. Can.
64. lunato-maculata Mots. 45–382 Or.Cal.Ut.Wy.
a. apicalis Csy. 99–81 Nev. Cal.
b. expurgata Csy. 08–400 Colo.
c. lengi Joh. 10–865 So.Cal.
III
65. sinuata Muls. 51–1011 Cal.
trivittata Csy. 99–81 Cal.
crotchi Csy. 99–80 Cal.
interrogans Muls. 56–139
a. spuria Lec. 67–358 Or. Wash.
b. complex Csy. 99–80 Vanc. [So.Cal.
66. cockerelli Joh. 10–849 Colo.-Wy.
lineata Joh. 10–46 Wash.
67. falcigera Cr. 73–368 H.B.T.
68. americana Cr. 73–368 ?Kan. H.B.T.
69. dispar Csy. 99–79 Colo.
70. oregonensis Cr. 73–367 Or.
71. glacialis (Fab.) 75–80 Pa.-Mo.-Ind. Mass. N.C. Dak.
abbreviata (Fab.) 87–54
remota (Web.) 01–49
72. quindecim-maculata Muls. 51–20 Mo. Kan. Ark.
73. convergens Guér. 46–321 U.S. & Can. Ind. So.Cal. Fla. Ariz.
modesta Melsh. 47–178
obsoleta Cr. nomen nudum
a. punctulata Lec. 52–131 Cal.
b. ambigua Lec. 52–131 So.Cal. Or.

Hippodamia Dej.
obliqua Csy. 99–79 Cal.
politissima Csy. 99–80 Cal.
11174. lecontei Muls. 51–1010 Colo. N.Mex. Cal. Ariz.
a. caseyi Joh. 10–21 Wash.
mulsanti Lec. 52–131 L.Sup.
b. vernix Csy. 99–79 Wy.Mont.Id.
c. subsimilis Csy. 99–79 Cal.
d. uteana Csy. 08–397 Ut. (Cal.?)
e. abducens Csy. 08–396 Colo.
pseudoglacialis Joh. 10–23
defecta Joh. 10–21
f. juncta Csy. 99–80 Cal.
75. quinquesignata Kby. 37–230 H.B.T.-Kan. Ariz. Nfld.
a. puncticollis Csy. 99–78 Can. Rocky Mts. So.Cal.
b. lilliputana Csy. 08–397 Colo.
c. coccinea Csy. 08–395 Colo.
d. leporina Muls. 56–135 Cal.
76. extensa Muls. 51–17 Cal.
77. moesta Lec. 54–16 Or.Vanc.B.C.
a. bowditchi Joh. 10–45 No.Rocky Mts.

Neoharmonia Csy. 99–90
11178. venusta (Melsh.) 46–175 M.&S.St. Ind. Ark.Kan.La.
a. dissimila Blatch. 14–66 Fla. Md.
79. notulata (Muls.) 51–83 La. Fla.
80. ampla (Muls.) 51–81 Mex.& So. U.S. Tex.

Coccinella L. 58–364
11181. perplexa Muls. 51–1021 No.St.Can. Ind.-Conn. N.Y.
?trifasciata L. 58–365 Eur.& Sib.
a. eugenii Muls. 66–95 Cal.
b. juliana Muls. 56–135 Or.Cal.
barda Lec. 60–286
c. subversa Lec. 54–19 Or.
82. humboldtiensis Nun. 12–448 No.Cal.
83. tricuspis Kby. 37–231 H.B.T.-Mich. Sib.
84. novemnotata Hbst. 93–269 Atl. St.-Or. Ind. So.Cal.
conjuncta Fitch 61–849 N.Y.
confluenta Fitch 61–849 N.Y.
inæqualis Fitch 61–849 N.Y.
parvamaculata Fitch 61–849 N.Y.
divisicollis Fitch 61–849 N.Y.
a. degener Csy. 99–88 N.Mex. Ariz.
oregona Csy. 08–403 Or. [Colo.
b. franciscana Muls. 53–19 Mex. U.S.?
c. johnsoni Csy. 08–403 So.Cal. [So.Cal.
85. transversoguttata Fald. 35–454 Sib. U.S.?Lab. Nev. Conn. Greenland
a. quinquenotata Kby. 37–230 Colo.-Mont.
transversalis || Muls. 51–117 [L.Sup. So.Cal.
interrupta Fitch 61–851 N.Y.
b. nugatoria Muls. 51–1021 Ut. Colo.
c. californica Mann. 43–312 So.Cal. Or. Wash.

Coccinella L.
d. vandykei Nun. 09–161 Nev.
e. nevadica Csy. 99–88 Nev.
f. melanocollis Joh. 10–62 Cal.
11186. bridwelli Nun. 13–76 Cal.
87. monticola Muls. 51–115 No. St. Vanc. L.Sup. Conn. Lab.
lacustris Lec. 52–131
sellica Joh. 10–63 Cal. N.H.
postica Joh. 10–63 Cal.
confluenta Joh. 10–63 Cal.
alutacea Csy. 99–89 N.Mex.
impressa Csy. 99–89 Cal.
biguttata Joh. 10–63 Colo.
a. difficilis Cr. 73–370 Ut. Colo.
b. suturalis Csy. 99–89 Colo.
c. prolongata Cr. 73–371 Ut.Kan.Cal.
(*Spilota* Billb. 20–61)
88. undecimpunctata L. 58–366 Eur.&N.Am.
menetriesi Muls. 51–104 Sib.&No.Cal. Alas.

Cycloneda Cr. 74–162
(*Daulis* || Muls. 51–296)
11189. sanguinea (L.) 63–11 No.& So.Am. Ind. Ariz.
a. immaculata (Fab.) 92–267 Fla. Ga. La.
90. munda (Say) 35–202 Me.-Man.-Pa.
a. polita Csy. 99–93 Cal. B.C. Id.
rubripennis Csy. 99–92 Tex. So.Cal. Colo.
91. atra Csy. 99–93 N.Am.?

Olla Csy. 99–93
11192. abdominalis (Say) 24–95 Tex.-So.Cal. Ind.
semilunaris Joh. 10–66 Ariz.-Tex.
minuta Csy. 08–406 Tex.
a. plagiata Csy. 99–94 So.Cal. So.& W. St. Tex.
fenestralis Csy. 99–95 N.Mex. [Ariz.
oculata ‡ auct. nec Fab.
b. sobrina Csy. 99–94 Fla.

Adalia Muls. 51–49
11193. bipunctata (L.) 58–364 Eur. & N.Am. Conn. Ind.
bioculata (Say) 24–94
quadrimaculata Scop. 63–80
94. frigida (Schn.) 92–172 Eur. Sib.& N.Am. Ind. Conn.
hyperborea (Payk.) 99–38
ornatella Csy. 99–86 Colo.
immaculata Joh. 10–68
melanopleura Lec. 60–286 Vanc. Cal.
parvula Weise 85–22 Eur. N.Am.?
siberica Weise 85–22 Mass. Eur.
facetta Weise 85–22 Mass. Eur.
postica Joh. 10–68 Mass.
a. disjuncta (Rand.) 38–33 Me. Mass. Wis.
b. humeralis (Say) 24–95 Can.-Cal. Ariz.
95. annectans Cr. 73–371 Colo.N.Mex.
ovipennis Csy. 99–86 Cal. [Cal.
transversalis Csy. 99–86 N.Mex.

Adalia Muls.
sexpustulata Joh. 10–71 Or.
ocellata Joh. 10–71 Or.
ophthalmica Muls. 51–56 Mo.Can.Mass.
coloradensis Csy. 08–401 Colo.
a. duplicata n.m.
humeralis ‡ Joh. 10–71 nec Say.
?ludoviciæ Muls. 51–36 N.Am.?

Cleis Muls. 51–208
(*Pseudocleis* Csy. 08–406)
11196. picta (Rand.) 38–51 U.S. & Can. Nfld. Mass. Ariz. So.Cal.
blanchardi Joh. 10–72
contexta Muls. 51–87
concinnata (Melsh.) 47–177
a. minor Csy. 99–95 Cal. Vanc.
97. hudsonica Csy. 94–96 H.B.T. N.H.

Agrabia Csy. 99–87
(*Harmonia* ‡ auct. nec Muls.)
11198. cyanoptera (Muls.) 51–82 Mex.&N.Mex.
99. sicardi Nun. 12–448 Cal. [Ariz.
a. complexa Nun. 12–448 Cal.

Anisocalvia Cr. 71–329
11200. duodecim-maculata (Gebl.) 32–76 Sib. & N.Am.
incarnata (Kby.) 37–231 [Conn. L.Sup.
a. elliptica Csy. 99–97 H.B.T.

Anisocalvia Cr.
11201. quatuordecimguttata (L.) 58–367 Eur. & N.Am.
a. similis (Rand.) 38–50 Mass. L.Sup.
b. cardisce (Rand.) 38–32 Me.
c. victoriana Csy. 99–96 B.C.
d. obliqua (Rand.)38–33 Me.
?hesperica Cr. 73–374 Ariz.

Anatis Muls. 51–133
11202. quindecimpunctata (Oliv.) 08–1027 Atl. St. Ind.
labiculata Say 35–288 [L.Sup.
?ocellata (L.) 58–366 Sib.
a. mali (Say) 24–93 Wis. Id. Atl. St. Ind.
03. rathvoni Lec. 52–132 Cal. Or.
04. lecontei Csy. 99–98 Ariz. N.Mex. Colo.

Neomysia Csy. 99–98
(*Mysia* ‡ auct. nec Muls. 46–129)
11205. pullata (Say) 25–301 L.Sup. Atl. St. Ind.
06. subvittata (Muls.) 51–138
notans (Rand.) 38–49 Mass. Lab.
07. horni (Cr.) 73–375 Or. So.Cal.
08. interrupta Csy. 99–99 N.Mex. Colo. Ariz.
09. randalli Csy. 99–99 L.Sup.-Lab.
10. montana Csy. 99–100 Colo.

CHILOCORINI

Axion Muls. 50–477
11211. pilatei Muls. 51–478 Tex.(So.Cal.?)
12. tripustulatum (DeG.) 75–395 R.I.-Tex. Fla.
verrucatus (Melsh.) 47–180
13. incompletus Nun. 11–71 Ill.
14. plagiatum (Oliv.) 08–1044 So.Cal.-Tex.
alutaceum Csy. 99–106 N.Mex. [Ind.
a. texanum Lec. 58–88 Tex. Ariz. N.Mex.
b. pleurale Lec. 59–90 So.Cal.

Chilocorus Leach 17–116
11215. tumidus Leng 08–37 Va.
16. cacti L. 67–584 Fla. Tex.
a. confusor Csy. 99–105 Ariz. So.Cal.
17. bivulnerus Muls. 51–460 U.S. & Can.
fraternus Lec. 57–70 [Ind. Fla.
a. orbus Csy. 99–105 So.Cal.
18. similis Rossi 90–68 †Ga. China

Arawana Leng 08–38
11219. arizonica (Csy.) 99–107 Ariz.

Exochomus Redt. 43–118
11220. marginipennis Lec. 24–174 N.Y.-Fla. Ind. L.Sup.

Exochomus Redt.
prætextatus Melsh. 47–178
deflectens Csy. 08–410 Mo.
a. childreni Muls. 41–1037 Fla.-So.Cal.
guexi Lec. 52–132 [Ariz.
contristatus Muls. 51–492 Mex.
b. latiusculus Csy. 99–108 Fla.-Mo. Tex.
c. californicus Csy. 99–107 So.Cal. Nev.
desertorum Csy. 99–108 Nev.
d. fasciatus Csy. 99–108 So.Cal.
11221. subrotundus Csy. 99–108 Tex.

(*Brumus* Muls. 51–492)
22. æthiops Bland 64–72 Neb.-Ariz.
a. mormonicus Csy. 08–411 Ut. [Colo.
23. orbiculatus Leng 08–41 Ariz.
24. högei Gorh. 94–180 Colo.-Mex.
25. septentrionis Weise 85–230 H.B.T. Man.-
a. nevadensis Leng 08–42 Nev. [Tex.
b. ovoideus Csy. 99–107 Colo. Ariz.
c. parvicollis Csy. 08–411 Ut.
26. davisi Leng 08–42 Atl. St.
27. histrio Fall 01–230 So.Cal.

Orcus Muls. 51–467
11228. chalybeus (Boisd.) 35–595 †Cal.

EPILACHNINÆ

Epilachna Chev. 44–359
11229. borealis (Fab.) 75–82 Fla. Conn. Ind.
30. mexicana Guér. 46–519 Mex. Border

Epilachna Chev.
11231. corrupta Muls. 51–815 Mex.
maculiventris Bland 64–72
juncta Joh. 10–79
a. cuprea Ckll. 18–153 Colo.
32. toweri Joh. 10–78 Tex.

† Introduced.