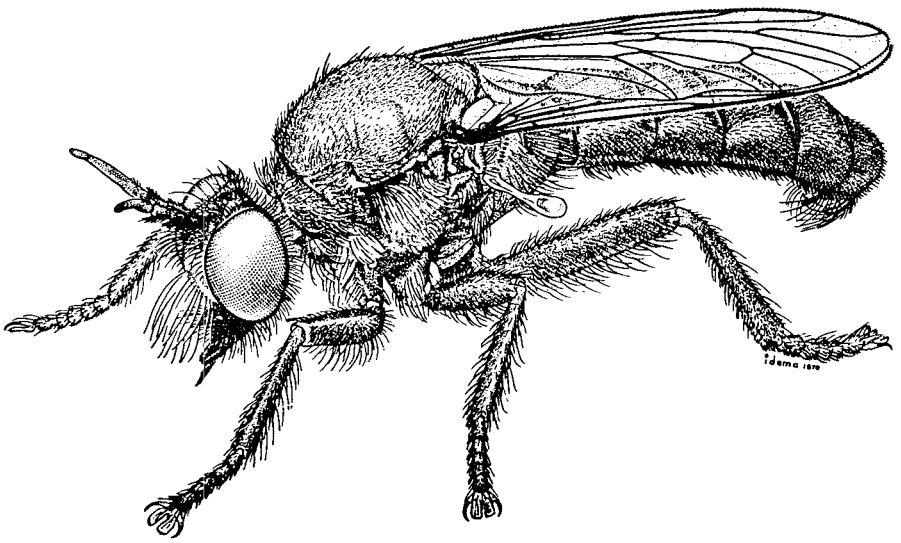

Frontispiece *Dicolonus sparsipilosum* Back, male.

THE NEARCTIC SPECIES OF *DIOCTRIA* AND SIX RELATED GENERA (DIPTERA, ASILIDAE)

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The North American members of the tribe Dioctriini, sensu *Hull, 1962, with the addition of* Bohartia, *are arranged in two tribes, Dioctriini s. str., with one genus and two subgenera,* Dioctria *and* Nannodioctria, *and a new tribe, Echthodopini, with six genera,* Bohartia, Dicolonus, Echthodopa, Eudioctria, Metadioctria, *and* Myelaphus. *A sister group relationship between the two tribes is postulated, with Dioctriini the more derived. Keys, descriptions, figures and phylogenetic analyses are provided for all nearctic species, as follows:* Dioctria, *nine species including two new species,* australis *and* wilcoxi; Bohartia, *seven species including six new species,* isabella, martini, munda, nitor, seneca *and* tenuis; Dicolonus, *five species, including three new species* medium, nigricentrum *and* pulchrum; Echthodopa, *three species;* Eudioctria, *14 species including three new species,* disjuncta, dissimilis *and* unica; Metadioctria, *one species; and* Myelaphus, *two species. The origin and dispersal of members of each tribe is discussed.*

Nous réarrangeons les membres nord-americains de la tribu des Dioctriini, selon Hull, 1962, avec l'addition du genre Bohartia *en deux tribus, les Dioctriini s. str., avec un genre et deux sous-genres,* Dioctria *et* Nannodioctria, *et une nouvelle tribu, Echthodopini, avec six genres,* Bohartia, Dicolonus, Echthodopa, Eudioctria, Metadioctria, *et* Myelaphus. *Nous postulons que les deux tribus forment des groupes-soeurs; les Dioctriini étant considérés comme les plus dérivés. Nous pourvoyons des clefs, des descriptions, des illustrations et des analyses phylogénetiques des espèces néarctiques comme suit:* Dioctria, *neuf espèces dont deux nouvelles,* australis *et* wilcoxi; Bohartia, *sept espèces dont six nouvelles,* isabella, martini, munda, nitor, seneca, *et* tenuis; Dicolonus, *cinq espèces dont trois nouvelles,* medium, nigricentrum *et* pulchrum; Echthodopa, *trois espèces;* Eudioctria, *quatorze espèces dont trois nouvelles,* disjuncta, dissimilis *et* unica; Metadioctria, *une espèce;* Myelaphus, *deux espèces. L'origine et la dispersion des membres de chaque tribu est discutées.*

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INTRODUCTION

The diverse family Asilidae contains over 400 genera distributed by most authors among four subfamilies, Dasypogoninae, Leptogastrinae, Laphriinae and Asilinae. Members of the family vary greatly in size, colour and proportions, but few reliable structural characters have been found on which to base tribal or generic group taxa. The tribe Dioctriini belongs to the Dasypogoninae, containing about three-fourths of the genera of the family, and in which the problem of determining relationships and phylogeny is particularly acute.

Hull (1962) was first to study the entire family at the generic level. His treatment, though phenetic, ranks as an important advance because it was world-wide in scope. More recently Papavero (1973) has initiated another analysis of the subfamilies and tribes. This study is especially valuable for its comprehensive review of previous classifications. Papavero raises many of Hull's tribes to subfamilial rank, yet his dendrogram of the family (fig. 1, p. 234) still reflects the classical tricotomy of Asilinae, Dasypogoninae and Laphriinae. He excluded the Leptogastrinae as a separate family. Papavero is the first to attempt a phylogenetic analysis of asilids, and we hope that he will in future instalments elaborate more fully his reasons for his choice of primitive and derived characters.

The tribe Dioctriini, as first proposed by Hull (loc. cit.) included four nearctic genera, *Dicolonus, Echthodopa, Myelaphus* and *Dioctria,* with subgenera *Nannodioctria, Metadioctria* and *Eudioctria.* These were grouped together, along with several Old World genera, because of their "generalized" appearance, open marginal and posterior wing cells, two-segmented palpi and absence of acanthophorites, or spine-bearing lobes of the female tenth tergum (Hull attributed them to the ninth). Hull believed all of these characters to be primitive, hence from a phylogenetic point of view his Dioctriini was based entirely on symplesiomorphy. While we concur with him that open marginal and posterior cells and two-segmented palpi are likely to be primitive, as they represent the condition in the Tabanomorpha, we cannot agree that a lack of acanthophorites is primitive. Nevertheless we are able to maintain his dioctriine assemblage, at least its nearctic members, essentially as he proposed it, but for rather different reasons, namely the synapomorphy of the absence of acanthophorites, coupled with an overall similarity in detailed structure of the antennae and terminalia, that also appears to us to be synapomorphic.

Acanthophorites, strictly speaking, are spine-bearing lobes of the tenth tergum of the female, although the term has also been used as if the spines alone are meant. These spines are stout, blunt and usually curved dorsally, and occur in a row along the posterior edge of each lobe of the tenth tergum which is more or less deeply emarginate mid-posteriorly (Fig. 136). They are assumed to be used for digging in the soil preparatory to oviposition and are present in the majority of Dasypogoninae, but other asilids lack these spines. Structures that appear to us to be closely similar to dasypogonine acanthophorites, in both appearance and position, are also present in the other families of Asilomorpha (viz., Therevidae, Scenopinidae, Mydidae and Apioceridae), all believed to be closely related to asilids (Hennig 1954, 1973).

As stated above, Hull (1962) believed that acanthophorites were derived structures and had evolved independently in each of the groups in which they are found. He placed emphasis on

this condition by grouping all those dasypogonine tribes lacking acanthophorites, viz. Dioctriini, Damalini, Laphystiini, Phellini and Chrysopogonini at the beginning of his classification.

We have reached the opposite conclusion, namely that acanthophorites are primitive structures, present in the ancestors of all the Asilomorpha, which have been lost subsequently several times. Consequently their presence in a genus or tribe of any one of these families must be considered as primitive, while their loss would be derived.

The relative plesiomorphy of acanthophorites has an important bearing on the position of the Asilidae within the Asilomorpha. If asilids were the most primitive member of the group it could be argued that acanthophorites evolved only twice, once in the dasypogonines and once in the ancestor of the rest of the Asilomorpha. Acanthophorites would then not be homologous between asilids and the other five families, and their presence in asilids would be derived. It is true that the asilids, along with therevids, have the least specialized wing venation (Hennig 1974) but we consider it unlikely that asilids are the most primitive member of the Asilomorpha in view of the unique specialization of their mouthparts. Unlike the biting Nematocera and Tabanomorpha, which primarily use their well-developed mandibles as cutting tools, asilids lack mandibles entirely, and instead have evolved a strong spear-like hypopharynx for stabbing and paralyzing their prey. The alterations in the labella, which have lost their lapping function entirely, and have become restructured into a guide for the hypopharynx, also have persuaded us that asilids have developed the biting habit *de novo,* quite independently of other biting Diptera, from a therevid-like ancestor in which the mandibles had already been lost.

Other unrelated evidence that acanthophorites have been secondarily lost can be found in the asiline genus *Proctacanthus.* All Asilinae lack true acanthophorites, but some species of *Proctacanthus,* which live in sandy areas, have acquired groups of strong curved spines on the cerci, analogous to acanthophorites, that evidently aid them in ovipositing in soil.

A third piece of evidence is in the presence of acanthophorites among some Bombyliidae, formerly placed in the Asilomorpha (Hennig 1954) now classified by Hennig (1974) with the Tabanomorpha.

In conclusion, therefore, we believe that possession of acanthophorites is symplesiomorphic, i.e., the ancestor of all Asilomorpha possessed them, therefore those Dasypogoninae still possessing them may be considered more primitive than those that lack them. In addition, their absence may be taken as evidence of closer relationship. This is not to suggest that all asilids, or even all dasypogonines, that lack acanthophorites are closely related, for other evidence mitigates against such a hypothesis. Of the five tribes stated by Hull to lack acanthophorites, the Phellini and Chrysopogonini are Australian, and no specimens were available for study. Nevertheless it is worth noting that not all of the members of either of these tribes lack acanthophorites. We have examined all the North American representatives of Damalini and Laphystiini, as well as *Damalus* itself, and find it impossible to visualize any close relationship between either of these tribes and the Dioctriini or Echthodopini. Therefore we can only conclude that at least two, and probably several groups of Dasypogoninae have independently lost their acanthophorites.

The nearctic species of *Dioctria* were last revised by Wilcox and Martin (1941), who proposed three subgenera, *Eudioctria, Metadioctria* and *Neodioctria;* the latter name was changed to *Nannodioctria* (Wilcox and Martin 1942) because of preoccupation. Martin and Wilcox (1965) transferred to *Dioctria* a fourth subgenus, *Bohartia* Hull, 1958, which Hull (1962) had earlier included in the Laphystiini. Many new species have since been discovered, and it is the purpose of the present study to treat all nearctic species of these genera.

During the course of this study it became apparent that *Dioctria s. str.* and *Nannodioctria* possess several synapomorphic features, especially in the structure of the proboscis, that are not shared with *Eudioctria, Metadioctria* or *Bohartia,* nor with other dasypogonines, as far as

we can determine. This was considered as grounds for restricting the tribe Dioctriini to *Dioctria* alone, with *Nannodioctria* as a subgenus. *Eudioctria, Metadioctria* or *Bohartia,* are each elevated to full generic rank, and are placed, along with *Dicolonus, Echthodopa* and *Myelaphus* in a new tribe, Echthodopini. As a group, this new tribe cannot readily be defined by synapomorphic characters, but no reason could be found to show that they did not form a monophyletic group, and they are considered in this paper as the primitive sister group of the Dioctriini *s. str.*

MATERIALS AND METHODS

During the preparation of this paper a total of about 4000 specimens were obtained from ten institutions and two private collections as follows: American Museum of Natural History (AMNH), New York City, N. Y.; Arizona State University (ASU), Tempe, Ariz.; California Academy of Sciences (CAS), San Francisco, Calif.; California Insect Survey (CIS), University of California, Berkeley, Calif.; Canadian National Collection (CNC), Biosystematics Research Institute, Ottawa, Ont.; Cornell University (CU), Ithaca, N. Y.; University of California, Davis (UCD), Calif.; University of California, Riverside (UCR), Calif.; University of Idaho (UI), Moscow, Ida.; United States National Museum (USNM), Washington, D. C.; Utah State University (USU), Logan, Utah and the private collections of Dr. C. H. Martin (CHM) and Dr. J. Wilcox (JW). The initials given above after each collection are those used below to indicate deposition of type material.

Preparation of mouthparts and genitalia was done by macerating these parts in 10% potassium hydroxide, neutralizing in 90% acetic acid, washing in 70% alcohol and then in water. These structural parts were then stored in glycerine in microvials and pinned below the specimens from which they came. Drawings were made with the aid of a camera lucida.

The species were then grouped into sister species (i.e., those two species sharing the largest number of apomorphic characters) and in turn pairs of sister species were grouped in similar fashion to form larger monophyletic units, i.e., species groups. Phylogenetic analysis has been presented in the form of dichotomous tables (Tables 1-6). The sister group which is believed to have the greatest number of apomorphic characters is placed on the right side of the table. In this way, the table has been used to show the interpretation of the direction of evolutionary changes, i.e., from left to right. However, each lineage usually develops some apomorphic characters of its own and thus it is not clear in every case which line of the two has diverged more.

Dendrograms were also constructed to indicate sister group relationships of species, species groups and higher taxa by repeatedly linking monophyletic units together with their sister groups. Each of the branches (lineages) and branching points in the dendrogram has been numbered to facilitate cross reference to the text and to the accompanying dichotomous table. For example, in the dendrogram for the genus *Dioctria* (Dendr. 2) the common ancestor of this group is given the number 2. Each of the two resulting lineages is numbered 2.1 and 2.2. The branch to the right (2.2), leading in this case to the subgenus *Dioctria,* is believed to have the greatest number of apomorphic characters. The left branch (2.1), leading to the subgenus *Nannodioctria,* is believed to be more primitive than the right branch. Subsequent points of divergence are distinguished by letters, i.e. 2A, 2B, etc. and the two lineages arising from 2A are numbered 2A.1 and 2A.2, from 2B, 2B.1 and 2B.2. By means of this numbering, the characteristics of each lineage can be more readily located in the accompanying dichotomous table.

MORPHOLOGY AND TERMINOLOGY

Head (Fig. 1, 21-32). Frons separated by bases of antennae into ventral preantennal region, pre-frons (Crampton 1942), or face (Fig. 1A, fc) (Walton 1909), also named frontoclypeus (Peterson 1916) and dorsal postantennal region, post-frons or

simply, frons; face well-developed, usually flattened, lower part convex in some taxa, in form of facial gibbosity, with group of hairs or bristles, the mystax (Fig. 1B, mx) arranged as cluster on gibbosity (Fig. 26-32) or reduced to transverse row along lower margin of face (Fig. 21-25); hairs or bristles of mystax varied from black or yellow to white or mixture of either; antennal bases (Fig. 1B, ant. b), i.e. region of frons immediately surrounding points of attachment of antennae varied from flat (Fig. 21, 22, 27) to strongly elevated, in form of tubercle-like structure (Fig. 23-26, 28, 29), in some taxa extended anterodorsally to level of vertex; mid-dorsal area of head at frontovertex moderately to strongly sunken or excavated between eyes, edges of frontovertex at eye margins and ocellar tubercle raised below lowest level of frontovertex, thus separated from one another by furrow or groove; furrows of various depths, extended from antennal bases around ocellar tubercle and convergent posteriorly on occiput, enclosing on occiput area here termed vertical extension, which may be posterior extension of vertex or part of occiput itself. Antenna (Fig. 7-20) three segmented, varied in shape, size and pile pattern; first segment cylindrical, varied in length and in texture, color, pattern and abundance of pile; second segment somewhat compressed laterally, widened dorsoventrally toward apex, usually shortest (except in *Dioctria albicornis* Wilcox and Martin (Fig. 7)), with pile only on apex dorsally and ventrally; third segment elongate, varied in thickness, from subcylindrical and slightly tapered apically to broadened in middle, or compressed laterally, terminated in one- or two-jointed apical appendage or style, varied in shape and size, from short subtruncate (Fig. 12-14), spoon-shaped (Fig. 15-18, 20), scaphiform (Fig. 11) or flattened laterally (Fig. 19) usually with small spine within its cupped dorsal or apical region.

Mouthparts (Fig. 33, 34). Labrum (b) relatively short, triangular; mandibles absent; lacinia unserrated (d); labium heavily sclerotized, more or less tubular, rounded (Echthodopini) or pointed (Dioctriini) apically, in form of rigid proboscis around hypopharynx (e, f); labella fused midventrally, but free apically and dorsally, folded with lateral edges in contact to form dorsum of proboscis; with (Echthodopini) or without (Dioctriini) notch near apex, here believed to be homologous to similar notch in thickened upper rim of labellum of other Brachycera; tip of labellum membranous, with sensory hairs; labial pile pale yellowish or whitish, either on apical dorsal edge of labella and apex of prementum in those forms with pointed proboscis (Dioctriini) (Fig. 33), or on apical ventral surface of labella and over most of prementum in remaining forms with apically blunt-tipped proboscis (Echthodopini) (Fig. 34). For a more detailed discussion see Melin (1923) and Adisoemarto (1965).

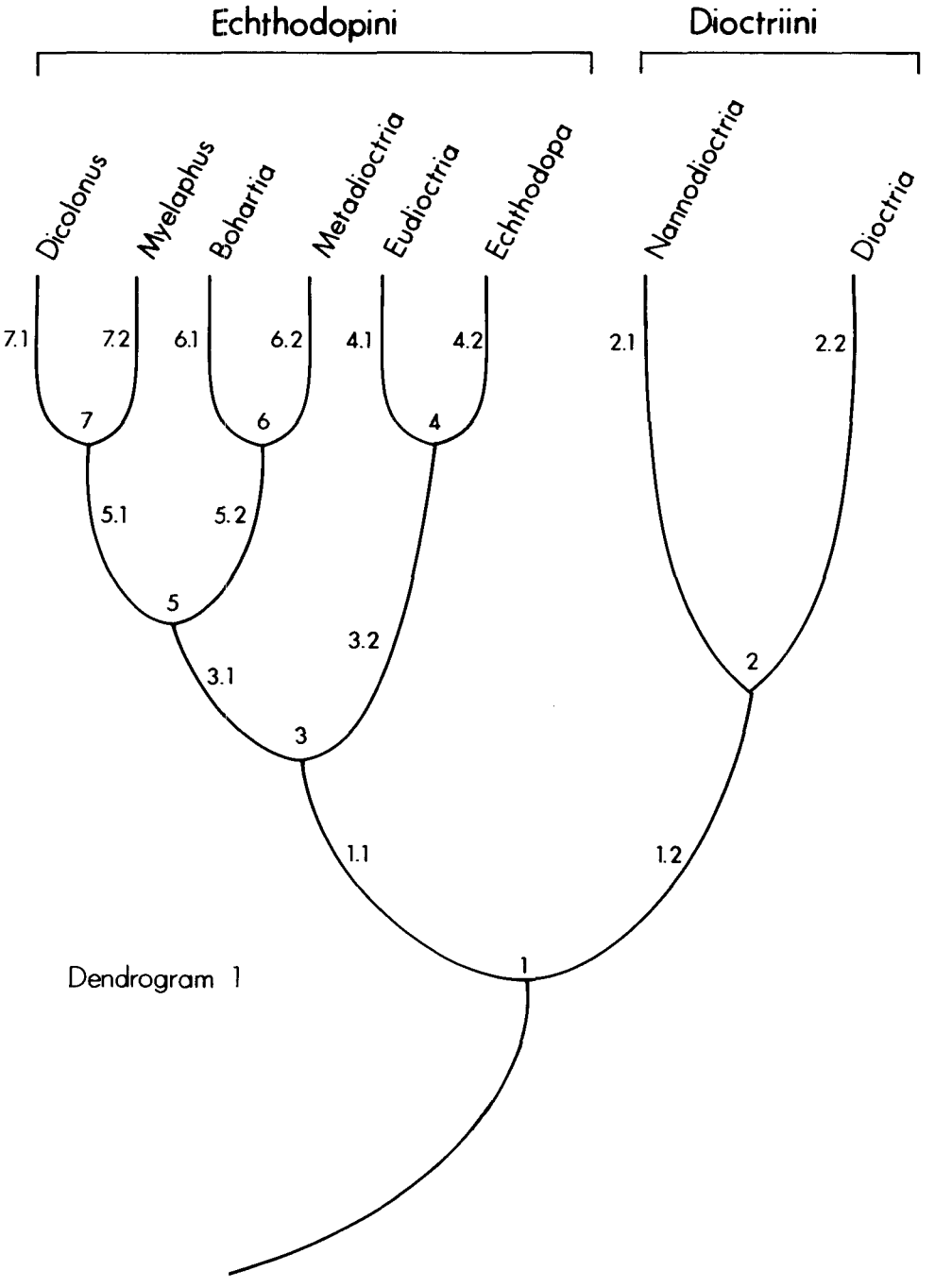
Thorax (Fig. 2, 35-53). Thoracic sclerites varied interspecifically in shape and size, in colour of integument and in colour and distribution of pollinosity and pile; lateral cervical sclerite (Fig. 2, lcs) either bare or pilose; prothorax well developed, antepronotum (apn) bare, pollinose, or pilose and traversed by furrow, post-pronotum or humerus (ppn) elongate and slanting (Fig. 35, 36) or short and upright (Fig. 37-44), with pile varied from short and sparse to long and abundant (Fig. 40); mesopleuron (Fig. 2, msp), in *Dioctria* subg. *Dioctria,* with ridge near posterior margin (Fig. 2, mpr; 37-39); sternopleuron (stp) in Echthodopini with furrow extended upward from point between front- and mid-coxal attachments (Fig. 40-44); scutellum bare or partly to largely pollinose (Fig. 49, 50), or with short fine hairs (Fig. 45, 46), appressed pile (Fig. 52), stiff erect hairs on edge (Fig. 47) or densely pilose on both edge and dorsal surface (Fig. 48, 51, 53).

Wing (Fig. 4, 54-59) either hyaline or slightly infuscated, paler along veins or with white or orange coloration on basal third; in general, one of two types, either narrower, with fourth branch of radial vein (R_4) ended at or behind wing tip and alula absent (Dioctriini) (Fig. 54-56), or wider with R_4 usually ended before wing tip and with alula (Fig. 3, al) usually well developed (Echthodopini) (Fig. 57-59).

Legs (Fig. 3, 60-76). All 3 pairs of legs varied in colour and in pilosity, from sparse and hair-like to abundant and bristle-like, in some species femur with both erect and appressed hairs (Fig. 64); hind femur (Fig. 3, fm) slender and club-shaped (*Dioctria*) (Fig. 60-62) or stouter, thickest subbasally or medially; hind tibia (tb) club-shaped (Fig. 60-62) or only gradually thickened apically (Fig. 63-70); hind legs tuberculate in some species (Fig. 66-68); in some species hind basitarsus conspicuously enlarged, longer than succeeding three segments (Fig. 60-62), and hind empodium comparatively shorter and completely covered with pollinosity (Fig. 71-73); in other species empodium slender, longer and pollinose only basally (Fig. 74-76).

Abdomen (Fig. 77-82). Pregenital part of male with eight segments, in female, eighth sternum part of ovipositor; first abdominal segment short with pile on posterolateral corner; second segment parallel-sided or narrower posteriorly with distinct subbasal groove turned forward laterally; third segment parallel-sided or slightly widened posteriorly; subsequent segments each a little shorter and wider than preceding, widest at apex of fifth segment; eighth tergite, in both sexes, concealed under seventh tergite; eighth sternite absent from male; in some species, abdominal segments relatively wider in female than corresponding segments of male.

Male genitalia (Fig. 5, 83-109). Ninth tergite or epandrium (Fig. 5, epa) trapezoidal with short pointed arms (Fig. 83-92, 107), deeply cleft posteriorly (Fig. 93-104), bifurcate (Fig. 105, 106) or in two halves (Fig. 108); ventral surface of epandrium with pair of sclerites, surstyli (ss), (= edita, Crampton 1942, Emden and Hennig 1956), well developed in some species (Fig. 83-88) or flat (Fig. 89-109) and in some taxa fused mesally (Fig. 105, 106); ninth sternite or hypandrium (hpa) trapezoidal (Fig. 83-88), heart-shaped (Fig. 90-92) or elongate (Fig. 94, 95, 109); gonocoxites (gc) articulated between epandrium and hypandrium, each with distal gonostylus (gs) and from one to three additional unarticulated processes, (1) lateral process (lp) (Karl 1959) originated on inner surface of gonocoxite lateral to base of gonostylus, and varied from club-shaped (Fig. 83-91) or T-shaped (Fig. 107, 108) to flat or scoop-like (Fig. 96-97) (absent from *Eudioctria media* Banks (Fig. 93)), (2) medioventral process (mvp) on ventral inner edge of gonocoxite mesal to base of gonostylus, varied from small and finger-like (Fig. 83-88) to broad (Fig. 98-100) (absent from *Eudioctria monroyia* Wilcox and Martin and *E. dissimilis* new species (Fig. 94, 95)), and (3), in some species, with lateral outgrowth on outer surface of gonocoxite, here termed lateral arm of gonocoxite (Fig. 93, gca); aedeagus (Fig. 5, ae) more or less funnel-shaped at base, narrowed to tube-like apex, and in some species with pair of short dorsolateral processes (adp), simple (Fig. 83-88) or lamellate (Fig. 89-92); apex of aedeagus in some other species



Dendrogram 1. Phylogeny of the genera of Dioctriini and Echthodopini (see Table 1 for explanatory notes).

directed more or less ventrally, associated with this is a variously shaped process on dorsal surface, sclerotized (Fig. 93-100) or membranous (Fig. 101-106), and here called dorsal process of aedeagus (Fig. 93, dpa).

Ovipositor (Fig. 110-139). *Ovipositor formed from eighth, ninth and tenth segments; eighth tergite* or epigynium (Fig. 6, epg) (Crampton 1942) reduced in size but unmodified in shape; eighth sternite or hypogynium (hpg) (Crampton 1942, Emden and Hennig 1956), ventral to epigynium, posteriorly with pair of lobes termed hypogynial valves (hv), and interpreted as homologous to anterior gonopophyses of Tabanidae (Mackerras 1955) or by Cole and Wilcox (1938), probably incorrectly, as *ninth sternite; vagina* (Reichardt 1929) in form of pouch-like space between epigynium and hypogynium; spermathecal opening (Fig. 6, gf) on dorsal wall of vagina, flanked by pair of sclerites, comprising ninth sternite, here believed to be homologous to genital fork of Nematocera and Rhagionidae, in some taxa fused at anterior ends in form of single inverted V- or U-shaped sclerite (Fig. 114-118, 127); pair of small sclerites each attached to apex of arm of genital fork here interpreted as remnants of ninth tergite rather than as part of ninth sternite as was interpreted by Reichardt 1929, Crampton 1942, Emden and Hennig 1956, (such sclerites absent from rhagionids *Rhagio* (Fig. 131), *Symphoromyia* (Fig. 132) or *Chrysopilus* (Fig. 133) in the bombyliid *Aphoebantus* (Fig. 138), and mydid *Nemomydas* (Fig. 137), all with clearly recognizable ninth tergite, undivided or in some taxa divided longitudinally into two halves (Fig. 132), dorsolateral in position, with unmistakable ventrolateral connection on each side to arm of genital fork); eighth and tenth tergites separated by extensive membranous gap, from which dorsal portion of ninth tergite is presumed to have disappeared; tenth tergite (Fig. 110-130) narrow transverse band, more or less emarginate posteriorly, without row of spines (acanthophorites).

TRIBAL AND GENERIC ARRANGEMENT

At the beginning of the following table (Table 1) are listed six characters used to group the Dioctriini (*sensu* Hull) into two tribes, the Dioctriini *s. str.*, with only one genus, and the Echthodopini, with the remaining genera (see Dendrogram 1 following). The Dioctriini *s. str.* is believed to be the more derived. The modification of the labella is peculiar to *Dioctria s. str.*, is not shared with any echthodopine or other dasypogonine genus; consequently it is considered a derived character. Similarly the bare ocellar triangle, reduced mystax, and reduced alula do not occur together in Echthodopini or in other dasypogonines.

A similar comparative analysis of the most important generic characters is also presented in this table. Our phylogenetic interpretation of these facts is shown in Dendrogram 1.

Table 1. Characters used in Interpretation of the Phylogeny of Dioctriini and Echthodopini.

1.1 Echthodopini	1.2 Dioctriini
labella cylindrical, rounded apically, with subapical membranous "notch" (Fig. 26-32).	*labella pointed, flattened dorsally near apex, heavily sclerotized and without subapical "notch" (Fig. 21-25).
ocellar triangle bristled.	*ocellar triangle without bristles.
mystax clumped.	*mystax usually reduced to a transverse row of bristles.
sternopleuron with a vertical furrow or "suture".	*sternopleuron evenly convex, without vertical "suture".
alula well-developed.	*alula reduced.
surstylus flattened or absent.	*surstylus usually with a small lobe.
2.1 *Dioctria (Nannodioctria)*	2.2 *Dioctria (Dioctria)*
*Prothoracic sclerites, especially postpronotum elongate.	Prothoracic sclerites short.
Mesopleuron without ridge.	*Mesopleuron with ridge near posterior margin (Fig. 37-39).
Occiput pollinose on lower half.	*Occiput with a pair of pollinose patches above foramen.
Antennal bases flat, not evident in profile (Fig. 21-22).	*Antennal bases protruding (Fig. 23-25).
Frontovertex pollinose.	*Frontovertex bare.
First antennal segment subequal in length to second segment.	*First antennal segment elongate, longer than second segment.
Lateral process of gonocoxite slender, not bulbous subapically.	*Lateral process of gonocoxite bulbous subapically.
3.1 *Dicolonus, Myelaphus, Bohartia* and *Metadioctria*	3.2 *Eudioctria* and *Echthodopa*
*Abdominal segments parallel sided.	Abdominal segments narrowest at intersegment between second and third segment.
*Upper half of face with hairs (except *Myelaphus*)	No hairs on upper half of face.
Hind margin of epandrium moderately concave, epandrial arms present.	*Hind margin of epandrium deeply cleft, epandrial arms lost.

Table 1. (concluded). Characters used in Interpretation of the Phylogeny of Dioctriini and Echthodopini.

Gonocoxite simple.	*Gonocoxite with lateral subapical outgrowth.
Lateral process of gonocoxite elongate.	Lateral process of gonocoxite flattened and broad.
Lateral process of aedeagus present.	*Lateral process of aedeagus absent.
4.1 *Eudioctria*	4.2 *Echthodopa*
Frontovertex pollinose.	Frontovertex bare.
Pteropleuron bare.	*Pteropleuron pollinose and pilose on anterior half.
*Scutellum bare.	Scutellum pilose.
*Hind femur and hind tibia tuberculate.	Hind leg smooth.
Epandrium deeply cleft.	*Epandrium divided into two lateral halves.
*Lateral outgrowth (arm) of gonocoxite long and curved.	Lateral arm of gonocoxite reduced.
*Aedeagus with distinct dorsal process.	Aedeagus without dorsal process.
5.1 *Bohartia* and *Metadioctria*	5.2 *Dicolonus* and *Myelaphus*
Pile on ventral surface of first antennal segment longer than that on dorsal surface.	*Pile on first antennal segment uniform in length.
Frontovertex narrowed toward antennal bases.	*Frontovertex parallel sided.
Sternopleuron pollinose.	*Sternopleuron bare.
Pile on upper face linear on each side.	Pile on upper face not linear.
Pile on mesonotum and abdomen erect.	Pile on mesonotum and abdomen recumbent.
Pile on mesopleuron marginal.	Pile on mesopleuron extended from upper margin to sternopleuron.
Pile on abdomen, especially on sides of second segment, differentiated in length.	Abdominal pile uniform in length.
Lateral process of aedeagus lamellate.	Lateral process of aedeagus not lamellate.
6.1 *Bohartia*	6.2 *Metadioctria*
Frontovertex and occiput pollinose.	Frontovertex and occiput not pollinose.
Mesonotum pollinose.	Mesonotum bare.
Mesonotal pile short and sparse.	Mesonotal pile long and dense.
Abdomen wider in the middle.	Abdomen parallel sided.
7.1 *Dicolonus*	7.2 *Myelaphus*
Antennal style spoon shaped, one segmented.	*Antennal style compressed laterally, two segmented.
Upper face around antennal bases pilose and pollinose.	*Upper face bare.
First antennal segment densely pilose.	*First antennal segment bare.
*Sternopleural suture absent.	Sternopleural suture present.
Lateral processes of aedeagus greatly reduced.	Lateral processes of aedeagus well developed.

* denotes apomorphic condition.

Key to the North American Genera of Dioctriini and Echthodopini.

1 Apex of proboscis pointed, opening between labella dorsal and subapical, hypopharynx protruded above and slightly proximad of apex; labella without subapical notch (Fig. 33a); prementum shorter than labella, with sparse pile restricted to apex; R_4 ended behind wing tip (Fig. 54-56); alula absent; ocellar tubercle without strong bristles; hind femur club-shaped, abruptly enlarged apically; hind metatarsus conspicuously enlarged, at least as long as subsequent three tarsal segments (Fig. 60-62) ..... Dioctriini 2

1' Apex of proboscis rounded, opening terminal; labella with subapical notch; prementum as long as or longer than labella, with abundant pile on entire lower surface; R_4 ended before wing tip (Fig. 57-59); alula present; ocellar tubercle with long hairs, or bristles curving forward (except in *Myelaphus*); hind femur thickest subbasally,

or at middle or gradually enlarged apically; hind metatarsus shorter than three subsequent tarsal segments (Fig. 63-70) ..... Echthodopini 3

2 (1) Antennal style short, one fifth as long as third antennal segment, subtruncate or spoon-shaped (Fig. 7-9); antennal bases not raised on tubercle, concealed behind eye margin in profile (Fig. 21B, 22B) ..... *Dioctria (Nannodioctria)*, p. 514

2' Antennal style long, one third to one half as long as third antennal segment, more or less scaphiform (Fig. 23B, 24, 25B); antennal bases raised on a conical tubercle visible beyond eye margin in profile ..... *Dioctria (Dioctria)*, p. 516

3 (1') Antenna with three well-developed flagellomeres, apical flagellomere arising between two flap-like apical extensions of second (Fig. 19); face pollinose at most only on lower margin (Fig. 30A); mystax narrow band of short, straight bristles along lower margin of face ..... *Myelaphus* Bigot, p. 528

3' Antenna with only two flagellomeres, second minute, styliform (Fig. 12-18, 20); face largely or entirely pollinose; mystax cluster of curved bristles (Fig. 26-29, 31, and 32) 4

4 (3') Upper half of face, below antennal bases, with abundant long hairs (Fig. 28 and 29); gibbosity without pollen; anatergite with hairs. ..... *Dicolonus* Loew, p. 524

4' Upper half of face without hairs or with at most single row along lateral margin (Fig. 26 and 27); face usually entirely pollinose; anatergite without hairs 5

5 (4') Upper half of face destitute of hairs (Fig. 31 and 32); R_{4+5} branched distal to end of discal cell 6

5' Upper half of face with a row of weak hairs on each side (best seen in profile); R_{4+5} branched proximal to end of discal cell 7

6 (5) Mesopleuron largely covered with smooth recumbent hairs; pollinosity on upper hind corner of sternopleuron extended forward to pollinosity of front corner; scutellum pilose (Fig. 51) ..... *Echthodopa* Loew, p. 549

6' Mesopleuron pilose at most on upper two thirds and along posterior margin; pollinosity on sternopleuron as two separate patches; scutellum pollinose or not, without pile (Fig. 49 and 50). ..... *Eudioctria* Wilcox and Martin, p. 537

7 (5') Frontovertex and occiput pollinose; scutal pile short and appressed, scutellar margin with short appressed hairs; notopleural and supraalar bristles thick. ..... *Bohartia* Hull, p. 529

7' Frontovertex and occiput shining black, without pollinosity; scutal pile long, abundant and suberect; scutellar margin with long fine erect hairs; notopleural and supraalar bristles hairlike ..... *Metadioctria* Wilcox and Martin, p. 535

Tribe Dioctriini Hull, 1962

As treated here, the tribe includes a single diverse genus, *Dioctria s. str.*, with two subgenera, *Nannodioctria*, a New World group with three species, and *Dioctria*, with two major species groups. One group of some 50 species (Engel 1930) is entirely palaearctic (*Dioctria baumhaueri* Mg., a member of this group has been introduced into eastern North America). The other is nearctic except for an unnamed Korean species, and includes only five species. *Nannodioctria* is considered the more primitive of the two, based on characters shown in Table 1.

Diagnosis. – Ocellar tubercle devoid of bristles; region of frons with antennal bases strongly elevated (except in *Nannodioctria*), in form of tubercle-like structure (Fig. 23, 26, 28, 29); facial gibbosity scarcely evident; mystax transverse row of strong bristles, in few taxa with tendency to form clump of bristles; proboscis pointed apically, opening from which hypopharynx protrudes is above and slightly behind pointed apex; dorsal margin at apex of proboscis

flat or slightly concave in profile (Fig. 33a), dorsal edges of labella infolded; labella longer than prementum, shining black, with distinct median longitudinal groove on ventral side, without subapical notch on dorsal side (Fig. 33a); sternopleuron without vertical "suture" or furrow; hind femur and hind tibia each club-shaped; alula absent; male surstylus with small lobe or tubercle (Fig. 83-88).

Genus *Dioctria* Meigen

Subgenus *Nannodioctria* Wilcox and Martin

Dioctria, subgenus *Neodioctria* Wilcox and Martin, 1941: 7. Type-species: *Dioctria (Neodioctria) albicornis* Wilcox and Martin, 1941: 7, by original designation. Preoccupied by *Neodioctria* Ricardo, 1918: 58.

Dioctria, subgenus *Nannodioctria* Wilcox and Martin, 1942: 35, as new name for *Neodioctria* Wilcox and Martin *nec* Ricardo.

Diagnosis. – Antennal style short, one fifth as long as third antennal segment, subtruncate or spoon-shaped; third antennal segment thickened in middle or subcylindrical; ratio of first to second segment variable; antennal bases flat; face flat or slightly convex on lower part, yellow to orange pollinose; occiput largely pollinose, only vertical extension bare; thorax black with brownish markings along prothoracic suture, on post-pronotum, posterior half of pteropleuron, posterodorsal corner of sternopleuron and upper margin of hypopleuron; prothoracic sclerites comparatively elongate (Fig. 35 and 36); postpronotum broad, slanted.

Wilcox and Martin (1941) included only *D. albicornis* in this subgenus, but two more species, *D. seminole* Bromley and *D. australis* new species are also placed here. Our interpretation of the phylogeny of these three species is in Dendrogram 2, below.

Key to species of subgenus *Nannodioctria*

1	First two antennal segments and basal third of third segment pale yellow; pollinosity on mesal area of frontovertex extended to ocellar tubercle; prothoracic and mesothoracic sclerites largely yellowish brown; scutum yellowish brown on sides .... *albicornis* Wilcox and Martin, p. 514
1'	All antennal segments black or dark colored; frontovertex entirely bare; prothoracic and mesothoracic sclerites largely or entirely black; scutum entirely black, bare or pollinose 2
2 (1')	Mesonotum bare; first antennal segment four times as long as its diameter (Fig. 8) ..... *seminole* Bromley, p. 515
2'	Mesonotum pollinose; first antennal segment only twice as long as its diameter (Fig. 9)..... *australis* new species, p. 515

Dioctria (Nannodioctria) albicornis Wilcox and Martin

Dioctria (Neodioctria) albicornis Wilcox and Martin, 1941: 7.

Dioctria (Nannodioctria) albicornis Wilcox and Martin, 1945: 35.

A slender-bodied species easily recognized by colour of antennal segments, shape of antennal style, shape of face, and pattern of pollinosity on the frontovertex.

Description. – Male: length 8.5-9.0 mm; first antennal segment shorter than second; third segment thickest at middle (Fig. 7); first two, and basal 0.33 of third, antennal segments pale yellow; remainder of third segment and antennal style black; face flat, yellowish white pollinose; frontovertex black, yellowish pollinose from anterior end of ocellar tubercle to antennal bases (Fig. 21A); anterior one third and posterodorsal corner of sternopleuron, dorsal 0.75 of mesopleuron, and posterior 0.50 of hypopleuron whitish yellow pollinose (Fig. 35A); scutum pollinose only on lateral margin; fore and mid

legs pale orange yellow; hind leg brown except for yellow coxa, trochanter and basal and apical one fourth of femur; tarsi brownish, darkened apically; abdomen dark brown with orange yellow band on each intersegment; epandrium (Fig. 83B) trapezoidal with pair of posterior arms; surstylus thick with flanged ventral surface (Fig. 83C); hypandrium trapezoidal; gonocoxite tapered apically; lateral process of gonocoxite curved, pointed at apex; medioventral process short, thumb-like; gonostylus gradually tapered apically, curved mesally; aedeagus funnel-shaped with widely separated dorsolateral processes; ovipositor with broad hypogynial valves, widely separated from each other; genital fork divided into two sclerites; portions of ninth tergite quadrangular, concave on ventral surface; tenth tergite semicircular narrow band.

Female: length 9.0-11.0 mm; otherwise same as male.

Distribution. – Central California, in the vicinity of Sequoia National Park, at an altitude of 7000 ft. (Map 1).

Specimens examined. – 6 ♂♂, 5 ♀♀.

Dioctria (Nannodioctria) australis new species

The mesonotal pollinosity readily distinguishes this species from the other two species of *Nannodioctria.*

Description. – Male: length 11 mm; antennal style spoon-shaped, 0.20 as long as third antennal segment (Fig. 9); third antennal segment subcylindrical; first antennal segment about twice as long as its diameter, as long as second segment; frontovertex black, bare, only anterior corners yellow pollinose; antennal bases flat; face slightly convex on lower part, orange pollinose; proboscis black, orange basally; occiput largely pollinose; lateral cervical sclerite and antepronotum largely black, orange along suture; postpronotum brownish; bristles on lateral cervical sclerite and along presutural antepronotum orange; mesothorax black with brownish patches on posterodorsal corner of sternopleuron, upper margin of hypopleuron and posterior half of pteropleuron; scutum black, largely orange yellow pollinose, with pair of bare streaks on anterior dorsocentral region, another pair above wing bases, and a pair across posterior calli; scutellum black, pollinose on basal half and along hind edge; pile on scutellar margin short, yellowish; pollinosity on mesothoracic pleura as in *D. albicornis* and *D. seminole;* mesothoracic hairs and bristles orange yellow; legs brownish orange and black; coxae and trochanters brownish orange; front and mid femora brownish orange, black dorsally; hind femur entirely black, except pale marking on ventral surface of apex; front and mid tibiae brownish orange; hind tibia entirely black; front and mid tarsi brownish orange basally, gradually darkened to black toward apices; hind tarsus entirely black; claws black, orange basally; wings hyaline, 1.75 times length of abdomen; wing veins dark brown; abdomen entirely black; genitalia orange with triangular black marking on base of epandrium. Length: 11.0 mm.

Female: same as male except hind femur black only on dorsal surface; abdomen black with orange markings on sides of second, third, sixth and seventh segments, four corners of fourth and hind corners of fifth segments; eighth segment and ovipositor orange.

Holotype: ♂, 8 mi. NE San Cristobal, Chiapas, Mexico, 10.V.1969 (H. J. Teskey) – CNC.

Allotype: ♀, Mexico City, 10,000′, VII.1936 (H. G. Meyer) – USNM.

Paratypes: 1 ♀, same data as allotype – USNM; 1 ♀, Desierto Leones, Mexico, III,IV,V,1965 (N. L. H. Krauss) – USNM.

Dioctria (Nannodioctria) seminole Bromley

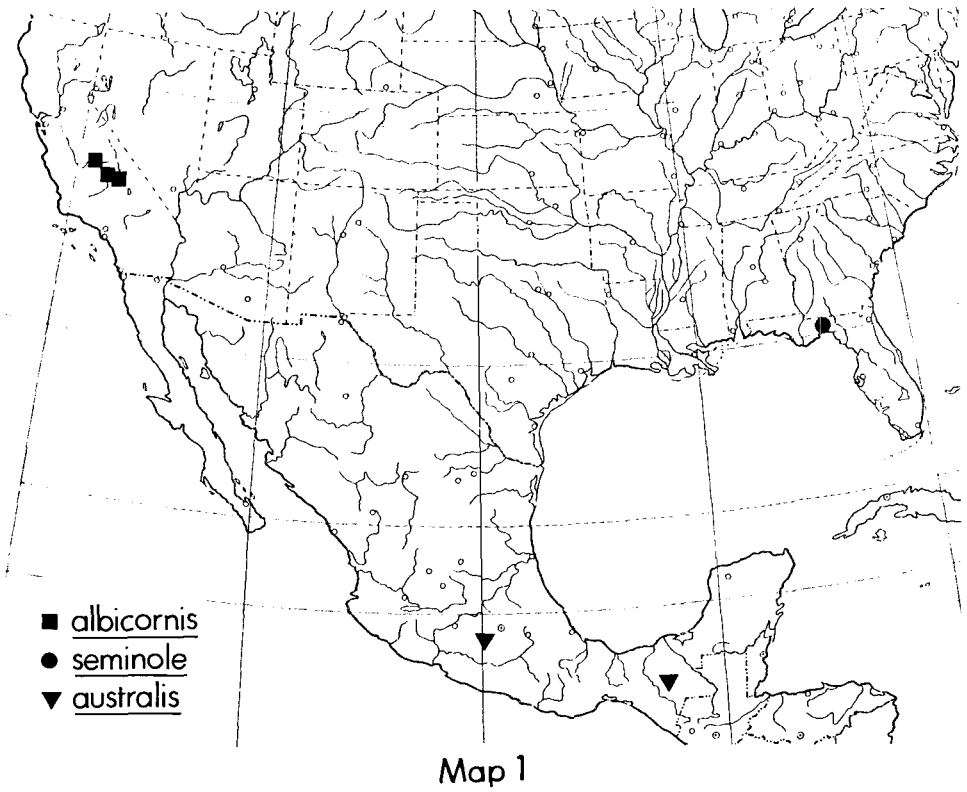
Dioctria seminole Bromley, 1924: 125.

Dioctria (Dioctria) seminole Bromley: Wilcox and Martin, 1941: 6.

Wilcox and Martin (1941) assigned this species to the subgenus *Dioctria.* However, shape of antennal style (Fig. 8), shape of antennal bases (Fig. 22), occipital pollen pattern, shape of postpronotum (Fig. 36) and absence of a mesopleural ridge, suggest a closer affinity to *Nannodioctria* than to *Dioctria.*

Description. – Female: length 10.5 mm; antennal segments black, first segment elongate, 1.66 as long as second segment; third segment slightly thickened at middle (Fig. 8); face slightly gibbose on lower part (Fig. 22); frontovertex black, pollinose only near antennal bases; occiput black, upper half pollinose; pollinosity on anterior margin of mesothoracic pleuron slightly interrupted on lower margin of mesopleuron (Fig. 36); color pattern of legs as in *D. albicornis;* abdomen black with orange intersegmented bands.

Only the female holotype, from Tallahassee, Florida, now in the Cornell University Collection, is known (Map 1).



Map 1. Distribution of the species of *Dioctria* subg. *Nannodioctria*.

Subgenus *Dioctria* Meigen

Dioctria Meigen, 1803: 270. Type-species: *Asilus oelandicus* Linnaeus, 1758, designated by Latreille, 1810 (see also Coquillett, 1910).

Diagnosis. – Antennae uniform (Fig. 10, 11); antennal style long, 0.33 to 0.50 as long as third segment, more or less scaphiform; third segment subcylindrical; second segment shorter than first segment; first segment four times as long as its diameter; antennal bases elevated in form of tubercle (Fig. 23-25); lower part of face slightly gibbous; frontovertex pollinose only on front corners, in some species pollinosity extended to antennal bases (Fig. 23B); occipital pollinosity as pair of patches above foramen; prothoracic sclerites comparatively shorter; lateral postsutural antepronotum convex; postpronotum short, in form of less obtuse angle with body axis (Fig. 37, 39B), usually black; mesopleural ridge near posterior margin (Fig. 37-39 A); male genitalia (Fig. 84-88) differing from *Nannodioctria* only by shape of lateral process of gonocoxite (bulbous subapically, pointed at apex); surstylus in some species with lateral projection (Fig. 85-88C); ovipositor (Fig. 110-112) similar to that of *albicornis*.

Remarks. – In North America members of this subgenus are more uniform than those of *Nannodioctria*. The fifty-odd Eurasian species can be grouped in the subgenus *Dioctria*, but they are morphologically more varied, and differ from the five North American species in patterns of pollinosity on the mesonotum, in abdominal color pattern and in shape of the

gonostylus which curves laterally instead of mesally.

Our interpretation of the phylogeny of the six species is shown below in Dendrogram 2.

Key to species of subgenus *Dioctria* in North America

1 Mesonotum largely pollinose except for two narrow bare dorsocentral stripes; coxae black. . . . . *baumhaueri* Meigen, p. 519

1' Mesonotum largely bare, at most pollinose marginally; coxae orange yellow . . 2

2 (1') Pollinose area of anterodorsal region of sternopleuron extended dorsally as broad band to or nearly to upper margin of sternopleuron, contiguous or nearly so with pollinose area on anterior margin of mesopleuron (Fig. 37A), or two areas separated by very narrow gap, several times longer than high 3

2' Pollinose area of anterodorsal region of sternopleuron reduced, separated from pollinose area on anterior margin of mesopleuron by broad gap at least as high as long (Fig. 39A) 5

3 (2) Anterodorsal corner of postpronotum pollinose . . . . . *pleuralis* Banks, p. 517

3' Anterodorsal corner of postpronotum bare 4

4 (3') Postpronotum, posterior margin of mesopleuron, posterior half of pteropleuron, posterodorsal corner of sternopleuron and upper half of hypopleuron reddish-brown in ground color; ventral corner of antepronotum pollinose . . . . . *wilcoxi* new species, p. 518

4' Prothorax and mesothoracic pleuron black in ground color . . . *vera* Black, p. 518

5 (2') Pollinosity of anterior part of mesopleuron almost completely hidden beneath hairs of prothoracic spiracle; pollinosity along dorsal margin narrower than pollinose band on notopleuron above it . . . . . *pusio* Osten Sacken, p. 518

5' Pollinosity of mesopleuron more extensive, extended in continuous strip along anterior, dorsal and posterior margins . . . . . *henshawi* Johnson, p. 517

Dioctria (Dioctria) henshawi Johnson

Dioctria flavipes Banks, 1917: 119, *nec* Meigen 1804.
Dioctria henshawi Johnson, 1918: 103 (n. name for *flavipes* Banks).
Dioctria vertebrata Cole, 1919: 230. NEW SYNONYMY.
Dioctria (Dioctria) henshawi Johnson: Wilcox and Martin, 1941: 5.

Description. – Male: length 7.0-8.0 mm; antennal bases bare on sides (Fig. 24); postpronotum bare; pollinosity on anterodorsal area of sternopleuron reduced in size, not extended to upper margin of sternopleuron (Fig. 38); surstylus with lateral projection (Fig. 86C).

Female: length 7.0-8.5 mm; otherwise as in male.

Distribution. – Southern British Columbia, southward along the Cascade Range to the northern Sierra Nevada, east to Idaho and Utah (Map 4).

Specimens examined. – 28 ♂♂, 29 ♀♀.

Dioctria (Dioctria) pleuralis Banks

Dioctria pleuralis Banks, 1917: 118.
Dioctria (Dioctria) pleuralis Banks: Wilcox and Martin, 1941: 5.

Description. – Male: length 8.0-10.0 mm; antennal bases pollinose on sides (Fig. 23B); anterodorsal 0.33 of postpronotum pollinose; pollinosity on anterior margin of mesopleuron contiguous with that on anterior part of sternopleuron (Fig. 37A); pile on scutum extended from behind postpronotum to mesonotal suture (Fig. 37B); surstylus on ventral surface of epandrium with lateral projection (Fig. 85C).

Female: length 9.0-11.5 mm; otherwise as in male.

Remarks. – A series of two males and six females from Laguna Mts., San Jacinto Mts., San

Bernardino Co., and San Diego Co., Calif., lack postpronotal pollinosity. Another series of both male and female specimens from Santa Cruz Island, California, are largely black, including the hind legs, with the postpronotal pollinosity only on anterior corner. Still another series of four males and four females from Santa Anna, California, possess postpronotal pollinosity like that of the Santa Cruz Island specimens, but with intersegmental orange bands present on the abdomen. We interpret this as intraspecific variation only.

Color of legs in *D. pleuralis* is similar to that in *D. wilcoxi.* The abdominal orange markings vary in both sexes. Some males have an extra orange band of varying size across the middle of the second segment while in some females the last few segments of the abdomen tend to be pale; in other females the hind legs are entirely orange.

Distribution. – Southwestern corner of California, from Santa Barbara County, including Santa Cruz Island, to San Diego County, with an isolated record from Flagstaff, Arizona (Map 2).

Specimens examined. – 23 ♂♂, 26 ♀♀.

Dioctria (Dioctria) pusio Osten Sacken

Dioctria pusio Osten Sacken, 1877: 288.
Dioctria (Dioctria) pusio Osten Sacken: Wilcox and Martin, 1941: 5.

Among the North American species of *Dioctria (sensu stricto)* this is the least pollinose; specimens appearing as shiny, almost bare.

Description. – Male: length 6.0-7.0 mm; sides of antennal bases bare (Fig. 25B); upper face below antennal bases of some specimens with median bare streak; mesopleuron bare except extremely narrow pollinose band along dorsal and posterior margins (Fig. 39A); legs largely orange, hind tibia darker; tarsi brown apically; abdomen mainly reddish brown, first segment and middle basal half of second segment black; surstylus with lateral projection (Fig. 88C).

Female: length 7.0-8.0 mm; otherwise as in male.

Distribution. – Southern British Columbia south along the Cascade and Coast Ranges to the Sierra Nevada, California, with an isolated record in central Colorado (Map 5).

Specimens examined. – 57 ♂♂, 50 ♀♀.

Dioctria (Dioctria) vera Back

Dioctria vera Back, 1909: 256.
Dioctria (Dioctria) vera Back: Wilcox and Martin, 1941: 6.

Description. – Male: length 8.0-9.0 mm; antennal bases of most specimens mainly bare on sides; postpronotum bare; pollinosity on anterior margin of mesopleuron broadly contiguous with that of sternopleuron; pile on mesonotum restricted to small triangle behind postpronotum continued posteriorly along dorsocentral region as narrow strip; surstylus with lateral projection (Fig. 87C).

Female: length 8.0-10.0 mm; otherwise as in male.

Remarks. – As in *D. pleuralis* this species also varies in coloration: the abdomen varies from largely orange with black markings on the middle of the first and the second segments to completely black; the legs are either entirely orange or with largely brown hind femur, and brown hind tibia and tarsus.

Distribution. – Widely distributed in western United States from northern California, northern Utah and northern Colorado to southern California and southeastern New Mexico (Map 3).

Specimens examined. – 82 ♂♂, 144 ♀♀.

Dioctria (Dioctria) wilcoxi new species

Description. – Male: frontovertex slightly more pollinose than in other species, especially on sides and above antennal bases; anterior half of lateral cervical sclerites, postpronotum, posterior margin of mesopleuron, posterodorsal corner of

sternopleuron, upper half of hypopleuron and posterior half of pteropleuron reddish brown contrasted with remaining black areas; pollinosity on sides of postsutural antepronotum yellowish orange; dorsal margin of postpronotum and adjacent scutum whitish pollinose; sternopleural and mesopleural pollinosity contiguous; anterior two pairs of legs and hind coxa orange yellow; hind femur darker, hind tibia and tarsus brown; basal half of claws brownish, remainder black; abdomen black with dorsal orange markings on sides of first three segments, anterior and posterior margins of third to sixth segments, and posterior margin of seventh segment; genitalia orange, surstylus without lateral projection (Fig. 84C).

Female: as in male; abdomen comparatively wider, ovipositor orange (Fig. 110).

Remarks. – Some specimens of both sexes have the first two antennal segments paler than the third.

Type material. –

Holotype: ♂, Strawberry, Tuolumne Co., Calif., 10.VII.1951 (W. C. Bentinck) – CIS.

Allotype: ♀, same locality, 15.VIII.1960 (C. A. Toschi) – CIS.

Paratypes: Calif.: 1 ♂, same locality, 14.VII.1951 (D. Burdick) – CIS; 1 ♂, Pinecrest, Tuolumne Co., 11.VIII.1948 (P. H. Arnaud, Jr.) – JW; 1 ♀, Strawberry, Tuolumne Co., 19.VI.1951 (A. T. McClay) – UCD; 1♀, Cow Creek, Tuolumne Co., 24.VI.1951 (E. Schlinger) – UCD; 2 ♀♀, Pinecrest, Tuolumne Co., 18.VII.1947, 16.VII.1948 (P. H. Arnaud, Jr.) – JW; 1 ♀, Huntington Lake, Fresno Co., 7000′, 22.VII.19(?) (F. E. Blaisdell) – JW.

Distribution. – Central Sierra Nevada, California (Map 2).

Dioctria (Dioctria) baumhaueri Meigen

Dioctria baumhaueri Meigen, 1820: 245.
Dioctria baumhaueri Meigen: Johnson, 1918: 102.
Dioctria (Dioctria) baumhaueri Meigen: Wilcox and Martin, 1941: 5.

This species was introduced from Europe (Johnson, 1918) and has become common in eastern North America.

Description. – Male: 10.0-13.0 mm; face whitish yellow pollinose, bare below antennal bases; mystax whitish, bristles on antennal segments dark brown; other pile on head yellowish; antepronotum without pollinosity; following whitish pollinose – postpronotum, procpimeron, anterior half of sternopleuron, anterior, dorsal and posterior margins of mesopleuron, posterodorsal corner and posterior margin of sternopleuron, hypopleuron, posterior half of pteropleuron and sides of coxae; scutum largely pollinose with two bare parallel dorsocentral streaks and submarginal bare spot on each intra-alar region; front and mid femur and tibia predominantly orange yellow except for narrow black band along dorsal surface of femur; hind femur varied from completely orange yellow to completely black; hind tibia varied from mainly orange yellow with black tip to mainly black with orange yellow base; all tarsi black; wing hyaline; abdomen black; genitalia black; surstylus without lateral projection; gonostylus curved laterally.

Female: as in male.

Distribution. – Southwestern Michigan (Oakland Co.) east to southern Quebec and New York.

Specimens examined. – approximately 300 of each sex.

Table 2. Characters used in Interpretation of the Phylogeny of the Nearctic species of *Dioctria*.

2A.1 *D. albicornis* and *D. seminole*	2A.2 *D. australis*
Intersegmental orange bands on abdomen.	*Abdominal segments black.
*Antepronotum longer.	Antepronotum shorter.
Scutum pollinose only on lateral margins.	Scutal pollinosity in form of a pattern.
Hind femur orange with black streak in both sexes.	Hind femur entirely black in male, black on dorsal half in female.
2B.1 *D. albicornis*	2B.2 *D. seminole*
First antennal segment shorter than second.	*First antennal segment longer than second.
Anterior half of frontovertex pollinose.	*Frontovertex without pollinosity.
First two antennal segments orange.	Antennal segments uniformly black.
2C.1 Nearctic line (inc. one Korean species)	2C.2 Palaearctic line
*Mystax linear.	Mystax usually clustered.
*Lateral process of gonocoxite curved mesad.	*Lateral process of gonocoxite curved laterad.

Table 2. (concluded). Characters used in Interpretation of the Phylogeny of the Nearctic species of *Dioctria.* (See Dendrogram 2, p. 521)

2D.1 *D. wilcoxi*	2D.2 four other Nearctic spp. (and Korean species).
Postpronotum orange brown.	*Postpronotum black.
Mesothoracic pleuron with brownish orange markings.	*Mesothoracic pleuron entirely black.
Mesonotal pollinosity on lateral margins wide.	*Mesonotal pollinosity on lateral margins narrow.
*Side of antepronotum pollinose.	Antepronotum bare.
*Mesonotum behind postpronotum pollinose.	Mesonotum behind postpronotum bare.
Surstylus without lateral projection.	*Surstylus with lateral projection.
2E.1 *D. pleuralis*	2E.2 *D. vera, D. henshawi, D. pusio,* and Korean sp.
*Postpronotum pollinose on anterodorsal corner.	Postpronotum bare.
*Mesonotal pile extended to mesonotal suture.	Mesonotal pile present only slightly behind postpronotum.
Intersegmental orange yellow bands from second to sixth segment.	*Intersegmental orange yellow bands only to fourth segment or less.
Abdominal segments long.	*Abdominal segments shorter.
2F.1 *D. vera*	2F.2 *D. henshawi, D. pusio,* and Korean species.
Sides of antennal bases pollinose.	*Sides of antennal bases bare.
Pollinosity on anterior edge of meso- and sternopleuron continuous.	*Pollinosity on anterior edge of meso- and sternopleuron interrupted.
Antennal style spoon-shaped.	*Antennal style scaphiform.
2G.1 *D. henshawi*	2G.2 *D. pusio* and Korean species.
Face entirely pollinose.	*Upper face below antennal bases bare.
Intersegmental bands on abdomen present.	*Abdomen without intersegmental bands.
Hind femur with dorsal black streak.	*Hind femur without black streak.
2H.1 *D. pusio*	2H.2 Korean species.
Bare marking on upper face only slightly below antennal bases.	*Bare marking on upper face occupies one third of face.
Abdomen orange.	Abdomen black.
Hind leg orange.	Hind leg black.

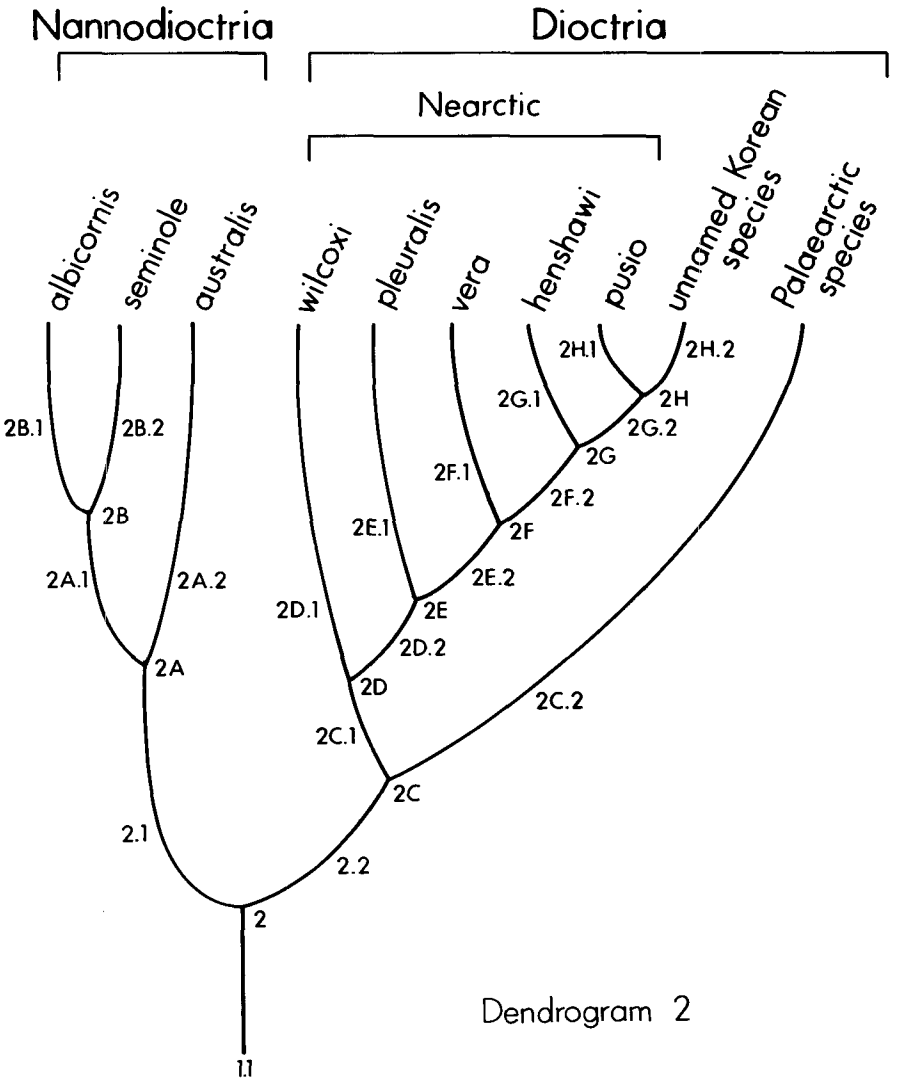
* denotes apomorphic condition

Distribution and Zoogeography of *Dioctria.*

The three species of *Nannodioctria* are more primitive than, and do not appear to be as closely related to one another as, those species of the subgenus *Dioctria,* suggesting they are older. They are widely allopatric in distribution, i.e., Central California, Florida and Mexico (Map 1), in what may be called a relict distribution. Such a pattern of distribution has been explained as a result of extinction of most species of the group, without further speciation, leaving a few survivors in peripheral areas of their former range.

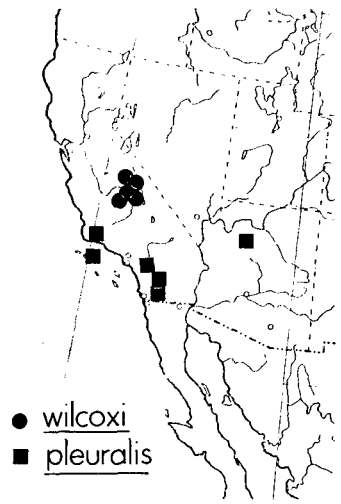
The Palaearctic species of the subgenus *Dioctria,* except for an undescribed Korean species are considered a monophyletic group (Dendr. 2, 2C.2), while the Nearctic species of *Dioctria,* together with the Korean species, form another monophyletic group (2C.1). Consequently of the several possibilities for the origin of the genus *Dioctria,* only two, North America or Asia, seem probable.

We believe that *Dioctria* originated in North America, and that the Palaearctic species group evolved from an ancestor that migrated some time ago from the New World to the Old. At a much later date, the ancestor of the Korean sister species of *D. pusio* moved in a similar direction. Both the Palaearctic species group of *Dioctria,* and the Korean species, have been interpreted here as being derived with respect to their Nearctic sister group counterparts, suggesting that all the Nearctic forms are more primitive. The latter have remained and continue to evolve at their site of origin. A Nearctic origin for *Dioctria* is also consistent with the exclusive occurrence of *Nannodioctria* and all but three species of the Echthodopini in the Nearctic Region.

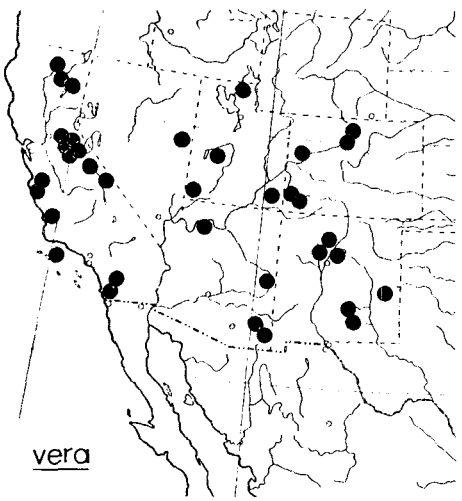


Dendrogram 2. Phylogeny of the Nearctic Species of *Dioctria*.

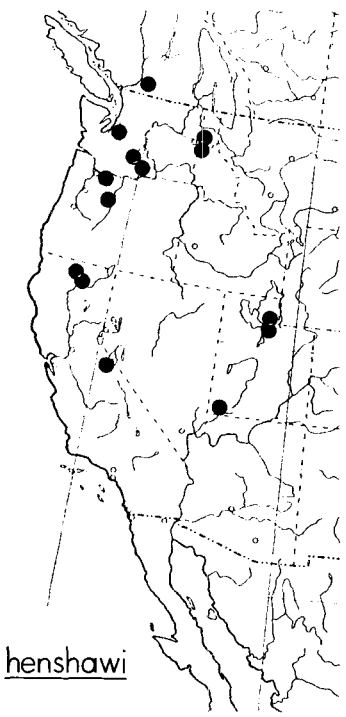
If, on the other hand, *Dioctria* originated in the Palaearctic region, migration must have taken place after the two subgenera, *Dioctria* and *Nannodioctria*, had differentiated. One of them, the ancestor of *Nannodioctria*, migrated to North America without leaving any known representatives in Asia. The other, the ancestor of the subgenus *Dioctria*, then split into two lineages, one migrating to North America to become the ancestor of the Nearctic species of the subgenus *Dioctria* (Dendr. 2, 2C.1), without leaving known representatives in Asia, the other remaining in Asia to develop into the Palaearctic species group (Dendr. 2, 2C.2). The presence of an unnamed species in Korea (2H.2), which shares a common ancestor with the most derived Nearctic species (*D. pusio*), indicates a more recent migration from North America



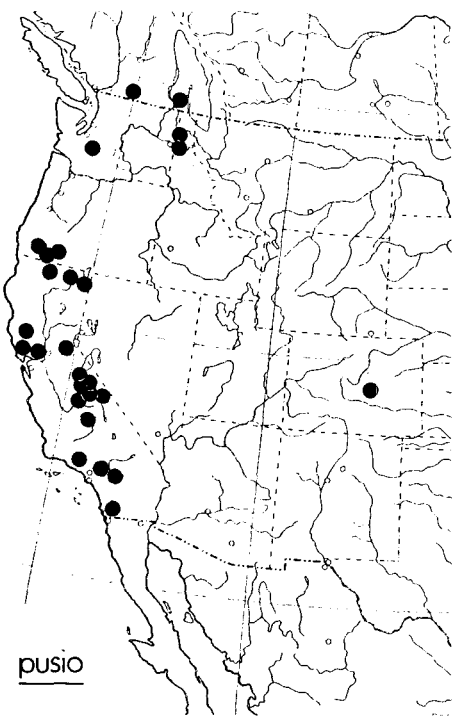
Map 2



Map 3



Map 4



Map 5

Maps 2-5. Distribution of the Nearctic species of *Dioctria* subg. *Dioctria*.

to Asia. A parallel case is found in the fish family Catostomidae which originated in Asia and radiated secondarily in North America, with one species, *Catostomus catostomus,* subsequently returning to Asia (Darlington, 1957).

There were at least five opportunities for these migrations to have occurred in the area of Beringia during the Tertiary, i.e., the early Eocene, late Eocene, early Oligocene, late Miocene and middle to late Pliocene (Simpson, 1947). To these possibilities one must also add the interglacial periods of the Pleistocene. It is believed that there were three major areas of connection between North America and Eurasia during the Tertiary period, i.e., transarctic, transatlantic and Beringian (Lindroth, 1957; Hopkins, 1967). Since the first two connections ceased to exist before or during early Tertiary time (Lindroth, 1957), the Beringian land bridge is the most likely one to be relevant to movement of *Dioctria.* The Korean species, because it has been the most recent species to evolve, probably left North America in the late Pliocene. The flora of the land bridge at that time consisted of muskeg vegetation and woodlands dominated by birch, aspen, alder and willow (Hopkins, 1967). A few species of the European group of *Dioctria* also occur today in this type of habitat.

In the Pliocene, coniferous forests, of the type where most *Dioctria* are now found both in Europe and North America, were dominant on both continents. The land bridge at that time was not of this type, however, but may have been so during the Miocene. Perhaps the earlier migration, i.e., that of the ancestor of the Palaearctic group of *Dioctria* took place during the Miocene.

Tribe Echthodopini new tribe

Diagnosis. – Ocellar tubercle with bristles; proboscis rounded apically, its opening apical; labellum with subapical notch; sternopleural suture present, extending upward from a point between front and mid coxal attachments; mesopleuron without prominent crest or ridge parallel to posterior margin in front of mesopleural bristles; hind femur thickened sub-basally or in middle; alula well developed; male surstylus flattened, reduced in size or absent, without lobe or tubercle.

Remarks. – Six genera are here assigned to this tribe: the type genus, *Echthodopa,* and *Dicolonus, Myelaphus, Bohartia, Metadioctria* and *Eudioctria.* Together they form a collection of rather dissimilar dasypogonine genera that do not have acanthophorites; they all share with *Dioctria* a prominent transverse groove on the second abdominal tergite, but they lack the distinctively pointed proboscis characteristic of *Dioctria.* As such, the Echthodopini may be an artificial assemblage, or more likely a paraphyletic group, for we have not been able to define it in terms of synapomorphic characters. It is treated here, for convenience, as a single tribe, the primitive sister group of the Dioctriini.

Nearly all of the species of Echthodopini are found in North America, and one might therefore conclude that the group arose on that continent. Two species of *Myelaphus* and one *Dicolonus,* however, are recorded from the central and eastern Palaearctic region (Hull, 1962; Engel, 1930). Unfortunately, these species were not available for study, and it should be noted that *Myelaphus* and *Dicolonus* appear to be the most primitive of the group (Dendrogram 1). Until the Palaearctic species can be analyzed phylogenetically to determine whether they or the nearctic species are the more primitive, it seems impossible to determine on which continent the tribe arose. Western North America seems, nevertheless, to have been the area of greatest radiation, for all the species of *Bohartia* and *Metadioctria* and the majority of *Eudioctria* are found there. This region was isolated by reduced rainfall as early as the Oligocene (MacGinitie, 1958); the isolation was reinforced during the Miocene by development of the Rocky Mountains and of the Great Plains in their rain shadow.

Genus *Dicolonus* Loew

Dicolonus Loew, 1866: 32. Type-species: *Dicolonus simplex* Loew (loc. cit.), by monotypy.
Dicolonus Loew: Back, 1909: 246.

Diagnosis. * – Face between mystax and antennal bases with dense tuft of long pile, pollinose except for triangular bare marking on gibbosity; occiput pollinose and densely pilose; frontovertex and vertical extension bare; prothoracic sclerites, upper half of mesopleuron, scutum, scutellum, anterior and posterodorsal corners of sternopleuron densely pilose but without pollinosity; abdomen parallel sided, uniformly and densely pilose; male genitalia uniform (Fig. 107); epandrium trapezoidal with pair of posterior arms; lateral process of gonocoxite T-shaped; aedeagus without processes; genital fork of ovipositor divided into two sclerites (Fig. 129A).

Remarks. – This genus is uniform; the species assigned here are distinguished only by variation of length, texture and colour of the pile. Our interpretation of the phylogeny of the five species is shown in Dendrogram 3 below.

Key to the Nearctic species of *Dicolonus*.

1	Pile on edge and surface of scutellum short, hardly exceeding thickness of scutellum; mesonotal pile short, recumbent 2
1'	Pile on edge and surface of scutellum at least as long as length of scutellum; mesonotal pile erect or at most only slightly reclining 3
2 (1)	Pile on centre of scutum reddish brown, surrounded by orange pile on margins; occipital bristles when viewed laterally orange mixed with black along margin ..... *sparsipilosum* Back, p. 525
2'	Pile on centre of scutum uniformly orange yellow, occipital pile entirely orange yellow ..... *pulchrum* new species, p. 525
3 (1')	Scutal hairs crinkled..... *simplex* Loew, p. 525
3'	Scutal hairs straight 4
4 (3')	Scutum with at most four or five longer black hairs along dorsocentral region; pile on front and dorsal surfaces of hind femur appressed (Fig. 69) ..... *medium* new species, p. 524
4'	Scutum with numerous long, strong, black hairs present along dorsocentral and supraalar regions extending beyond yellow pile; pile on hind femur uniformly erect or semi-erect (Fig. 70) ..... *nigricentrum* new species, p. 525

Dicolonus medium new species

Length of pile, especially on the scutum, is intermediate between that of *D. sparsipilosum* and *D. simplex*.

Description. – Male: Length 9.5 mm; head black, pile long, abundant and suberect; gibbosity rather abruptly constricted above (Fig. 28); area occupied by mystax slightly less than half of face; frontal, ocellar and occipital bristles as long as first antennal segment; thorax with erect orange yellow pile; scutal pile suberect, as long as or slightly longer than diameter of first antennal segment, slightly brownish on central area; few orange bristles on dorsocentral and supraalar regions; scutellar bristles longer than length of scutellum; remaining thoracic pile pattern as in *D. sparsipilosum* but longer and suberect; abdomen with long and erect pile, in form of fringes along lateral margins when viewed from above.

Type material. – Female: Length 10.0 mm; mesonotal pile uniformly orange yellow; otherwise same as male.

Holotype: ♂, Mineral King, Tulare Co., Calif., 8000 ft., 7.VII.1942 (R. Bohart) – USNM.

Allotype: ♀, same data – USNM.

**D. argentatus* Matsumura, from Japan, not seen.

Paratype: 1♂, Charleston Mt. Park, Nevada, 9000 ft., 21.VI.1940 (R.M. Bohart) – USNM. (Map 7).

Dicolonus nigricentrum new species

Description. – Male: Length 9.0-12.0 mm; as in *medium*, but with numerous long black bristly hairs on dorsocentral region distinctly longer than remaining pile; scutellar pile orange, longer than length of scutellum; legs with suberect pile on hind femur (Fig. 70).

Female: Length 12.0-14.0 mm; otherwise as in male.

Remarks. – This species is very similar to *D. medium* but can be distinguished by numerous distinct black hairs on the scutum, extended beyond the yellow pile.

Type material. –

Holotype: ♂, Potlatch, Idaho, 20.VI.1907 (J.M. Aldrich) – USNM.

Allotype: ♀, Pullman, Wash., 2.VI.1907 (J.M. Aldrich) – USNM.

Paratypes: 1♂, 1♀, Rock Lake, Wash., (J.M. Aldrich) – USNM; 1 ♂, Pullman, Wash., 4.VI.07 – USNM; 1♂, Twisp, Wash., 12.VII.1960 (F.C. Harmston) – USNM; 1♂, White Lake, Oliver, B.C., 28.V.1959 (R.E. Leech) – CNC; 1♀, Keremeos, B.C., 29.VI.1923 (C.B. Garrett) – CNC. (Map 7)

Dicolonus pulchrum new species

This species is similar to *D. sparsipilosum* but is distinguished by the following characteristics:

Description. – Male: Length 9.5 mm; frontal bristles black, slightly shorter than first antennal segment; ocellar bristles black, 0.33 as long as frontal bristles; occipital bristles orange; scutal pile orange, dense, covering scutum as velvety orange layer, obscuring its ground colour; dorsocentral bristles absent; posterior edge of scutellum without long bristles, but with only short pile not exceeding thickness of scutellum.

Female: Length 10.5 mm, otherwise same as male.

Type material. –

Holotype: ♂, Tallac, Lake Tahoe, Calif., 25.VII.1915 – USNM.

Allotype: ♀, same locality, 17.VII.1915 (E.P. VanDuzee) – USNM.

Paratype: 1 ♀, Yosemite, Calif., 3880-4000 ft., 19.VI.1931 – USNM; 1 ♀, same locality, 22.VI. 1931 (E.O. Essig) – USNM; 1♂, 1♀, L. Tahoe, Calif. – USNM. (Map 7).

Dicolonus simplex Loew

Dicolonus simplex Loew, 1866: 32.

Dicolonus simplex Loew: Back, 1909: 247.

This species is easily recognized by the long, erect orange yellow pile with tip of each hair curled.

Description. – Male: Length 13.0-14.0 mm; pile in general long, dense and erect, each hair curled at tip; frontal bristles black, 1.5 times as long as first antennal segment; ocellar bristles black, as long as frontal bristles; bristles on upper face black, mixed with few orange hairs on lower part; ocellar bristles black mixed with orange; scutal pile orange, dense, erect, obscuring dorsocentral bristles; scutellum with dense erect orange pile and long bristles on posterior edge (Fig. 52); pile and bristles on legs orange; pile on abdomen orange.

Female: Length 12.0-15.0 mm; bristles on upper face below antennal bases and ocellar bristles largely orange; otherwise same as male.

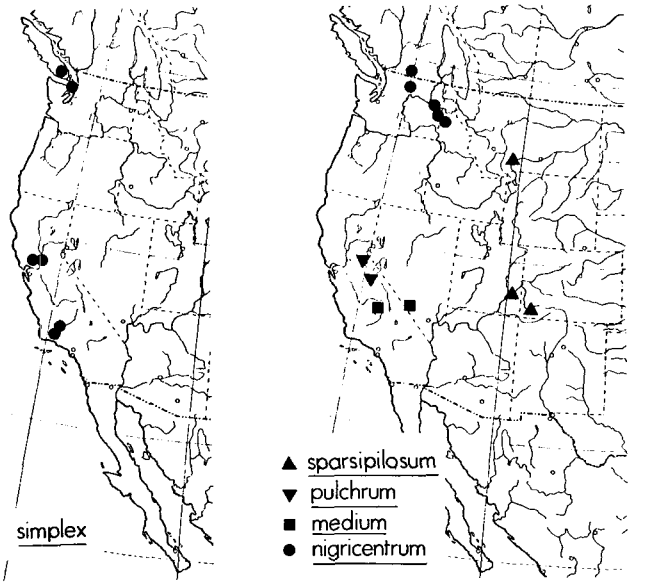
Distribution. – Cascade and Coast Ranges, from Victoria, B.C., to Los Angeles Co., Calif. (Map 6).

Specimens examined. – 10♂♂, 13♀♀.

Dicolonus sparsipilosum Back

Dicolonus sparsipilosum Back, 1909: 247.

Description. – Male: As in frontispiece. Length 8.5-9.5 mm; pile in general very sparse, short and recumbent; frontal and ocellar bristles black, equal in length, slightly shorter than first antennal segment; occipital bristles orange, mixed with black



Map 6 Map 7

Maps 6-7. Distribution of Nearctic species of *Dicolonus*.

along margin of occiput; scutal pile orange on anterior margin of scutum, reddish brown on remainder of scutum, short and sparse, on posterior edge of scutellum not exceeding thickness of scutellum.

Female: Length 9.0-10.0 mm; otherwise same as male.

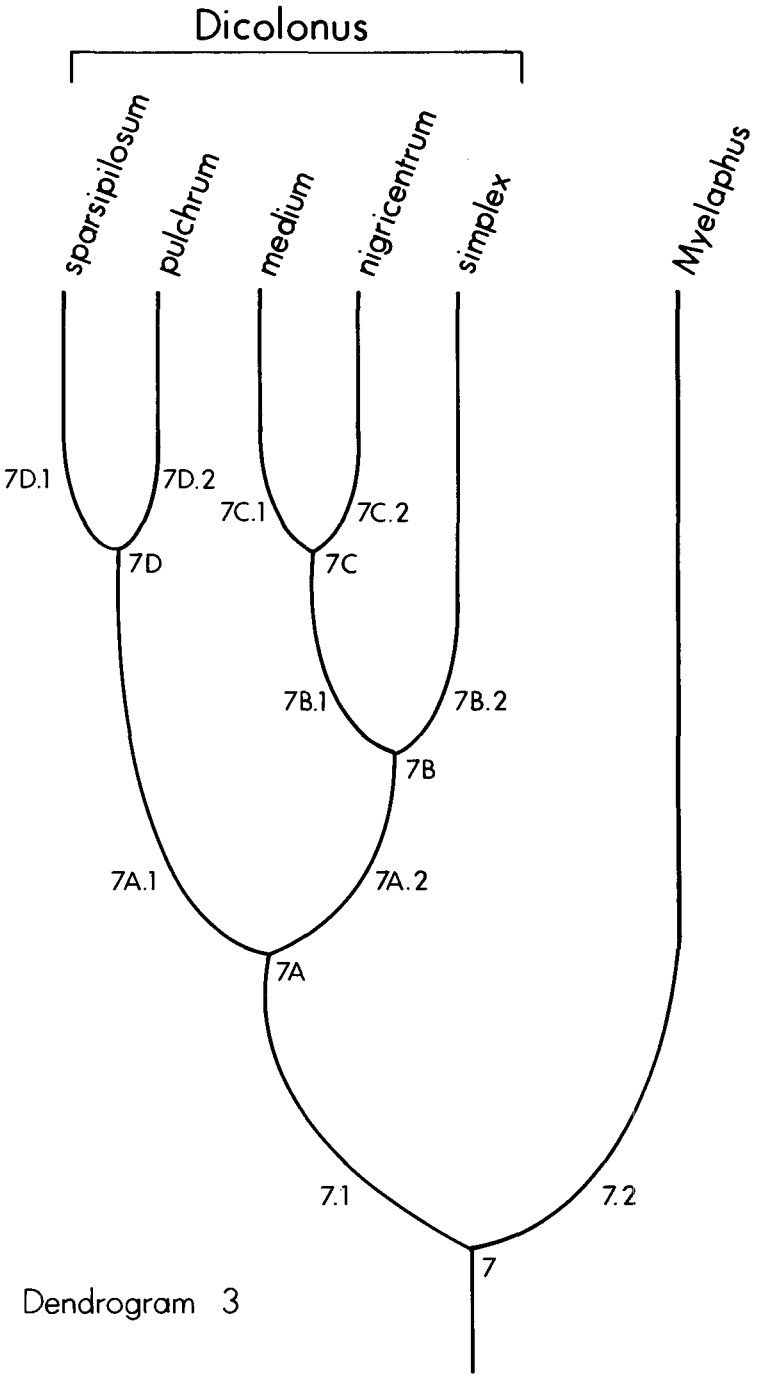
Distribution. – Western slopes of the Rocky Mountains from Montana to Colorado (Map 7).

Specimens examined. – 6 ♂♂, 4 ♀♀.

Table 3. Characters used in the Interpretation of the Phylogeny of *Dicolonus*. (See Dendrogram 3, p. 527)

7A.1 *D. sparsipilosum* and *D. pulchrum*	7A.2 *D. medium, D. nigricentrum,* and *D. simplex*
Pile on mesonotum, dorsum of abdomen, and femora appressed.	*Pile in general long and somewhat erect.
Pile on posterior edge of scutellum as long as thickness of scutellum.	*Pile on posterior edge of scutellum longer than thickness of scutellum.
Mesonotal bristles absent.	*Mesonotal bristles present.
7B.1 *D. medium* and *D. nigricentrum*	7B.2 *D. simplex*
Pile on mesonotum shorter making mesonotal bristles easily distinguished.	*Mesonotal bristles obscured by long pile.
Pile of straight hairs.	Tip of each hair curled.
7C.1 *D. medium*	7C.2 *D. nigricentrum*
Dorsocentral bristles orange yellow.	*Dorsocentral bristles black.
Mesonotal pile uniformly orange yellow.	*Pile on posterior 0.66 of mesonotum brownish.
7D.1 *D. sparsipilosum*	7D.2 *D. pulchrum*
Pile on mesonotum sparse, orange yellow on anterior 0.25 of mesonotum, brownish on the rest.	Pile on mesonotum dense, uniformly orange yellow, obscuring the ground colour of integument.
Ocellar bristles about equal in length to the first antennal segment.	*Ocellar bristles short, only 0.33 length of first antennal segment.

* denotes apomorphic condition



Dendrogram 3. Phylogeny of the species of *Dicolonus*.

Genus *Myelaphus* Bigot

Myelaphus Bigot, 1882: xci. Type-species: *Myelaphus melas* Bigot, 1882: xci; by monotypy.

*Diagnosis**. – First antennal segment twice or more as long as second, four times longer than wide, with hairs mostly on dorsal surface; third antennal segment as long as first two segments together, cleft apically, with triangular flange-like extension on each side enclosing base of antennal style; style two-segmented (Fig. 19), compressed laterally, half as long as third segment; first segment of style also deeply cleft apically as in third segment, terminating in two triangular extensions enclosing apical segment of style; face with small median pit below or furrow between antennal bases (Fig. 30); mystax of relatively short straight straw-coloured bristles confined to lower margin of face; face almost or completely devoid of pollen; frontovertex with row of reddish proclinate bristles close to eye margin; ocellar bristles short; thoracic pile strongly appressed; prothorax densely and evenly pilose; anterior corner and most of posterior half of sternopleuron, mesopleuron, posterior half of hypopleuron, katatergite and scutellum evenly pilose; tibiae gradually thickened apically; wing more or less infuscated, with R_4 ended before wing tip; epandrial arms directed mesally (Fig. 109B); lateral process of gonocoxite T-shaped with lateral arm curved (Fig. 109A, F); aedeagus with lateral processes (Fig. 109G, H); ovipositor with genital fork of two small sclerites (Fig. 130A).

Key to Nearctic species of *Myelaphus*

1 Face reddish-brown, with prominent transverse oval protuberance, just below middle, whose lower surface is sculptured with 2 or 3 curved concentric grooves; first antennal segment, and thorax, mostly reddish in ground colour. . . . . *melas* Bigot, p. 528

1' Face, antennae and thorax black; face evenly rounded, without prominent oval protuberance. . . . . *lobicornis* Osten Sacken, p. 528

Myelaphus lobicornis Osten Sacken

Ceraturgus lobicornis Osten Sacken, 1877: 187.
Myelaphus lobicornis (Osten Sacken): Williston 1884: 7-8.

Description. – Face, frontovertex, antennae and occiput black in ground colour; face evenly rounded below middle, yellow pollinose along lower margin; slight transverse depression between antennal bases and middle of face; 2 to 3 pairs of faintly impressed lines radiating out and down from small median pit below antennal bases (Fig. 30A); mystax bristles shorter than in *M. melas*, in length about 0.5 to 0.66 width of face; thorax largely black in ground colour; pilosity straw coloured, denser than in *M. melas*, obscuring ground colour on postpronotum, mesopleuron and upper part of sternopleuron, and extended, on sternopleuron, to mid-coxa; coxae and trochanters black; legs orange, darkened on apices of tarsi; claws black; first two, three in some specimens, abdominal segments black, basally as well as laterally, remaining segments orange to reddish brown dorsally, black laterally and ventrally.

Distribution. – British Columbia to southern California and northern Utah (Map 8).

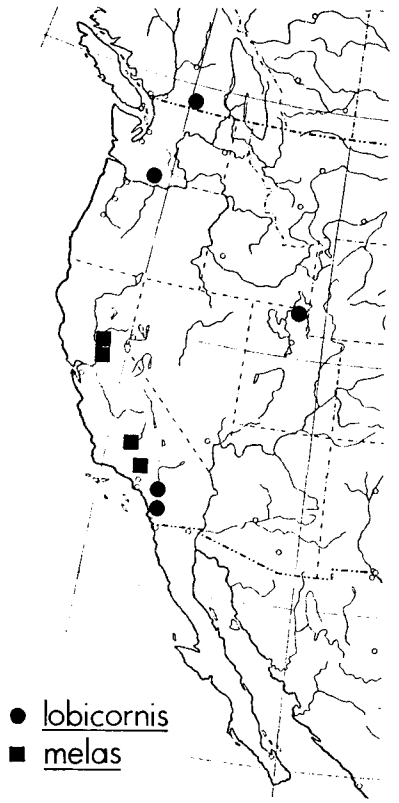
Specimens examined. – 6♂♂, 8♀♀.

Myelaphus melas Bigot

Myelaphus melas Bigot, 1882: 112.
Myelaphus rufus Williston, 1884: 7.

Description. – Face, frontovertex and first antennal segment shining reddish brown, pollen, if any, sparse and confined to lower corners of face; prominent oval protuberance or tubercle, extended across most of face just below middle, sculptured

**M. dispar* Loew, from the central Palaearctic Region and *M. jozanus* Matsumura, from Japan, not seen.



Map 8

Map 8. Distribution of Nearctic species of *Myelaphus*.

on lower surface with two or three curved concentric grooves; mystax bristles as long as width of face; thorax mainly reddish in ground colour; pilosity yellow, sparse, nowhere obscuring ground colour and not extended to lower edge of sternopleuron; legs reddish-orange; claws red basally; black apically; abdomen entirely reddish brown.

Distribution. – Southern Sierra Nevada, California (Map 8).

Specimens examined. – 7♂♂, 3♀♀.

Genus *Bohartia* Hull

Bohartia Hull, 1958: 317. Type-species: *Bohartia bromleyi* Hull, 1958: 318, by monotypy.

Diagnosis. – Head mainly pollinose, at most ocellar tubercle and surrounding area bare; occiput and vertical extension pollinose; antennal bases flat; upper face below antennal bases with row of hairs on each side; mystax cluster of hairs; pile on prementum abundant, occupying anterior half; postpronotum and scutum entirely pollinose; scutellum pollinose basally, bare on posterior edge; scutal pile appressed, short, distributed evenly; bristles on supra-alar region and posterior callus; scutellum with two patches of suberect pile on basal half, and row of erect marginal bristles; wing hyaline; alula well developed; anterior branch of third vein (R_4) ended before wing tip; first two abdominal segments parallel sided, third segment slightly broader posteriorly; male genitalia quite uniform throughout the genus (Fig. 90-92), differing only in shape of hypandrium and surstylus; epandrium trapezoidal with pair of posterior arms; surstyli flat;

lateral process of gonocoxite bulbous; hypandrium triangular or heart-shaped; aedeagus with lamellate aedeagal processes. Ovipositor with lateral arms of genital fork fused at anterior ends, in form of U-shaped structure (Fig. 114 and 115A).

Remarks. – This genus was considered an aberrant member of the Laphystiini (Hull 1958, 1962) but Martin and Wilcox (1965) transferred it to *Dioctria (sensu latiore)* as an additional subgenus. However, in this treatment *Bohartia* is considered as a separate genus.

Adults of the seven species assigned to this genus, *B. bromleyi, B. isabella, B. martini, B. munda, B. nitor, B. senecta* and *B. tenuis*, are closely related to one another and are distinguished only by the combination of the pattern of pollinosity, size, colour, and abundance of pile, and integumental coloration. The genitalia and other structural characters are quite uniform. The available characters are rather unsuitable for assessing phylogeny; nevertheless, an attempt has been made to interpret their phylogeny (Dendrogram 4) tabulated in Table 4 below.

Key to the species of *Bohartia*

1	All femora entirely light reddish brown	*nitor* new species, p. 532
1'	Femora partly or entirely black	2
2 (1')	Femora only partly darkened, at least hind pair largely or entirely light reddish brown	3
2'	Femora entirely dark brown to black, at most hind pair brownish on extreme bases or apices	4
3 (2)	Tibiae orange basally, darkened apically; hind femur uniformly orange brown.	*munda* new species, p. 532
3'	Tibiae uniformly reddish brown; hind femur reddish brown at base and on apical third, separated by a dark brown band	*senecta* new species, p. 532
4 (2')	Occipital bristles entirely black; second antennal segment with at least two distinct dark reddish or dark brown bristles on ventral surface	*bromleyi* Hull, p. 530
4'	Bristles on upper occiput partly or entirely white; bristles on ventral surface of second antennal segment whitish	5
5 (4')	Bristles on head and thorax entirely white; abdomen light orange except at base.	*tenuis* new species, p. 533
5'	Bristles on head black and white; mesonotal bristles black; abdomen dark reddish brown or black	6
6 (5')	Abdomen entirely black; postsutural anteprontum pollinose on dorsal fourth to third; tibia entirely black	*isabella* new species, p. 531
6'	Abdomen with reddish areas; postsutural anteprontum pollinose on more than upper half; tibiae dorsally, at base, usually paler than femora	*martini* new species, p. 531

Bohartia bromleyi Hull

Bohartia bromleyi Hull, 1958: 318-320.

Dioctria (Bohartia) bromleyi Hull: Martin and Wilcox 1965: 370.

Description. – Male: length 8.0-9.0 mm; frons, face and occiput silvery-grey pollinose; bristles on frontovertex, on ocellar tubercle and along upper margin of occiput black; mystax whitish yellow mixed with few black bristles; second antennal segment with reddish bristles, two distinct strong bristles on ventral surface (Fig. 14); first antennal segment with whitish pile; anteprontum pollinose only on dorsal 0.33; scutal bristles and bristles on scutellar edge black; genitalia with elongate trapezoidal hypandrium (Fig. 92A) and broad surstylus (Fig. 92C).

Female: as in male.

Distribution. – This species has been recorded only from Charleston Mt. Park, Nevada, at 9000 ft. (Map 9).

Specimens examined. – 2♂♂, 2♀♀.

Bohartia isabella new species

A species with entirely black integument, with white pile, and with pollinosity mostly silvery-grey or slightly yellowish. It can be distinguished from *bromleyi* by the presence of white bristles on the occiput and antennae.

Description. – Length 5.5-6.0 mm; frons, face and occiput silvery-grey pollinose, frontal and ocellar bristles entirely black; occipital bristles mostly white with some bristles on upper half black; antennal pile and bristles entirely white; mystax mostly white, few black bristles on upper part; pile on head white; postsutural antepronotum pollinose only on dorsal 0.25 to 0.33, in some specimens extended downward along anterior margin; front margin of pollinosity on posterodorsal corner of sternopleuron straight; prothoracic bristles entirely white; scutum evenly covered with short recumbent white pile and silvery pollinosity; scutal and scutellar bristles black; pile on scutellar disc white; legs entirely black, sparsely pollinose, bristles mostly white, pile whitish; claws black; abdominal pile sparse, entirely white; genitalia with triangular hypandrium (Fig. 90A); pile on genitalia black except for whitish pile on cerci.

Female: Length 6.0-6.5 mm; same as male; pile on ovipositor white.

Type material. –

Holotype: ♂, 3 mi. N. Westgard Pass, Inyo Co., Calif., 26.VI.1953 (J. W. MacSwain) – CIS.

Allotype: ♀, same data.

Paratypes: California: 1♂, Rumsey, Yolo Co., 30.VI.1956 (R. M. Bohart) – UCD; 1 ♂, 2♀♀, Independence, 17.V.1956 (J. Wilcox) – JW; 2 ♂♂, 2 ♀♀, Mariposa, Mariposa Co., 17,19.VI.1968 (R.M. Bohart) – UCD; 2 ♂♂, Rosemond, 29.IV., 3.V.1941 (J. Wilcox) – JW; 1 ♂, 1 ♀, 13.8 mi. NE Trona, State Range, Inyo Co., 17.IV.1962 (C. A. Toschi) – CIS; 1 ♀, San Jose, Santa Clara Co., 9.VII.1955 (A. M. Barnes) – CIS; 1 ♀, Little Lake, Inyo., 13.V.1962 (A. S. Menke) – UCD; 1 ♀, Poiute Butte, Los Angeles Co., 26.IV.1957 (J. Wilcox) – JW; 1 ♀, Lovejoy Buttes, Llano, 9.V.1955 (J. E. H. Martin) – CNC. Nevada: 1 ♂, 1 ♀, Crystal, 9.V.1961 (G. E. Bohart) – USU; 1 ♀, Montgomery Pass, 4.VII.1958 (J. Wilcox) – JW.

Distribution. – Sierra Nevada, California, west and northwest of Death Valley (Map 10).

Bohartia martini new species

Most specimens of this species are readily distinguished from the other six species of *Bohartia* by the reddish brown abdominal segments and the long fringelike hairs on the posterior surface of front tibia; specimens with the abdomen predominantly black may be separated from *isabella* by the more pollinose postsutural antepronotum.

Description. – Male: Length 6.0-7.5 mm; head as in *isabella*, but second antennal segment usually with some reddish or brown bristles; postsutural antepronotum pollinose at least on dorsal half; pollinosity on posterodorsal corner of sternopleuron slightly extended forward on lower part; scutal pile short, sparse, and appressed; femora black; tibiae reddish at least at base dorsally; front tibia with fringe-like hairs on posterior surface; first abdominal segment and basal half of second segment black, from middle of second to seventh segment reddish brown varying to mostly black with reddish areas; eighth segment black; male genitalia black with black bristles; hypandrium varied, but always bulged ventrally near base (Fig. 91D).

Female: Length 6.5–8.0 mm; same as male; ovipositor (Fig. 115) reddish brown, bristles on hypogynium black.

Type material. –

Holotype: ♂, Hy. 395, June Lane Jct., Calif., 20.VI.1954 (Dorothy Martin) – CHM.

Allotype: ♀, same data.

Paratypes: California: 4 ♂♂, 3 ♀♀, same data; 23 ♂♂, 3 ♀♀, same data (C. H. Martin) – CHM; 3 ♂♂, 4 mi. SW Tom's Place, Mono Co., 13.VII.1961 (G. I. Stange) – CIS; 1 ♂, 7 mi. E. Bodie, Mono Co., 2.VII.1964 (P. Rude) – CIS; 1 ♂, Lee Vining, Mono Co., 2.VII.1967 (Eric Jessen) – CIS; 2 ♂♂, 1 ♀, Hallelujah Jct., Lassen Co., 18.VII.1953 (R. M. Bohart) – UCD; 1 ♂, same locality, 17.VII.1955 (R. M. Bohart) – UCD; 1 ♂, same locality, 2.VII.1964 (R. M. Bohart) – UCD; 2 ♂♂, 2 ♀♀, same locality, 22.VI.1964 (R.M. Bohart) – UCD; 4 ♂♂, same data (F. D. Parker) – UCD; 1 ♂, same data (M. E. Irwin) – UCR; 1 ♂, 1 ♀, same locality 1.VII.1965 (F. D. Parker) – UCD; 1 ♂, same locality, 4.VI.1952 (E. I. Schlinger) – CHM; 1 ♀, same locality, 29.VI.1966 (R.M. Bohart) – UCD; 1 ♀, same

locality, 7.VII.1968 (R. M. Bohart) – UCD; 2 ♀♀, same locality, 2.VII.1964 (M. R. Irwin) – UCR; 1 ♀, same locality, 12.VII.1962 (M. I. Irwin) – UCD; 18 ♂♂, 11 ♀♀, same locality, 4.VII.1967 (J. Wilcox) – JW; 5 ♂♂, 1 ♀, Mammoth, 9.VII.1957 (J. Wilcox) – JW; 14 ♂♂, 8 ♀♀, Pinecrest, 31.VII. 1948 (P. H. Arnaud, Jr.) – JW; 1 ♂, Woodfords, Alpine Co., 17.VI.1958 (W. W. Middlekauff) – CIS; 1 ♂, 1 ♀, Strawberry, Tuolumne Co., 14,15.VII.1951 (J. W. MacSwain) – CIS; 1 ♂, Truckee, 5.VII.1936 (A. E. Pritchard) – USNM; 1 ♀, Truckee, 6000′, Tahoe Co., 14.VII.1961 (B. H. Poole) – CNC; 1 ♀. Lake Tahoe, Tallac, 25.VI. (?) (E. P. VanDuzee) – CIS; 1 ♀, Lake Tahoe, 7.VII.1938 – UCD; 1 ♂, Strawberry, Tuolumne Co., 18.VII.1957 (J. M. Burns) – CIS; Arizona: 1 ♂, 8 mi. S. Cay Creek, Maricopa Co., 22.VI.1962 (D. M. Zohner) – ASU; Nevada: 1 ♂, Kingsbury Gd., Douglas Co., 19.VI. 1964 (F. D. Parker) – UCD; 1 ♂, Orovada, 6.VI.(G.E. Bohart) – USU; Washington: 1 ♂, Odessa, 27.VI. 1960 – (E. I. Schlinger) – UCR; Wyoming: 1 ♂, Mesa Conserv. Area, So. of Pinedale, 17-18.VII.1968 (R. J. Lavigne) – CHM; Idaho: 16 ♂♂, 10 ♀♀, 6 mi. NE. Malta, Cassia Co., 22.VI.1965 (R. L. Westcott) – UI (Map 11).

Bohartia munda new species

Adults of this species are separated from those of other *Bohartia* by the wholly orange hind femora and the darker brown tibiae and tarsi.

Description. – Male: Length 6.5 mm; frons, face and occiput silvery-grey pollinose; ocellar, frontal and upper occipital bristles dark; postsutural antepronotum silvery pollinose only on upper 0.25; mesonotal pile short, sparse, appressed; coxae black, trochanters light reddish brown; front femur black with reddish brown markings on extreme base and ventral apical 0.25; apical 0.25 of mid femur entirely light reddish brown, hind femur entirely light reddish brown; tibiae brownish basally, gradually darkened apically; tarsi and claws dark brown; pile on legs pale yellow; abdomen black, with pale yellowish pile; male genitalia black with black pile. Genitalia not dissected or figured.

Female: Length 6.5-7.0 mm; otherwise same as male; two paratype female specimens with hind femur black on extreme base and entirely black tibiae; pile on hypogynium black.

Type material. –

Holotype: ♂, Bear Valley, Calif., 27.VI.1948 (J. Wilcox) – JW.

Allotype: ♀, in copula with holotype.

Paratypes: 1 ♀, Upper Deep Canyon at Horsethief Creek, Riverside Co., Calif., 3400′, 11.VI.1965 (M. E. Irwin) – UCR; 1 ♀, 2 mi. W. Phelan, San Bernardino County., Calif., 22.V.1957 (E. I. Schlinger) – UCD (Map 10).

Bohartia nitor new species

This species is easily recognized by the distinctive long appressed white pile on the scutum and abdomen, and by the entirely light reddish brown legs.

Description. – Female: Length 7.5 mm; head black, yellowish white pollinose; pile entirely pale yellow; (third antennal segments missing); thorax black with pattern of pollinosity as in *isabella;* scutal pile long, distinctly appressed; coxae black with extreme apices reddish; all femora, tibiae, and tarsi bright reddish brown; claws reddish on extreme bases; pile of legs yellow, abdominal pile appressed on terga, recumbent on sterna.

Holotype: ♀, Tracy, Calif., 2.VI.1920 (E.P. Van Duzee) – CAS (Map 9).

Bohartia senecta new species

Adults of this species are also black with reddish brown legs, somewhat like *munda* adults but different in having darker hind femora each with a black band near the base and in having paler tibiae and tarsi.

Description. – Length 7.0 mm; mystax yellow, mixed with few black bristles; bristles on second antennal segment and upper occiput black; pattern of pollinosity on thorax as in *isabella;* coxae black; trochanters reddish; front and mid femora black with apical 0.25 of front and apical 0.33 of mid femora entirely reddish brown; hind femur reddish brown with subbasal black band; tibiae uniformly reddish brown; tarsi darker brown, darkened to black apically; claws black; pile of legs yellowish; abdominal segments and male genitalia black; pile on abdominal segments yellowish, on genitalia black. Genitalia

not dissected or figured.

Type material. –

Holotype: ♂, 15 mi. N. Colonia Guerrero, Baja California, Mexico, 9.V.1949 (R.C. Dickson) – UCR (Map 10).

Bohartia tenuis new species

Adults of this species are somewhat like those of *B. martini* but they are distinguished by absence of black bristles on head and thorax, and by the pale orange abdomen.

Description. – Length 6.0 mm; pile on head, antennae and thorax entirely white, thoracic pollen pattern as in *martini*; bristles on head and thorax entirely white; legs almost entirely dark brown; joints between femora and tibiae lighter brown; claws black; pile on legs white; first abdominal segment black, second segment black basally, orange apically, third to seventh segments pale orange; abdominal pile yellowish; genitalia brown with brownish orange pile. Genitalia not dissected or figured.

Female: Length 7.0 mm; otherwise same as male except for sexual differences.

Type material. –

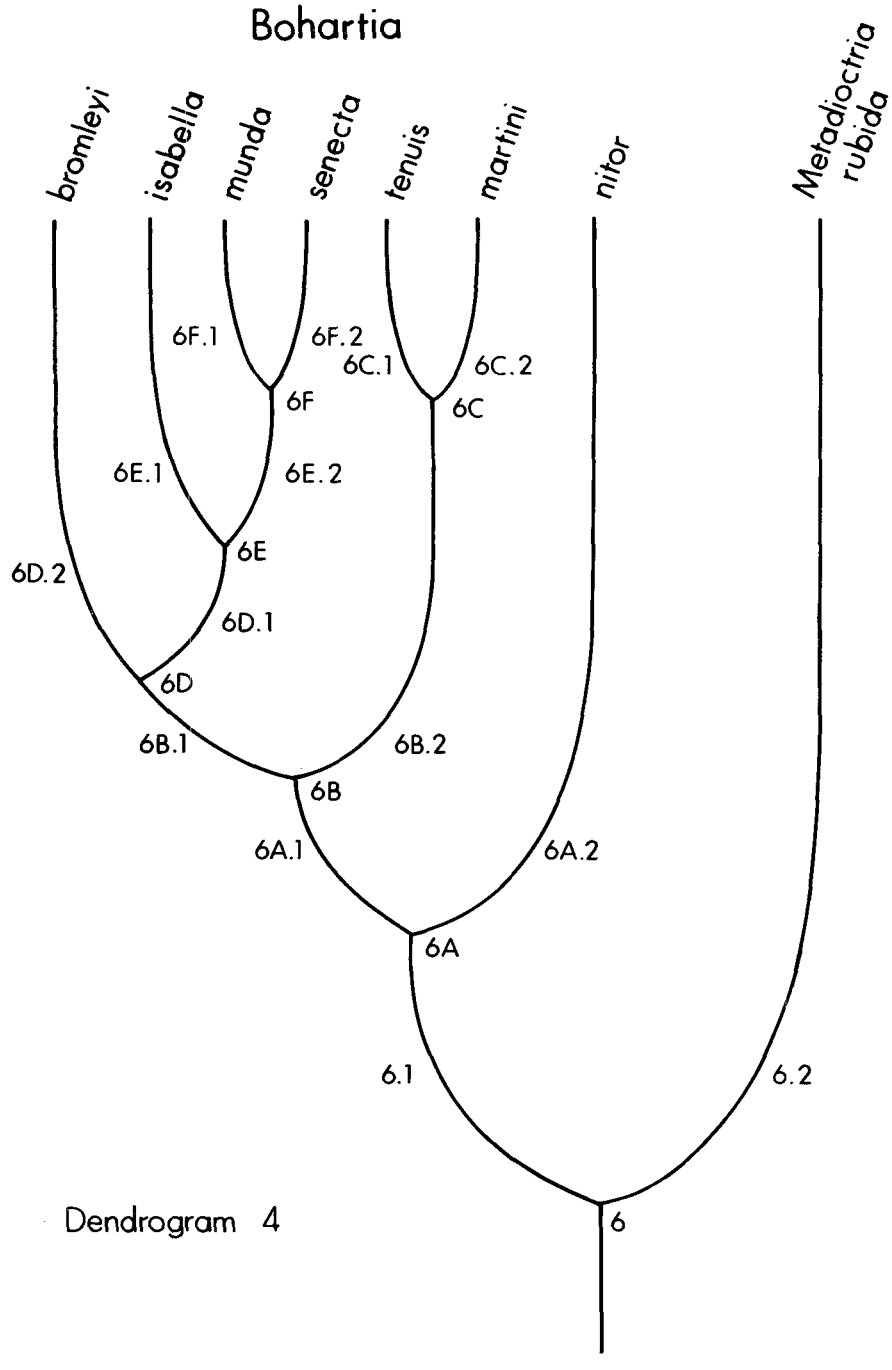
Holotype: ♂, Tempe, Arizona, 17.V.1926 (A.A. Nichol) – JW.

Allotype: ♀, Florence Jct., Ariz., 18.IV.1935 (F.H. Parker) – USNM (Map 11).

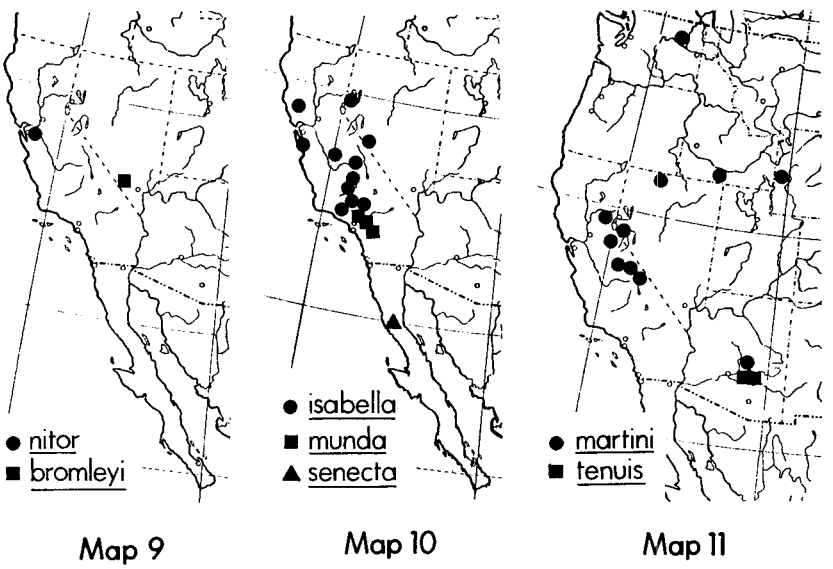
Table 4. Characters used in the Interpretation of the Phylogeny of *Bohartia.* (See Dendrogram 4, p. 534)

6A.1 *B. bromleyi, B. isabella, B. munda, B. martini, B. senecta* and *B. tenuis*	6A.2 *B. nitor*
Pile on mesonotum and abdomen short.	*Pile on mesonotum and abdomen distinctly long and appressed.
Wing veins dark brown	*Wing veins reddish brown.
Fore and mid femora black.	*Legs (except coxae) entirely reddish brown.
6B.1 *B. bromleyi, B. isabella, B. munda, B. senecta*	6B.2 *B. tenuis* and *B. martini*
Abdomen entirely black.	*Abdomen from middle of second to seventh segment reddish brown.
Pollinosity on anteprenotum on upper 0.33.	*Pollinosity on antepronotum at least on upper 0.5.
6C.1 *B. tenuis*	6C.2 *B. martini*
Hypandrium of equal thickness throughout.	*Hypandrium bulged subbasally.
Antennal pile entirely white.	Antennal pile reddish brown and black.
6D.1 *B. isabella, B. munda* and *B. senecta*	6D.2 *B. bromleyi*
One bristle on ventral surface of second antennal segment weak.	*Two bristles on ventral surface of second antennal segment strong, distinct.
Smaller, 6-7 mm.	*Larger, 8-9 mm.
6E.1 *isabella*	6E.2 *munda* and *senecta*
Legs entirely black.	*Tips of front and mid femora, part or all of hind femur, and basal 0.5 of each tibia brownish.
6F.1 *munda*	6F.2 *senecta*
Apical 0.5 of each tibia black; tarsi black	*Tibiae entirely reddish brown; tarsi reddish brown basally gradually darkened to black toward apices.

* denotes apomorphic condition



Dendrogram 4. Phylogeny of the species of *Bohartia*.



Maps 9-11. Distribution of the species of *Bohartia*.

Genus *Metadioctria* Wilcox and Martin

Dioctria, subgenus *Metadioctria* Wilcox and Martin 1941: 19. Type-species: *Dioctria rubida* Coquillett; by original designation.

Diagnosis. – Antenna with short truncate style (Fig. 12); third segment subcylindrical, somewhat compressed laterally on base; first segment four times as long as wide, subequal in length to second segment; frontovertex with two patches of bristles; antennal bases slightly elevated, with cluster of bristles on each side (Fig. 26); ocellar bristles in two curved rows, each with 4-5 bristles; face flat with distinct gibbosity on lower part; mystax cluster of bristles; pile on prementum dense; pollinosity on occiput confined to margin; anterior corner of postpronotum, anterodorsal one third of mesopleuron, anterior and posterodorsal corners of sternopleuron and posterior third of hypopleuron pollinose; pronotum, scutum, dorsal and posterior margins of mesopleuron and anterior and posterodorsal corners of sternopleuron with long, dense pile; scutellum with erect marginal bristles (Fig. 47); front and midfemora thickest subbasally, gradually tapered at both ends (Fig. 63); tarsi without conspicuous swollen hind metatarsus, empodium pollinose only basally (Fig. 74); wing 2.5 times as long as wide, infuscated; alula well-developed; abdomen parallel sided; epandrium trapezoidal, with blunt epandrial arms (Fig. 89B); surstylus flat (Fig. 89C); hypandrium,somewhat rounded on base, extended apically as long median point (Fig. 89 hpa); lateral process of gonocoxite thick and broadened on dorsal part, at apex pointed ventrally (Fig. 89D, E, F); medioventral process not well developed; gonostylus flattened, tapered apically, curved mesally; aedeagus with lamellate lateral processes (Fig. 89G,H); ovipositor (Fig. 113) with genital fork semicircular.

Remarks. – Adults of *M. resplendens* Loew are in general appearance quite suggestive of, and the species has been included in, *Metadioctria* (Wilcox and Martin 1941), Martin and Wilcox 1965). They have a shiny black integument, with slight greenish-gold reflections, all bristles and pile are a rich golden yellow, and pollinosity is lacking except for a strip extended from the base of each antenna to the ventrolateral corner of the face, a narrow band behind each eye and a small spot on the anterodorsal and posterodorsal corners of the sternopleuron. The antennal style is two-

segmented. The proboscis appears to be characteristic of Echthodopini but the second abdominal segment lacks all traces of the broad transverse groove characteristic of both Dioctriini and Echthodopini (Fig. 77-82). We suspect it belongs elsewhere taxonomically, and have therefore omitted it from the present study.

Metadioctria rubida Coquillett

Dioctria rubidus Coquillett 1893: 80.
Dioctria (Metadioctria) rubida Coquillett: Wilcox and Martin 1941: 19.
Dioctria (Metadioctria) rubida nigripilosa Wilcox and Martin 1941: 19.
Dioctria (Metadioctria) rubida atripes Wilcox and Martin 1941: 20.

Description. – Face silvery-white pollinose; frontovertex and occiput (except for a pollinose band behind eye) shining black; thorax, coxae and trochanters black; wing infuscated.

Remarks. – In males of the typical form of *rubida*, all pile and bristles (except on tarsi) are orange yellow; fore and mid legs, hind femora and bases of hind tibiae are orange. Males of form *atripes* are distinguished from the other two forms by having entirely black legs, black abdominal segments and black pile, except on lower occiput and mesothoracic pleura; males of *nigripilosa* are intermediate between typical *rubida* and *atripes*, having femora and basal halves of anterior tibiae orange and the last two abdominal segments orange. These forms are apparently only colour variants and consequently the names have no nomenclatural status.

Distribution. – Southern California from Ventura to San Bernardino and Riverside Counties (Map 12).

Specimens examined. – 7♂♂ *"atripes"*, 3♂♂ *"nigripilosa"*, 11♂♂ typical *rubida* and 13♀♀.

Map 12

Map 12. Distribution of *Metadioctria rubida.*

Genus *Eudioctria* Wilcox and Martin

Dioctria, subgenus *Eudioctria* Wilcox and Martin 1941: 8. Type-species: *Dioctria albius* Walker, by original designation.

Diagnosis. – Antennal style spoon-shaped, short, 0.20 as long as third segment (Fig. 15-17); third segment thickened in middle; second segment of equal length to first; first segment twice as long as its diameter; bristles on ocellar tubercle in curved rows; antennal bases slightly elevated, with cluster of bristles on each side; face slightly concave in middle, gibbosity distinct; bristles of mystax clustered (Fig. 31); prementum densely pilose; labellum notched subapically (Fig. 34); occipital bristles long, dense, absent from vertical extension; frontovertex and occiput mainly pollinose; lateral cervical sclerites densely pilose; anteprontotum pilose along front margin and on sides; scutum entirely pollinose to nearly bare with pollinose markings; scutal pile on margins, on dorsocentral and acrostichal regions; upper and front margins of mesopleuron, front margin and upper hind corner of sternopleuron and posterior half of hypopleuron pollinose; scutellum pollinose on basal third in some species; legs either entirely black or black with orange markings on basal half of each tibia; hind femur thickest subbasally, gradually tapered apically with short recumbent dorsal and longer erect ventral pile, each hair arising from tubercle (Fig. 66-68); fore and mid tibiae subcylindrical with sparse long pile, distinctly erect on ventral surfaces; hind tibia tuberculate, with sparse erect pile and row of bristles on dorsal, front and ventral surface respectively; hind metatarsus not swollen, at most twice as long as succeeding segments; empodium bare, pollinose only at extreme base (Fig. 76); wing infuscated, whitish basally in male, in some forms of some species orange on basal half; R_4 ended before wing tip (Fig. 59); alula distinct; abdominal segments black, with base of third segment narrowest (Fig. 82); epandrium long with posterior margin deeply cleft; posterior part of epandrium short and stumpy (Fig. 101-103), club-shaped (Fig. 104-106) or broad and flat (Fig. 93-100); hypandrium short, narrow or broad or long; lateral process of gonocoxite flat, broad and scooplike or absent; lateral arm of gonocoxite long, somewhat curved; medioventral process of gonocoxite broad or insignificant; gonostylus blade-shaped; aedeagus pointed ventrally with dorsal process of various shapes, sclerotized or membraneous; ovipositor (Fig. 116-127) with hypogynium convex ventrally and narrow hypogynial valves; genital fork of separate sclerites (Fig. 119-125) or these fused to each other at anterior ends (Fig. 117 and 118); portions of ninth tergite quadrangular; tenth tergite band-like, with or without lateral indentation.

Remarks. – This genus is quite uniform especially in shape of antennae, facial gibbosity, thoracic sclerites, wings and abdominal segments. Colour and pattern of pollinosity vary more substantially and provide the principal characters on which the key has been based.

Males of some species and the females of *E. sackeni* also show polymorphism in the form of two or more colour variants. The variants in *E. albius* and *E. sackeni* are particularly striking and have been given names. Similar polymorphism also exists in *E. propinqua*, in which all four variants have been collected together in the same forest clearing at the same time, each taken in copula with indistinguishable females. Less pronounced variation also occurs in *E. doanei, E. media, E. brevis* and *E. tibialis.*

Based on structure of the male genitalia, members of this genus are arranged in six species groups as follows:

1. *albius* group – *E. albius* and *E. propinqua* (Fig. 96 and 97);
2. *doanei* group – *E. doanei* and *E. beameri* (Fig. 101-104);
3. *media* group – *E. media* (Fig. 93);
4. *monrovia* group – *E. dissimilis* and *E. monrovia* (Fig. 94 and 95);
5. *nitida* group – *E. denuda, E. nitida* and *E. unica* (Fig. 98-100); and
6. *sackeni* group – *E. brevis, E. disjuncta, E. sackeni* and *E. tibialis* (Fig. 105 and 106).

The characters used to arrive at an interpretation of the phylogeny (Dendrogram 5) of the 14 species are indicated in Table 5.

Wilcox and Martin (1941) and Martin and Wilcox (1965) also included *Dioctria parvula* Coquillett in *Eudioctria*, but this species appears to us to be at least congeneric, if not conspecific, with *M. resplendens* Loew, which we have excluded from the Echthodopini (see *Remarks* under *Metadioctria*).

Key to the species of *Eudioctria*

1 Facial gibbosity without pollen ..... *unica* new species, p. 543
1' Facial gibbosity, at base of mystax, pollinose as in upper part of face 2
2 (1') Posterior edge of mesopleuron with thin band of pollen extended down to margin of sternopleuron (as in Fig. 36) 3
2' Lower half of mesopleuron without pollen (Fig. 43) 8
3 (2) Postpronotum bare of pollen except for narrow band adjacent to scutum ... 4
3' Postpronotum pollinose on upper half or more 6
4 (3) Scutum yellow pollinose with a pair of narrow parallel bare dorsocentral stripes on anterior third, and a large oval bare spot on each intraalar region extending from level of prothoracic spiracle to level of squama (see Fig. 43) ..... *disjuncta* new species, p. 544
4' Scutum without bare dorsocentral stripes 5
5 (4') Scutum entirely yellowish-grey or brown pollinose; scutellum pollinose at base .. .. *sackeni* Williston, p.
5' Scutum brown pollinose with bare anterior margin, and with a large oval bare spot on each intraalar region ..... *brevis* Banks, p. 543
6 (3') Eastern species; bristles of mystax, antennae, frontovertex and upper occiput either all yellow or all black ..... *propinqua* Bromley, p. 540
6' Western species; bristles of antennae, frontovertex and upper occiput yellowish-brown contrasting with mainly or entirely black mystax..... 7
7 (6') Tibiae orange basally, black apically; bristles on antennae, frontovertex and upper occiput orange-brown ..... *doanei* Melander, p. 540
7' Tibiae entirely black; bristles on upper half of head pale yellow .... *beameri* Wilcox and Martin, p. 540
8 (2') Scutum mainly bare of pollen except triangular area between postpronotum and dorsocentral hairs, narrow strip along supraalar margin, and (in *tibialis*) pair of small triangles anterior to scutellum 9
8' Scutum mainly pollinose, especially median area..... 10
9 (8) Mesopleuron without pollen ..... *tibialis* Banks, p. 544
9' Mesopleuron pollinose on anterodorsal third .... *dissimilis* new species, p. 541
10 (8') Scutellum pollinose dorsally at least on basal half ..... *media* Banks, p. 541
10' Scutellum without pollen except for possibly a narrow strip along anterior margin 11
11 (10') Eastern species; scutum pollinose to anterior margin; bristles of antennae, upper part of head and mystax and bases of tibiae, concolorous, either all orange or all black ..... *albius* Walker, p. 539
11' Western species; scutum bare of pollen along anterior margin between postpronota; bristles of antennae, upper part of head and mystax not concolorous with bases of tibiae 12
12 (11') Tibiae entirely black; bristles of antennae, frontovertex upper occiput and at least lower part of mystax orange-brown ..... *monrovia* Wilcox and Martin, p. 542
12' Tibiae orange basally, black apically; bristles of antennae, frontovertex, upper occiput and mystax black..... 13

13 (12') Scutum entirely pollinose. . . . . *nitida* Williston, p. 542
13' Scutum with oval bare spot on each side extended nearly to scutellum . . . . . *denuda* Wilcox and Martin, p. 542

The *albius* group

The two species assigned to this group, *E. albius* and *E. propinqua*, are similar to each other but males are distinguished by shape of aedeagus (Fig. 96 and 97) and pattern of pollinosity on the scutum and mesopleuron.

Males of both species show pronounced polymorphism. The face is either white or yellow, and basal half of the wing, either orange or brown. The orange wing base is correlated with orange-yellow hairs on the head and scutum, with lighter pollinosity on the scutum and with orange bases to all tibiae, resulting in an insect strikingly different from its dark-winged counterpart. All four combinations have been found in *E. propinqua*, all taken in copula with virtually identical females. Only three of the four theoretically possible variants, however, are known for *E. albius*. A white-faced, orange winged variant has not yet been discovered, but probably would be found by more extensive collecting.

The presence of an apparently homologous set of variants in males of both *E. albius* and *E. propinqua* has led us to assume that this polymorphism was also present in their common ancestor, and that the alleles have persisted in both species unaltered.

Eudioctria albius Walker

Dioctria albius Walker 1849: 301.
Dioctria (Eudioctria) albius Walker: Wilcox and Martin 1941: 10.
Dioctria (Eudioctria) albius f. *aurifacies* Wilcox and Martin 1941: 11.
Dioctria (Eudioctria) albius f. *xanthopennis* Wilcox and Martin 1941: 12.

Description. – Male: length 10.0-12.0 mm; pile on mouthparts and lower part of occiput white; side of antepronotum with orange pollinosity on posterior half; scutum orange yellow pollinose with submarginal bare spot on each side; dorsal half of mesopleuron yellowish pollinose; pile on legs and abdomen orange yellow; male genitalia with broad posterolateral part of epandrium (Fig. 96B), aedeagus with dorsal process formed into a hook with blunt tip (Fig. 96G).

Female: length 10.0-13.0 mm; uniformly black; face orange yellow; mystax black; bristles on frontovertex, on antenna, on ocellar tubercle, on upper occiput and on mesonotum black; ovipositor with genital fork of two lateral sclerites (Fig. 119A); hypogynial valves slender, wide apart (Fig. 119B).

Remarks. – In the male the face is either silvery white or golden yellow, and the wing is either uniformly infuscated (with slight whitish tinge at base) or infuscated on apical half and orange on basal half. Specimens with orange wing bases have the basal part of the tibiae orange and orange pile on head, scutum, pronotum and mesonotum. Those with uniformly infuscated wings have a black mystax, black bristles on the antennal segments, on the frontovertex, on the ocellar tubercle and on the upper part of the occiput. Three of the four theoretically possible variants have been described by Wilcox and Martin (1941), as follows: form *albius* (white-faced, dark-winged), from form *aurifaces* (orange-faced, dark-winged), and form *xanthopennis* (orange-faced, orange-winged). As they now appear to be colour variants only, these names are here considered as having no formal nomenclatural status.

In addition to the colour variants, there are four types of aedeagus (Fig. 96G 1, 2, 3, 4) that cannot be correlated with the colour variation. Each of these colour variants has all four types of aedeagus. All other parts of the male genitalia are essentially uniform within the species. It is conceivable that four species could be represented among the material, each possessing the three colour variants; unfortunately, it was not possible to conduct the necessary studies to resolve the problem.

Distribution. – All three forms are found intermingled along the Appalachians from New

Hampshire to Tennessee and North Carolina, with scattered records in Ontario and Wisconsin (Map 18).

Specimens examined. – 77♂♂ typical *albius*, 11♂♂ *"aurifacies"*, 5♂♂ *"xanthopennis"* and 137 ♀♀.

Eudioctria propinqua Bromley

Dioctria propinqua Bromley 1924: 125.
Dioctria (Eudioctria) propinqua Bromley: Wilcox and Martin 1941: 13.

Description. – Male: Similar to *E. albius*, except scutum entirely pollinose, without submarginal bare spots, and hind margin of mesopleuron pollinose along its entire length.

Female: uniformly black with pattern of pollinosity as in male; pollinosity uniformly orange yellow; legs black; wing infuscated; ovipositor with genital fork of two separate sclerites (Fig. 120A), slightly different from that of *E. albius*.

Remarks. – Colour combinations homologous to those in *albius* also occur in this species. All four possible combinations are known. The aedeagus also shows four variants (Fig. 97G), which likewise cannot be correlated with the colour variation.

Distribution. – Along the Appalachians from eastern Quebec, Maine and Nova Scotia to Tennessee and North Carolina (Map 17).

Specimens examined: 17 white-faced, dark-winged; 52 orange-faced, dark-winged; 9 white-faced, orange-winged; 23 orange-faced, orange-winged; 121 ♀♀.

The *doanei* group

The two species assigned to this group are characterized by the membranous structure on the dorsum of the aedeagus (Fig. 101-104, G, H), as well as by a pair of sclerites situated behind the portions of the ninth tergite of the ovipositor (Fig. 124 and 125A).

Eudioctria beameri Wilcox and Martin

Dioctria (Eudioctria) beameri Wilcox and Martin 1941: 13-14.

Description. – Male: length 13.0-16.0 mm; face and frons brassy yellow; mystax black, some specimens with few orange bristles on lower part; pile on head and antenna orange yellow; antepronotum pollinose dorsally, bare laterally; dorsal half of postpronotum pollinose; scutum entirely yellowish-brown pollinose; dorsal half and posterior margin of mesopleuron yellowish-brown pollinose; legs entirely black; epandrium with postlateral projection (Fig. 104B, C); aedeagus with dorsal membranous bulb-like structure (Fig. 104G, H).

Female: length 13.0-17.0 mm; ovipositor with pair of sclerites posterior to genital fork (Fig. 125A); genital fork of two separate sclerites; posterior edge of lateral valve of hypogynium brim-like (Fig. 125B, C); otherwise as in male.

Distribution. – Vicinity of Sequoia National Park in the southern Sierra Nevada, California (Map 19).

Specimens examined. – 6♂♂, 11♀♀.

Eudioctria doanei Melander

Dioctria doanei Melander 1923: 214.
Dioctria (Eudioctria) doanei Melander: Wilcox and Martin 1941: 14.

Colour and patterns of pile and pollinosity of this species are similar to those of *beameri*, it is distinguished by the following characteristics.

Description. – Male: length 12.0-16.0 mm; face silvery white, orange in some specimens (Wilcox and Martin 1941); front and midtibiae orange-yellow with black apices, hind femur orange-yellow on basal 0.66, remaining 0.33 black; postlateral projection on epandrium short, stumpy (Fig. 101B, C).

Female: length 12.0-16.0 mm; face orange yellow or silvery white; ovipositor different from that of *beameri* in shape of genital fork (Fig. 124A); lateral valve of hypogynium (Fig. 124B, C) without brim-like posterior edge.

Remarks. – A male from Crescent City, California and two males and one female from Forest Hill, Placer Co., California, in the collection of C.H. Martin, have the posterior half of the scutum mainly bare. The male genitalia (Fig. 102 and 103) and other characters do not differ, however, from those of *E. doanei.*

Distribution. – Southern Coast Range and southern Sierra Nevada, California. The four aberrant specimens mentioned above are from the northern Californian Coast Range and northern Sierra Nevada, California (Map 19).

Specimens examined. – 26♂♂, 19♀♀.

The *media* group

This species is sufficiently isolated to warrant placing it in a group by itself. It is characterized by absence of the lateral process of the gonocoxite and lateral flap-like structure on the aedeagus (Fig. 93).

Eudioctria media Banks

Dioctria media Banks 1917: 118.

Dioctria (Eudioctria) media Banks: Wilcox and Martin 1941: 15.

Description. – Male: length 8.0-11.0 mm; frons and face brassy pollinose; bristles on head and antennae black; pile on lower occiput and mouthparts yellowish; supraalar and dorsocentral bristles black; remaining bristles and pile orange yellow; dorsal surface of antepronotum pollinose; dorsal half of postpronotum pollinose; mesonotum entirely yellowish brown to grey pollinose; dorsal half of mesopleuron yellow pollinose; scutellum pollinose dorsally; legs black; male genitalia with lateroposterior part of epandrium broad (Fig. 93B); aedeagus with pair of lateral flap-like projections (Fig. 93G, H); hypandrium longer than gonocoxite, slightly constricted at middle (Fig. 93 hpa).

Female: length 9.0-11.0 mm; otherwise as in male.

Remarks. – Three males, from Marin and Butte Counties, California, have a silvery face, greyish pollinose scutum, and whitish lower half of the wing, and thus appear to belong to a colour variant analogous to those found in *E. albius* and *E. propinqua.*

Distribution. – Along the Cascade Range, the Coast Range and on the northern parts of the Sierra Nevada, California, with a single isolated record from northern Idaho (Map 13).

Specimens examined. – 33♂♂, 31♀♀.

The *monrovia* group

The two species assigned to this group are closely related, but distinguished from each other by patterns of pollinosity on the scutum, male genitalia (Fig. 94 and 95), and ovipositor (Fig. 117 and 118).

Eudoctria dissimilis new species

Description. – Male: length 7.0-9.0 mm; frons and face brassy pollinose, head and antennal bristles and pile orange-yellow; mystax with few brownish bristles above; frontovertex pollinose only on sides, bare on area anterior to ocellar tubercle; dorsal half of occiput bare; prothoracic sclerites without pollinosity; scutum shining black except for triangular spot posterior to pollinosity between edge of postpronotum and dorsocentral hairs; dorsal third of mesopleuron yellow pollinose; scutellum bare; legs black; male genitalia with lateroposterior part of epandrium broad (Fig. 95B, C); hypandrium elongate, extended posteriorly into brim-like structure (Fig. 95D); aedeagus with dorsal process compressed laterally, projected dorsally (Fig. 95G, H).

Female: length 8.0-9.0 mm; ovipositor with genital fork as inverted U-shaped structure (Fig. 118A); otherwise same as male.

Type material. –

Holotype: ♂, Idyllwild, San Jacinto Mts., Calif., 18.VI.1940 (C. D. Michener), length:

Allotype: ♀, Harkey Creek, San Jacinto Mts., Calif., 4.VI.1940 (C. D. Michener) – CAS.

Paratypes: 1 ♂, same data as holotype; 1 ♂, same locality, 23.V.1940; 1 ♂, Pinon Flat, San Jacinto Mts., 21.V.1940; 1 ♀, same locality as allotype, 1.VI.1940; 1 ♂, 1 ♀, Ribbonwood, San Jacinto Mts., 18.V.1940 (all by C. D. Michener) – CAS. – 1 ♂, 1 ♀, Crystal Lake, Los Angeles Co., Calif. (J. W. MacSwain) – UCB. (Map 15).

Eudioctria monrovia Wilcox and Martin

Dioctria (Eudioctria) monrovia Wilcox and Martin 1941: 15-16.

Description. – Male: length 8.0-9.0 mm; face brassy pollinose; mystax yellow below with few black bristles above; frontovertex entirely yellowish-brown pollinose; bristles of antennae and upper part of head brown; scutum largely pollinose with pair of lateral bare spots; mesopleuron yellow pollinose on upper half; male genitalia similar to those of *E. dissimilis* but hypandrium without brim-like structure on posterior edge (Fig. 94D) and dorsal process of aedeagus without dorsal projection (Fig. 94G).

Female: length 8.0-10.0 mm; ovipositor with genital fork widened at middle (Fig. 117A); otherwise as in male.

Distribution. – Coast Range of southwestern California, from Los Angeles to the Laguna Mts. (Map 16).

Specimens examined. – 2♂♂, 8♀♀.

The *nitida* group

Structure of the male genitalia and ovipositor suggest a relationship between this group and the *albius* group. However, the pattern and texture of the pile and the pattern of distribution of the *nitida* group readily distinguish this group from the *albius* group.

Diagnosis. – Male genitalia with lateroposterior part of epandrium flat and somewhat parallel sided, lateral arm of gonocoxite short and dorsal process of aedeagus broad, somewhat appressed dorsoventrally (Fig. 98-100).

Eudioctria denuda Wilcox and Martin

Dioctria (Eudioctria) nitida f. *denuda* Wilcox and Martin 1941: 17.

In addition to the pattern of pollinosity and of pile on the mesonotum, structure of the male genitalia (Fig. 99) indicates that this species is distinct from *E. nitida.*

Description. – Male: length 10.5-12.0 mm; face brassy; frontovertex and occiput (except vertical extension) orange-brown pollinose; mystax and bristles of antennae and upper half of head black; prothoracic sclerites with dorsal surface and posterolateral corner of antepronotum, and posterodorsal edge of postpronotum, orange-brown pollinose; scutum mainly orange-brown pollinose with pair of lateral bare spots; dorsal half of mesopleuron yellow pollinose; scutellum bare; remaining thoracic pile orange-yellow; front femur black on dorsal, orange on ventral, half; mid and hind femora black; tibiae largely orange yellow, black on apices; tarsi black; male genitalia with lateroposterior part of epandrium broad (Fig. 99B, C); dorsal process of aedeagus narrowed at middle (Fig. 99H).

Female: length 8.5-12.0 mm; front femur entirely black; otherwise same as male.

Distribution. – Western slopes of the Sierra Nevada, California (Map 15).

Specimens examined. – 9♂♂, 31♀♀.

Eudioctria nitida Williston

Dioctria nitida Williston 1884: 8.

Dioctria (Eudioctria) nitida Williston: Wilcox and Martin: 1941: 16.

Description. – length 11.0-13.0 mm; face brassy yellow pollinose; frons paler yellow pollinose; occiput bare of pollen on upper half; mystax and bristles of antennae and upper half of head black; pile of lower occiput and of proboscis white; dorsal surface and posterior corner of antepronotum with small patch of pollen; postpronotum pollinose only on posterodorsal edge; scutum entirely yellowish-brown pollinose; scutal pile rather long and suberect; front femur entirely black; male genitalia with

dorsal process of aedeagus broadened at middle (Fig. 98H); otherwise similar to *E. denuda.*

Female: length 11.0-15.0 mm; coloration and pollinosity as in male.

Distribution. – Southern British Columbia south along the Coast Range and on the Western slopes of the Northern Sierra Nevada, California to the level of San Francisco (Map 14).

Specimens examined. – 24♂♂, 40♀♀.

Eudioctria unica new species

Description. – Male: length 14.0-15.0 mm; face orange pollinose except for shining black gibbosity; frontovertex orange pollinose; bristles of mystax, antennae and upper half of head black; pile on lower half of occiput, prementum and front coxae white, crinkled, exceptionally long; postpronotum yellow pollinose on upper half; scutum with thin brownish pollen, and long yellow pile on acrostical, dorsocentral and supraalar regions; upper half and posterior margin of mesopleuron yellow pollinose; tibiae orange except at apices; rest of legs black; male genitalia with dorsal process of aedeagus slender but broadened at middle (Fig. 100H); lateroposterior part of epandrium short (Fig. 100B); lateral arm of gonocoxite short (Fig. 100A); otherwise similar to *nitida.*

Female: length 12.5-13.0 mm; hind femur distinctly stouter than that of male (compare Fig. 67 and 68); otherwise as in male.

Type material. –

Holotype: ♂, 4 road mi. E. Shasta City, Siskiyou Co., Calif., 23.VII.1962, McBride Camp Bround (D. C. Rentz, C. D. MacNeill) – CAS.

Allotype: ♀, Meadow Valley, Plumas Co., Calif., 5-6000′, 20.VI.1924 (E. C. VanDyke) – CAS.

Paratypes: 1 ♂, Sagehen Creek, near Hobart Mills, Nevada Co., Calif., 17.VI.1964 (M. E. Irwin) – UCR; 1 ♀, Fallen Leaf Lake, Lake Tahoe, 24.VII.1915 (E. C. VanDyke) – CAS. (Map 14).

The *sackeni* group

Four species are assigned to this group: *E. brevis, E. disjuncta, E. sackeni,* and *E. tibialis.* Of these, only *E. sackeni* is found west of the Rocky Mountains.

Good distinguishing characters for this group are in the male genitalia and ovipositor. The posterior part of the epandrium is elongated to form a club-shaped structure and the dorsal process of the aedeagus is broad and membranous (Fig. 105 and 106). In the female the genital fork is fused to adjacent portions of the ninth tergite (Fig. 126 and 127).

Eudioctria brevis Banks

Dioctria brevis Banks 1917: 117.

Dioctria (Eudioctria) brevis Banks: Wilcox and Martin 1941: 12.

Description. – Male: length 8.5-11.0 mm; face either reddish to coppery brown or yellow pollinose; frontovertex yellowish pollinose; occiput pollinose on lower 0.66, bare on remainder; mystax, bristles of antenna, frontovertex, ocellar tubercle and upper part of occiput either black (when face is coppery brown) or yellow (when face is yellow); pile on lower part of occiput and on mouthparts white; bristles on lateral cervical sclerite yellowish; prothorax without pollinosity except narrow brown band on postpronotum adjacent to scutum; scutum largely reddish brown pollinose, except large bare spot on each side and bare area along anterior margin between postpronota; pronotal and scutal bristles either black (when face is coppery) or yellow (when face is yellow); dorsal third and posterior margin of mesopleuron yellowish white pollinose; scutellum bare; wings usually uniformly brown, rarely paler on basal half but not correlated with yellow face; legs either entirely black (when face is coppery) or tibiae orange basally (when face is yellow); pile on legs and on abdomen yellowish; male genitalia with lateroposterior part of epandrium elongate, club-shaped (Fig. 106B, C); membranous structure present on dorsal process of aedeagus (Fig. 106G, H).

Female: length 8.0-12.0 mm; face yellow; mystax, head, antennal and scutal hairs and bristles orange yellow; legs black; ovipositor with genital fork fused to adjacent portion of ninth tergite (Fig. 127A); otherwise same as male.

Distribution. – Along the Appalachian Mountains from New Hampshire to Tennessee and North Carolina with an isolated record in eastern Ohio (Map 20).

Specimens examined. – 184 reddish brown-faced ♂♂, 9 orange-faced ♂♂ and 201♀♀.

Eudioctria disjuncta new species

Description. – Female: length 9.0 mm; pollinosity orange yellow; pile orange yellow; face yellow; frontovertex entirely yellowish white pollinose; upper third of occiput bare; mystax light brown; bristles of antennae and upper half of head yellow; posterior corner of antepronotum yellow pollinose; scutum largely pollinose with pair of parallel, longitudinal bare streaks on anterior dorsocentral region and a bare spot on each side; dorsal half and posterior margin of mesopleuron yellowish white pollinose; basal 0.66 or more of each tibia orange yellow.

Male unknown.

Type material. –

Holotype: ♀, Kerrville, Texas, 21.IV.1959 (J. F. McAlpine) – CNC.

Paratype: ♀, same locality, 17.IV.1959 (J. F. McAlpine) – CNC.

Distribution. – Known only from the type locality (Map 20).

Eudioctria sackeni Williston

Dioctria sackeni Williston 1884: 8.
Dioctria sackeni f. *rivalis* Melander 1923: 215-216.
Dioctria (Eudioctria) sackeni Williston: Wilcox and Martin 1941: 17-18.
Dioctria (Eudioctria) sackeni rivalis Melander: Wilcox and Martin 1941: 18-19.

This is the only species of the *sackeni* group found west of the Rocky Mountains. Two strikingly different colour morphs occur, each in both sexes, with males showing greater differentiation. In the typical morph (*sackeni*) the face is yellowish-white, frons slightly darker yellow, mystax, and bristles of antennae and upper half of head yellow, front and mid femora black dorsally, orange ventrally while all the tibiae are orange except for black apices. The male wing is orange basally, infuscated on apical half. In the other morph (*rivalis*) the face is silver in the male, brassy in the female, the pollen of the frontovertex, scutum and scutellum is coppery-brown, the mystax and bristles of antennae and upper half of head are black, legs are black (except for extreme apices of femora and extreme bases of tibiae which are orange), and the wings are completely infuscated. No differences have been found between the genitalia of either morph.

Description. – Male: length 6.0-8.0 mm; face, frontovertex and occiput (except vertical extension) completely pollinose; anteprono tum pollinose on dorsal suface; scutum entirely pollinose; dorsal 0.66 and posterior margin of mesopleuron yellowish-white pollinose; basal third of scutellum pollinose (Fig. 50); lateroposterior part of epandrium club-shaped (Fig. 105B); membranous structure present on dorsal process of aedeagus (Fig. 105G, H).

Female: length 7.0-9.0 mm; patterns of pollinosity as in male; genital fork of two separate sclerites, each fused to adjacent portion of ninth tergite (Fig. 126A).

Distribution. – Southern British Columbia, northern Idaho and northwestern Montana, to Los Angeles, California, along the Cascade Range and the Northern Sierra Nevada.(Map 21).

Specimens examined. – 64♂♂, 74♀♀ of *sackeni (s.s.)*, and 37♂♂, 67♀♀ of *rivalis*.

Eudioctria tibialis Banks

Dioctria longicornis Banks 1917: 118, *nec* Meigen 1820.
Dioctria longicornis var. *tibialis* Banks 1917: 118.
Dioctria banksi Johnson 1918: 103; (new name for *D. longicornis* Banks).
Dioctria (Eudioctria) banksi Johnson: Wilcox and Martin 1941: 12.
Dioctria (Eudioctria) tibialis Banks: Wilcox and Martin 1965: 371.

This species is the least pollinose in the *sackeni* group.

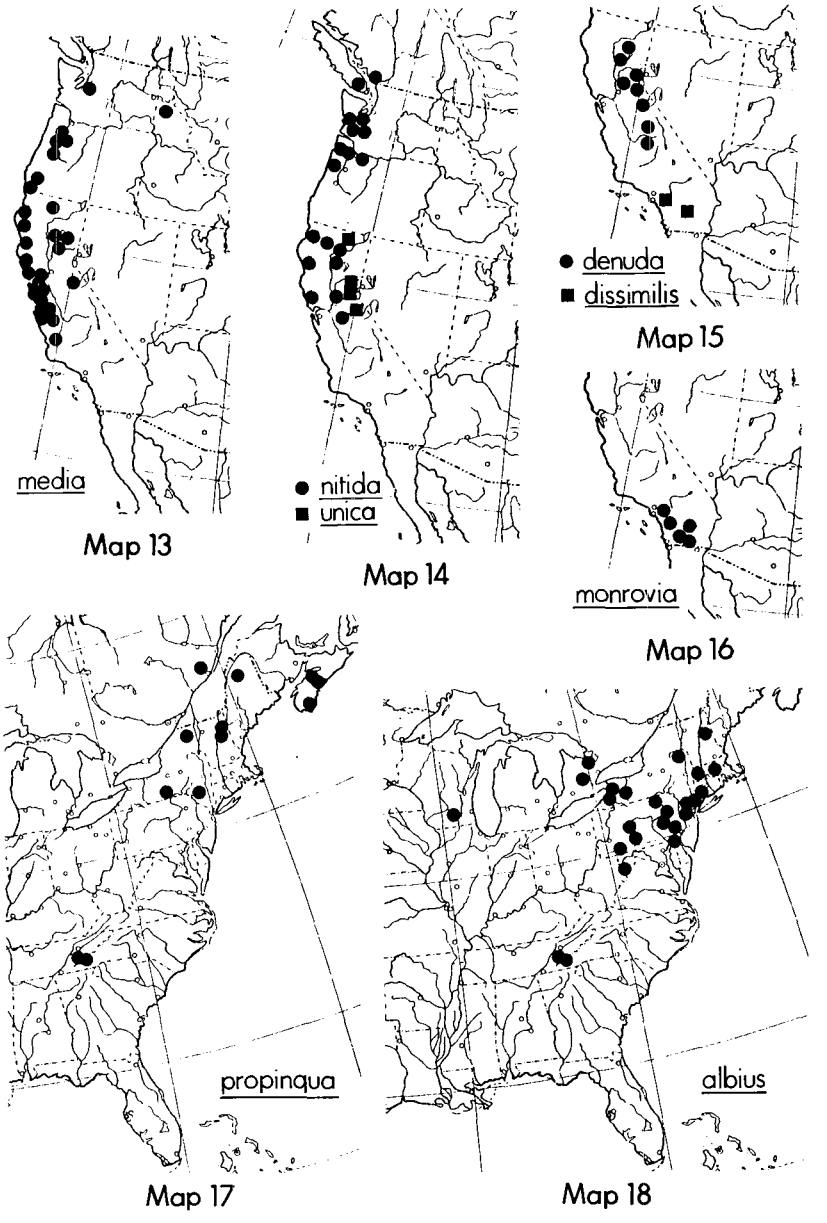
Description. – Male: length 8.5-10.0 mm; face reddish brown pollinose; frontovertex completely orange yellow pollinose; upper third of occiput bare; mystax reddish brown with a few white bristles below; bristles of antenna, frontovertex, ocellar tubercle and occiput brownish; prothoracic sclerites without pollinosity; scutum bare, shining black except for small spot between postpronotum and dorsocentral hairs; mesopleuron without pollinosity; legs usually black (some specimens that have

basal halves of tibiae yellowish were described as var. *tibialis* (Banks 1917); wing infuscated.

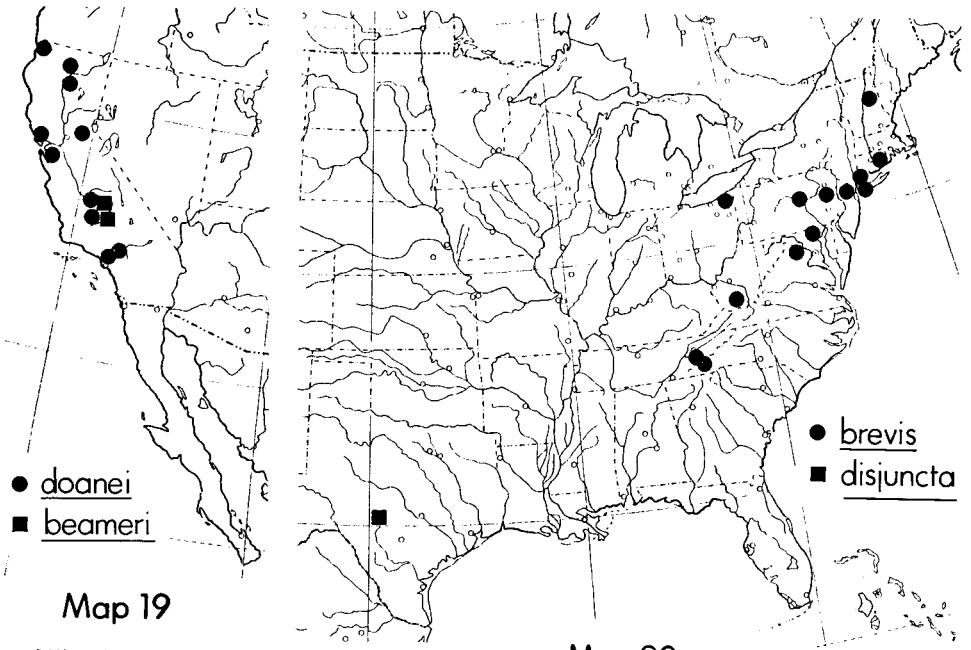
Female: length 9.5-11.0 mm; face orange yellow; otherwise similar to male.

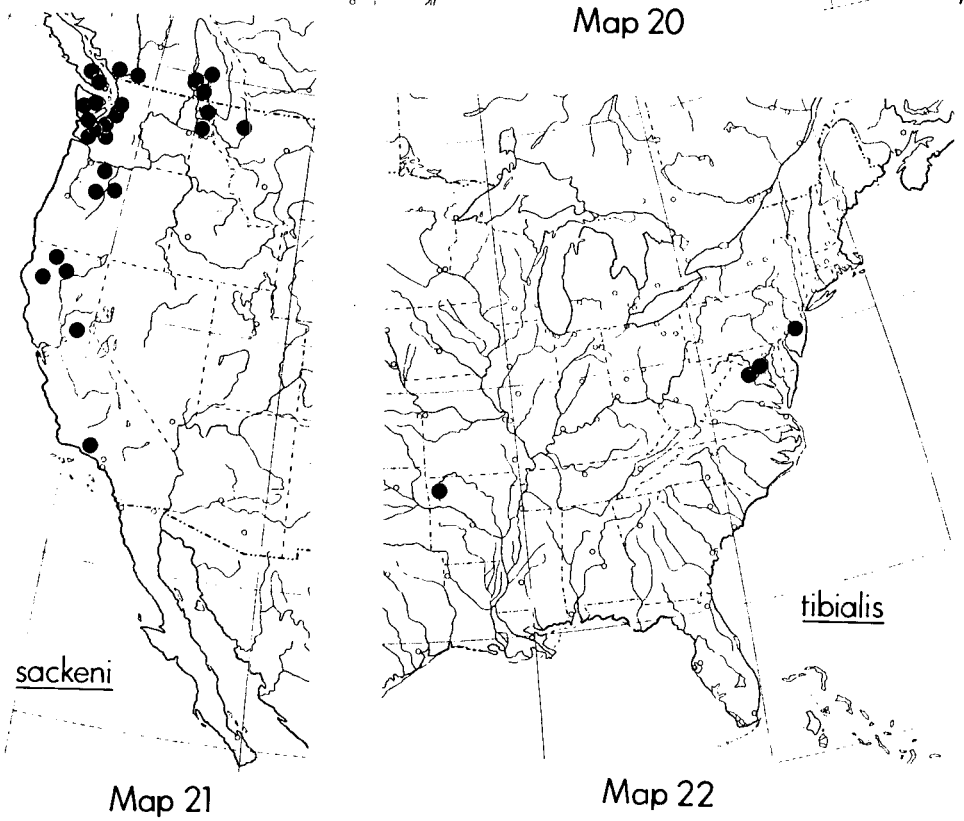
Distribution. – New Jersey, Maryland and Virginia, also northwestern Arkansas (Mt. Magazine, 2800′) (Map 22).

Specimens examined: – 37♂♂, 46♀♀.



Maps 13-18. Distribution of the species of *Eudioctria*.

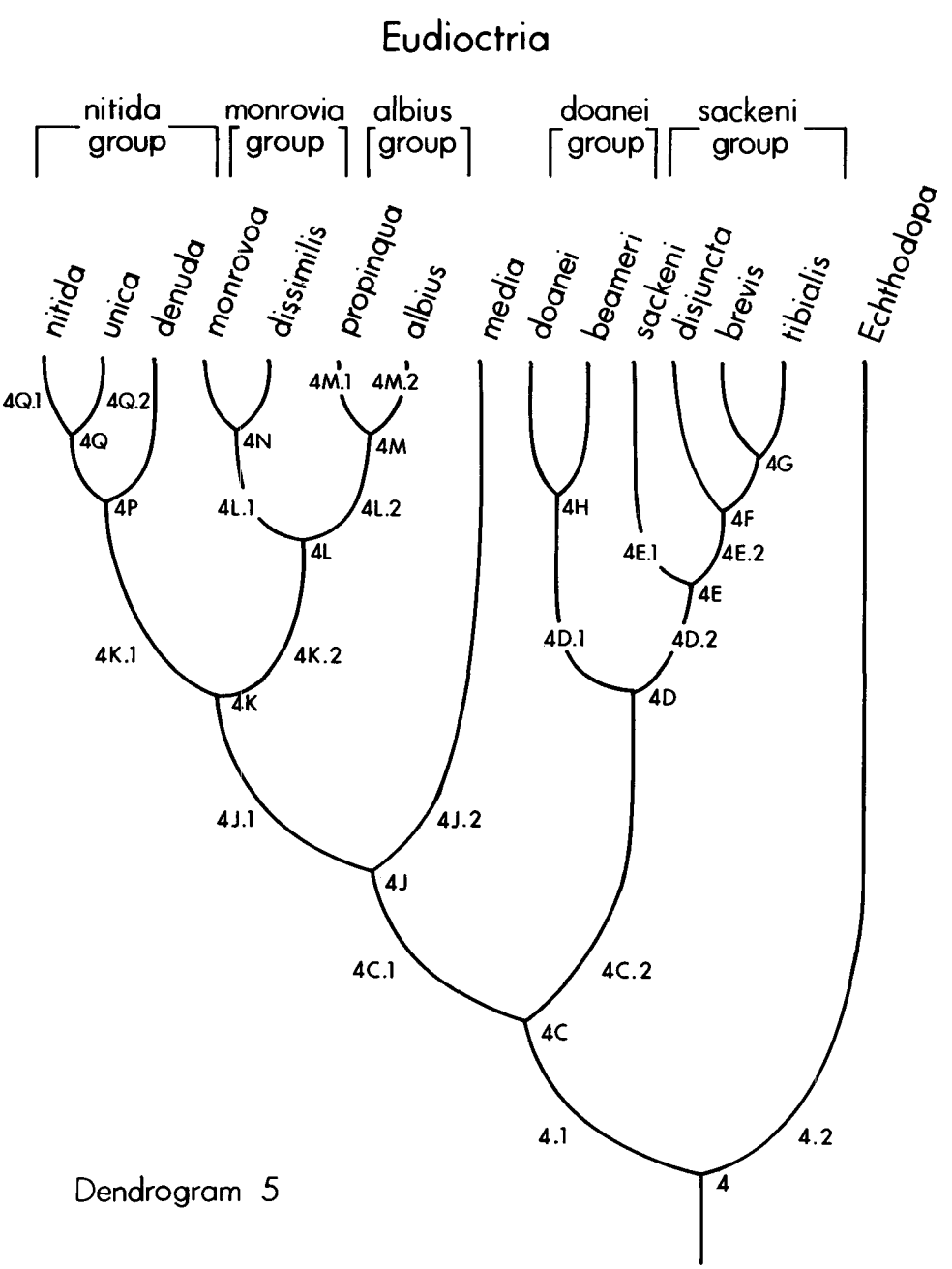




Maps 19-22. Distribution of the species of *Eudioctria*.

Table 5. Characters used for Interpretation of the Phylogeny of *Eudioctria.* (See Dendrogram 5, p. 548)

4C.1 *albius–, media–, monrovia,* and *nitida* groups	4C.2 *doanei–* and *sackeni* groups
Lateroposterior part of epandrium broad and flat.	*Lateroposterior corner of epandrium extended into outgrowth.
Dorsal process of aedeagus curved sclerotized structure.	Dorsal process of aedeagus extended into membranous structure.
Gonostylus tapered apically.	*Gonostylus with subapical bulge.
Lateral process of aedeagus not extended along inner edge of gonocoxite.	*Lateral process of aedeagus extended as flap along inner edge of gonocoxite.
4D.1 *doanei* group	4D.2 *sackeni* group
Posterior part of epandrium, lateral to cleft, broad and short, half as long as epandrial length.	*Posterior part of epandrium elongated as club-shaped structure, 0.66 as long as epandrial length.
*Dorsal process of aedeagus extended as long membranous bulbous structure.	Dorsal process of aedeagus extended as short bubble-like membranous structure.
*Pair of sclerites present posterior to portions of ninth tergite.	No sclerites behind portions of ninth tergite.
Genital fork not fused to ninth tergite.	*Genital fork fused to ninth tergite.
4E.1 *E. sackeni*	4E.2 *E. disjuncta, E. brevis, E. tibialis*
Occiput, except vertical extension, entirely pollinose.	*Upper 0.33 of occiput bare.
Mesonotum entirely pollinose.	*Mesonotum with bare markings.
*Scutellum pollinose.	Scutellum bare.
Genital fork not fused to each other.	*Genital fork fused on anterior ends.
4F.1 *E. disjuncta* and *E. brevis*	4F.2 *E. tibialis*
Mesonotum pollinose with pair of bare markings above wing bases.	*Mesonotum largely bare, pollinosity present only posterior to postpronotum.
Mesopleuron pollinose.	*Mesopleuron bare.
4G.1 *E. disjuncta*	4G.2 *E. brevis*
Posterior corner of antepronotum pollinose.	Antepronotum bare.
*Anterior dorsocentral region with bare streak.	Anterior dorsocentral regions entirely pollinose.
Mesopleural pollinosity on anterior edge extended to lower margin of mesopleuron.	Mesopleural pollinosity not extended to lower margin of mesopleuron.
*Pollinosity on posterodorsal corner of sternopleuron extended forward on lower part almost to sternopleural suture.	Pollinosity on posterodorsal corner of sternopleuron not extended forward.
4H.1 *E. doanei*	4H.2 *E. beameri*
Tibiae orange basally.	Tibiae black.
Outgrowth on epandrium short, stumpy.	*Outgrowth on epandrium elongate.
Lateral arm of hypogynium gradually tapered posteriorly.	*Lateral arm of hypogynium abruptly tapered posteriorly in form of posterior brim.
4J.1 *nitida–, monrovia–,* and *albius* groups	4J.2 *media*
Scutellum bare.	*Basal half of scutellum pollinose.
Lateral process of gonocoxite present.	*Lateral process of gonocoxite absent.
Aedeagus without lateral flap-like structure.	*Aedeagus with pair of lateral flap-like structures.
4K.1 *nitida* group	4K.2 *albius–* and *monrovia* groups
Dorsal process of aedeagus flattened dorsoventrally.	Dorsal process of aedeagus compressed laterally.
4L.1 *monrovia* group	4L.2 *albius* group
Side of pronotum not pollinose.	Side of pronotum pollinose.
*Hypandrium elongate, longer than gonocoxite.	Hypandrium short, at most half as long as gonocoxite.
No polymorphism.	*Polymorphism in males.
Western.	*Eastern.
*Medioventral process of gonocoxite greatly reduced.	Medioventral process of gonocoxite broad.
Lateral process of gonocoxite flat.	*Lateral process of gonocoxite concave, scoop-like.
*Genital fork fused on anterior ends, in form of inverted U-shaped structure.	Genital fork as two separate sclerites.



Dendrogram 5

Dendrogram 5. Phylogeny of the species of *Eudioctria*.

Table 5. (concluded). Characters used for Interpretation of the Phylogeny of *Eudioctria.*

4M.1 *E. propinqua*	4M.2 *E. albius*
Mesonotum entirely pollinose.	*Mesonotum with pair of sublateral bare markings.
Posterior margin of mesopleuron pollinose.	*Posterior margin of mesopleuron pollinose only on upper half.
Tip of dorsal process of aedeagus pointed.	*Tip of dorsal process of aedeagus blunt, in form of hook.
4N.1 *E. monrovia*	4N.2 *E. dissimilis*
Mesonotum mainly pollinose with pair of bare markings.	*Mesonotum largely bare, pollinose only posterior to post-pronotum.
Posterior edge of hypandrium not formed as brim-like extension.	*Posterior edge of hypandrium extended as brim.
Dorsal process of aedeagus without dorsal projection.	*Dorsal process of aedeagus with dorsal projection.
*Genital fork broadened at middle.	Genital fork horse-shoe shaped.
4P.1 *E. nitida* and *E. unica*	4P.2 *E. denuda*
Mesonotum entirely pollinose.	*Mesonotum with bare spots.
*Mesonotal and mesopleural hairs longer.	Mesonotal and mesopleural hairs shorter.
*Dorsal process of aedeagus broadened in middle.	*Dorsal process of aedeagus narrowed in middle.
4Q.1 *E. nitida*	4Q.2 *E. unica*
Face entirely pollinose.	*Face with triangular bare marking on gibbosity.
*Posterior part of epandrium more horizontal than vertical.	Posterior part of epandrium more vertical.

* denotes apomorphic condition

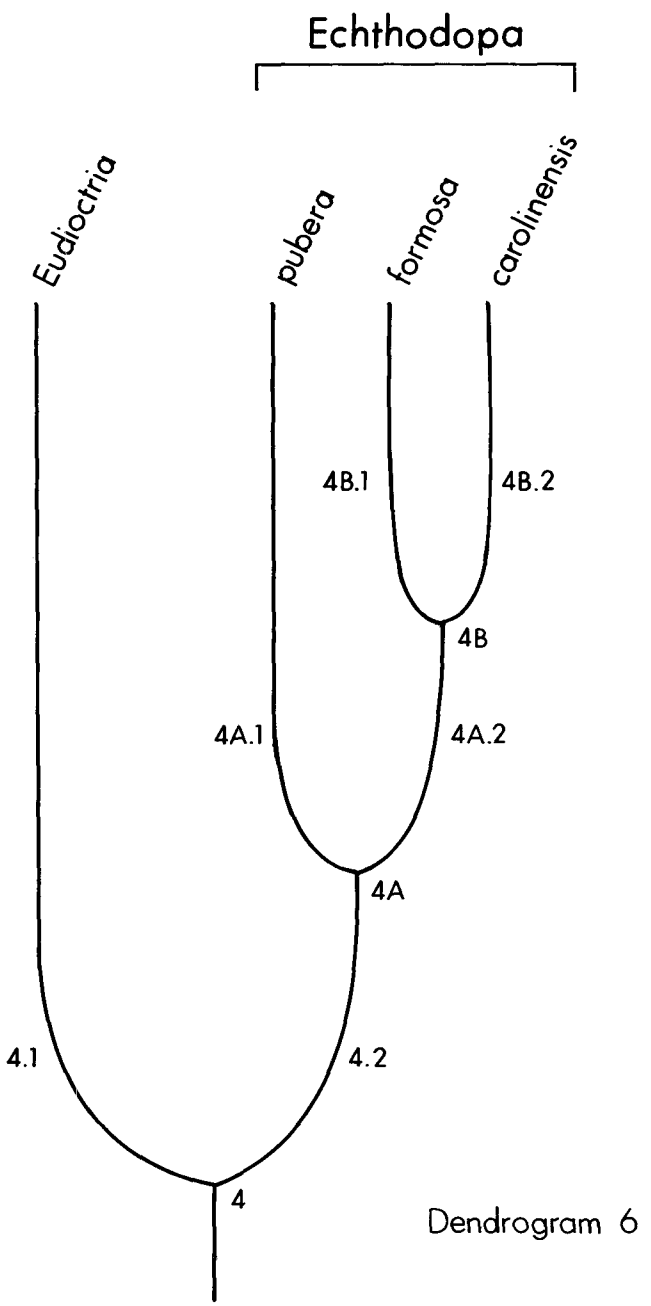
Genus *Echthodopa* Loew

Echthodopa Loew 1866: 15. Type-species: *Echthodopa pubera* Loew (loc. cit.), by monotypy.
Echthopoda Loew 1872: 62, unjustified emendation of *Echthodopa.*

Diagnosis. – Antennal style spoon-shaped, third segment of antenna subcylindrical and elongate, first segment 1.33 as long as second, with hairs on ventral surface not uniform in length (Fig. 20); frontovertex without pollinosity, bristles along margins, pair of patches of bristles near antennal bases; ocellar bristles in curved rows; occiput pollinose; face pollinose, with gibbosity on lower part (Fig. 32); mystax of clustered hairs; prementum densely pilose; labellum notched subapically; thorax black; prothoracic sclerites densely pilose, pollinose on side of antepronotum; mesonotum not pollinose, evenly pilose; mesothoracic pleuron pollinose on almost entire surface of mesopleuron, along dorsal margin of sternopleuron, on pteropleuron, and on posterior half of hypopleuron; scutellum pilose with long bristles along posterior edge (Fig. 51); basal 0.66 of each tibia orange, remainder of legs black; pile on legs orange-yellow; hind and mid femora each with a patch of short strong bristles on subapical anterior surface; wing hyaline, alula well developed, R_4 ended before wing tip; abdomen black, narrowest at intersegment between second and third segment; second abdominal segment with transverse subbasal groove turned forward on sides; abdominal pile orange yellow, longest on sides of second segment; male genitalia almost uniform (Fig. 108), with hypandrium either parallel sided (Fig. 108A) or constricted subapically; epandrium split into two lateral halves, without epandrial arms (Fig. 108B, C); aedeagus with dorsal bulge (Fig. 108G, H); ovipositor with genital fork split at anterior end (Fig. 128A).

Remarks. – Although various emended spellings of the name, e.g. *Echtodopa, Echtopoda, Echthopoda,* have been used, there is no indication in the original publication that *Echthodopa* was an inadvertant printer's error, thus the original spelling is accepted in accordance with Article 32(a)ii, International Code of Zoological Nomenclature.

This genus is represented in both eastern and western North America by three quite similar species. The characters used to deduce their phylogeny (Dendrogram 6) are tabulated in Table 6.



Dendrogram 6. Phylogeny of the species of *Echthodopa*.

Key to the species of *Echthodopa*

1	Mystax black	*carolinensis* Bromley, p. 551
1'	Mystax orange or yellow	2
2 (1')	Bristles on male and female genitalia black; hypandrium constricted subapically..	*formosa* Loew, p. 551
2'	Bristles on male and female genitalia orange yellow; hypandrium parallel sided (Fig.108)	*pubera* Loew, p. 551

Echthodopa carolinensis Bromley

Echthodopa carolinensis Bromley 1951: 9.

Description. – Male: length 20.0 mm; mystax black, remaining pile and bristles orange yellow; hypandrium constricted subapically.

Female: Unknown.

Distribution. – Known only from the type locality, Linville Falls, N.C., at 3000-3200' (Map 23).

Specimens examined. – 2♂♂ (holotype and paratype).

Echthodopa formosa Loew

Echthodopa formosa Loew 1872: 62.

Echthodopa formosa Loew; Back 1909: 248.

Description. – Male: length 18.0-19.0 mm; pile of two slightly different colors, that on frontovertex, occiput and mesonotum bright orange yellow, on remaining parts pale yellowish; bristles on genitalia black; hypandrium constricted subapically.

Female: same as male.

Distribution. – Massachusetts to Mississippi (Map 23).

Specimens examined. – 6♂♂, 6♀♀.

Echthodopa pubera Loew

Echthodopa pubera Loew 1866: 15.

Description. – Male: length 17.0-19.0 mm; pile uniformly pale yellowish; hypandrium parallel sided (Fig. 108A).

Female: same as male.

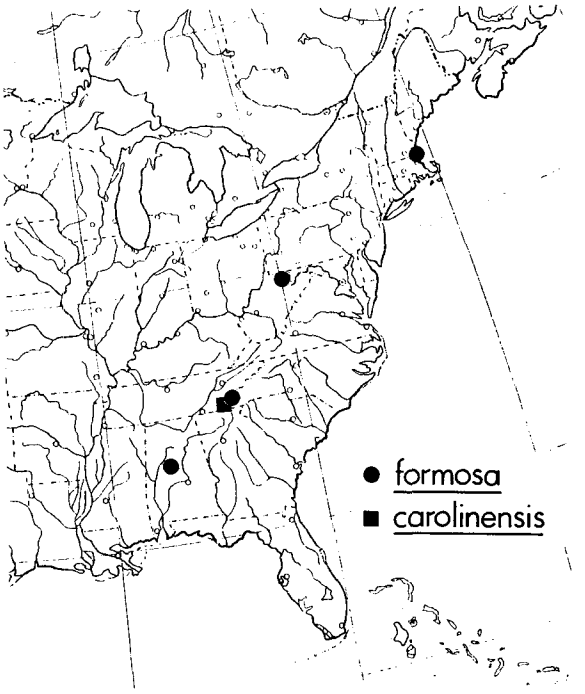
Distribution. – Rather widely distributed in two disjunct areas, Washington and Idaho, and Wisconsin to Michigan, south to Texas (Map 24).

Specimens examined. – 36♂♂, 56♀♀.

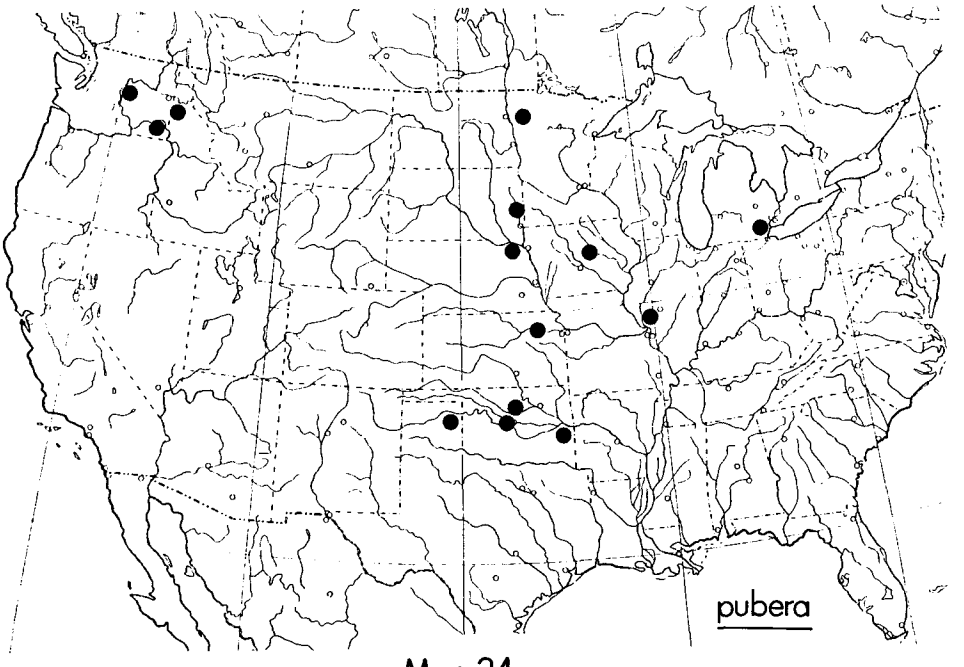
Table 6. Characters used for Interpretation of the Phylogeny of *Echthodopa.*

4A.1 *E. pubera*	4A.2 *E. formosa* and *E. carolinensis*
Hypandrium parallel sided.	*Hypandrium constricted subapically.
Western.	*Eastern.
4B.1 *E. formosa*	4B.2 *E. carolinensis*
Mystax orange yellow.	*Mystax black.
*Bristles on male and female genitalia black.	Bristles on male and female genitalia orange yellow.

* denotes apomorphic condition



Map 23



Map 24

Maps 23-24. Distribution of the species of *Echthodopa*.

List of Nearctic Species of Dioctriini and Echthodopini

Dioctriini Hull, p. 513*

Dioctria Meigen, p. 514		
subg.	*Nannodioctria* Wilcox and Martin, p. 514	
	albicornis Wilcox and Martin, p. 514	Calif.
	australis new species, p. 515	Mexico
	seminole Bromley, p. 515	Fla.
subg.	*Dioctria,* p. 516	
	baumhaueri Meigen, p. 519	introduced from Europe to eastern N.A.
	henshawi Johnson, p. 517	B.C., and Ida., to Calif. and Utah.
	pleuralis Banks, p. 517	Calif., Ariz.
	pusio Osten Sacken, p. 518	B.C. to Calif.
	vera Back, p. 518	Calif. to Colo. and N. Mex.
	wilcoxi new species, p. 518	Calif.

Echthodopini new tribe, p. 523

Dicolonus Loew, p. 524	
medium new species, p. 524	Calif., Nev.
nigricentrum new species, p. 525	B.C., Wash., Ida.
pulchrum new species, p. 525	Calif.
simplex Loew, p. 525	B.C., Wash., Calif.
sparsipilosum Back, p. 525	Rocky Mts. – Mont. to Colo.
Myelaphus Bigot, p. 528	
lobicornis Osten Sacken, p. 528	Wash., Utah, Calif.
melas Bigot, p. 528	Calif.
Bohartia Hull, p. 529	
bromleyi Hull, p. 530	Nev.
isabella new species, p. 531	Calif., Nev.
martini new species, p. 531	Wash. and Wyo. to Calif. and Ariz.
munda new species, p. 532	Calif.
nitor new species, p. 532	Calif.
senecta new species, p. 532	Baja Calif., Mexico
tenuis new species, p. 533	Ariz.
Metadioctria Wilcox and Martin, p. 535	
rubida Coquillett, p. 536	Calif.
Eudioctria Wilcox and Martin, p. 537	
albius Walker, p. 539	Wisc. and N.H. to Tenn., and N.C.
beameri Wilcox and Martin, p. 540	Calif.
brevis Banks, p. 543	N.H. to Tenn. and N.C.
denuda Wilcox and Martin, p. 542	Calif.
disjuncta new species, p. 544	Texas
dissimilis new species, p. 541	Calif.
doanei Melander, p. 540	Calif.
media Banks, p. 541	Wash. and Ida. to Calif.
monrovia Wilcox and Martin, p. 542	Calif.
nitida Williston, p. 542	B.C. to Calif.

propinqua Bromley, p. 540	Que. and N.S. to Tenn. and N.C.
sackeni Williston, p. 544	B.C. and Mont. to Calif.
tibialis Banks, p. 544	N.J. to Va., also Ark.
unica new species, p. 543	Calif.
Echthodopa Loew, p. 549	
carolinensis Bromley, p. 551	N.C.
formosa Loew, p. 551	Mass. to N.C.
pubera Loew, p. 551	Wash., Mich. to Texas

*Reference is to present text

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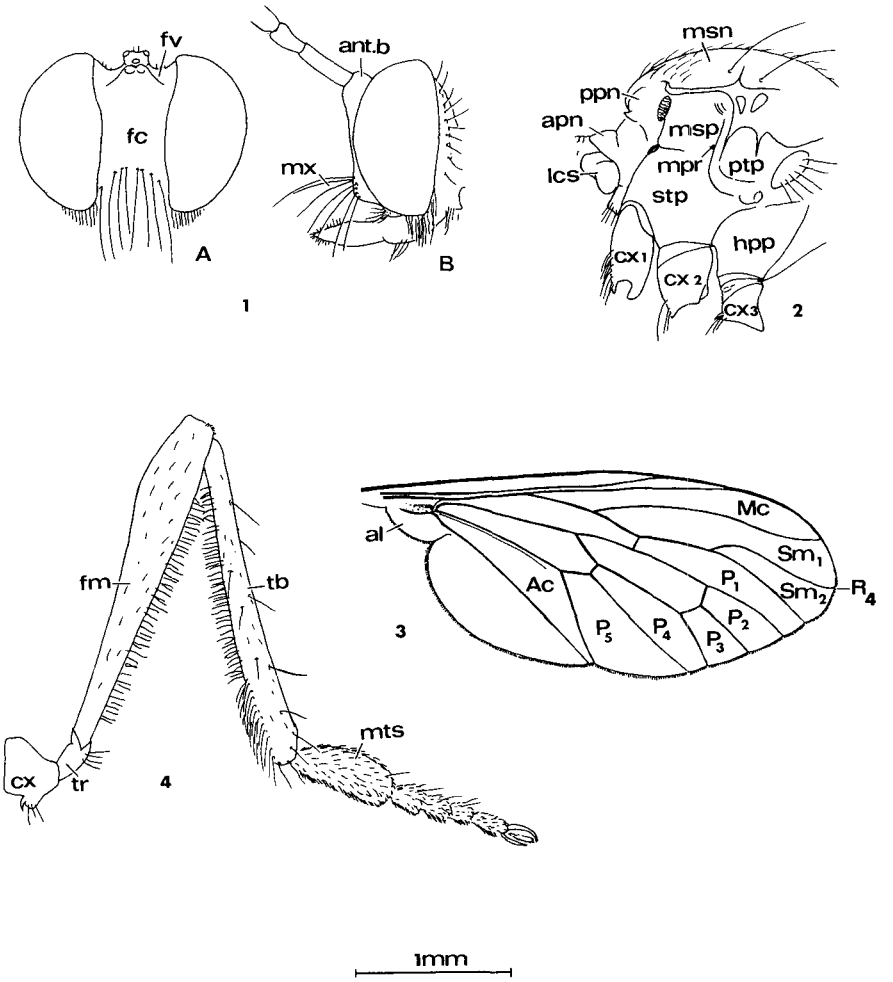

Fig. 1. Head; A. frontal aspect; B. lateral aspect; ant. b – antennal bases; fc – face; fv – frontovertex; mx – mystax. Fig. 2. Thorax, lateral aspect; apn – antepronotum; hpp – hypopleuron; lcs – lateral cevical sclerite; mpr – mesopleural ridge; msp – mesopleuron; msn – mesonotum; ppn – postpronotum; ptp – pteropleuron; stp – sternopleuron. Fig. 3. Hind leg, lateral aspect; cx – coxa; fm – femur; mts – metatarsus; tb – tibia; tr – trochanter. Fig. 4. Wing; R_4 – anterior branch of third vein; Ac – anal cell; Mc – marginal cell; P – posterior cell; Sm – submarginal cell; al – alula.

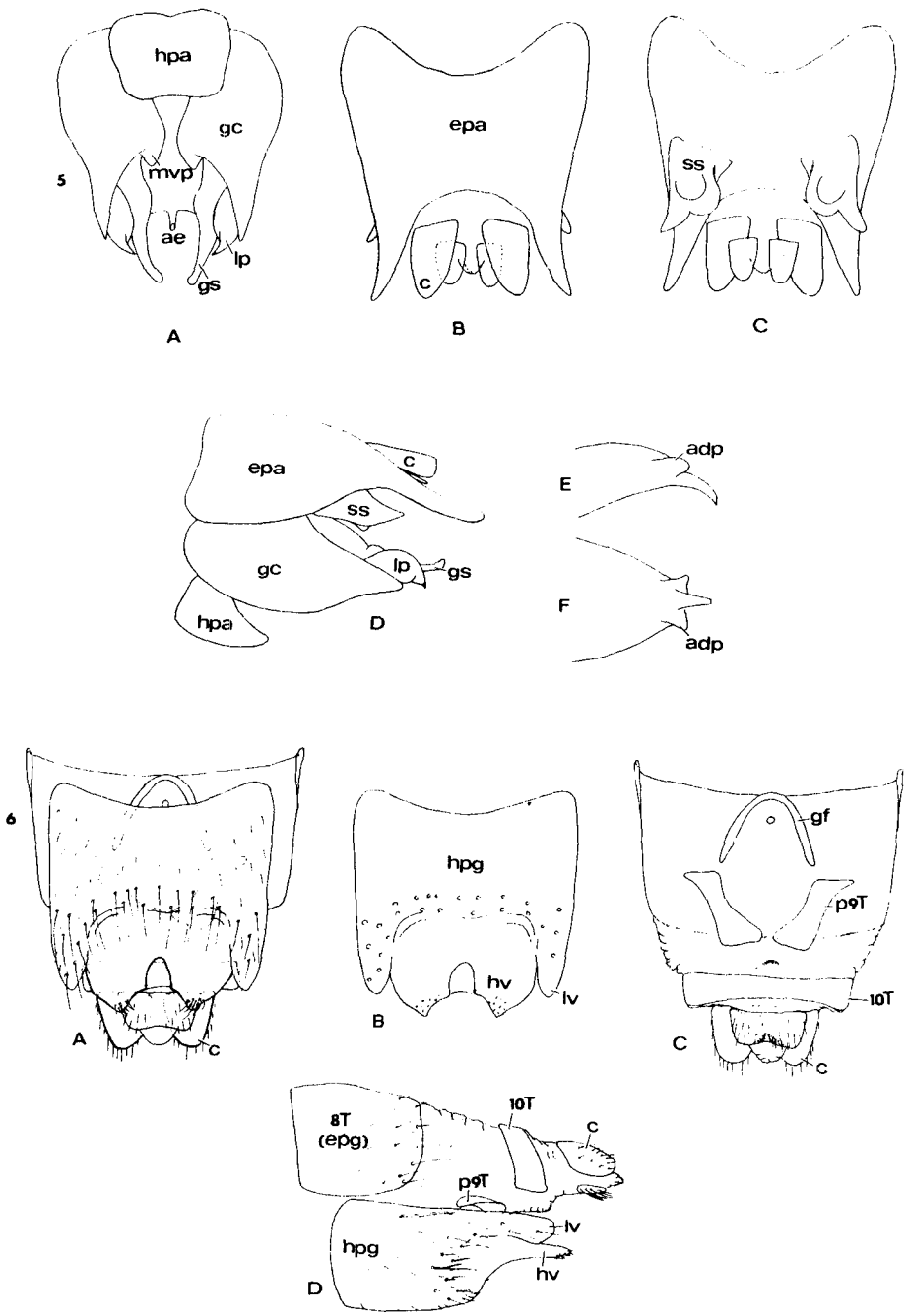

Fig. 5. Male genitalia; A. ventral aspect, epandrium omitted; B. epandrium, dorsal aspect; C. epandrium, ventral aspect; D. lateral aspect of genitalia; E. aedeagus, lateral aspect; F. aedeagus, dorsal aspect; adp – lateral process of aedeagus; epa – epandrium; hpa – hypandrium; gc – gonocoxite; gs – gonostylus; lp – lateral process of gonocoxite; mvp – medioventral process of gonocoxite; ss – surstylus. Fig. 6. Ovipositor; A. ventral aspect; B. hypogynium; ventral aspect; C. lateral aspect of ovipositor; c– cercus; gf – genital fork; hpg – hypogynium; hv – hypogynial valve; lv – lateral valve of hypogynium; p9T – portion of ninth tergite; 8T – eighth tergite or epygynium (epg); 10T – tenth tergite.

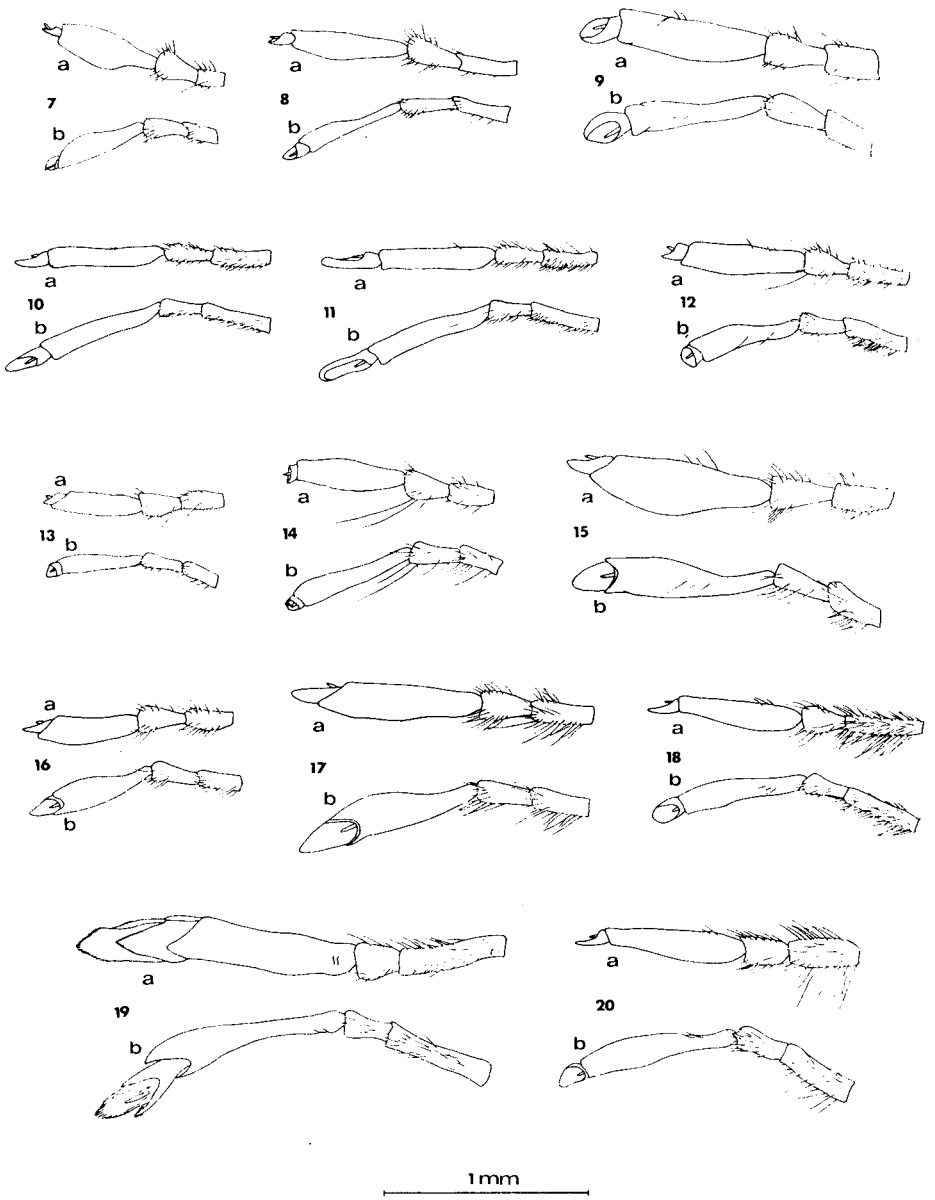

Fig. 7-20. Antenna; a. lateral aspect; b. dorsal aspect; Fig. 7. *Dioctria albicornis*; Fig. 8. *D. seminole*; Fig. 9. *D. australis*; Fig. 10. *D. pleuralis*; Fig. 11. *D. pusio*; Fig. 12. *Metadioctria rubida*; Fig. 13. *Bohartia isabella*; Fig. 14. *B. bromleyi*; Fig. 15. *Eudioctria albius*; Fig. 16. *E. sackeni*; Fig. 17. *E. brevis*; Fig. 18. *Dicolonus simplex*; Fig. 19. *Myelaphus lobicornis*; Fig. 20. *Echthodopa pubera*.

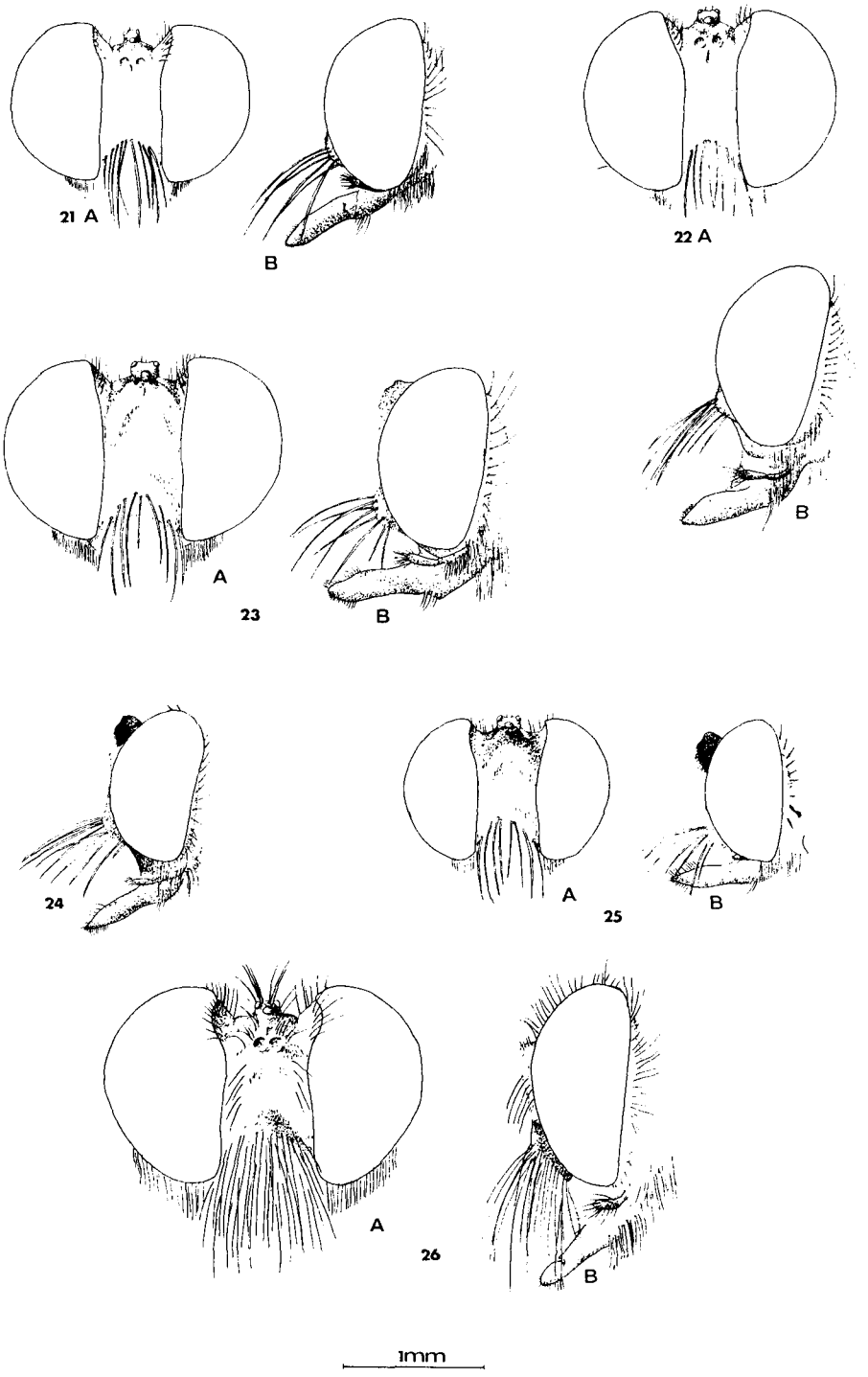

Fig. 21-26. Head; A. frontal aspect; B. lateral aspect; Fig. 21. *Dioctria albicornis*; Fig. 22. *D. seminole*; Fig. 23. *D. pleuralis*; Fig. 24. *D. henshawi*; Fig. 25. *D. pusio*; Fig. 26. *Metadioctria rubida.*

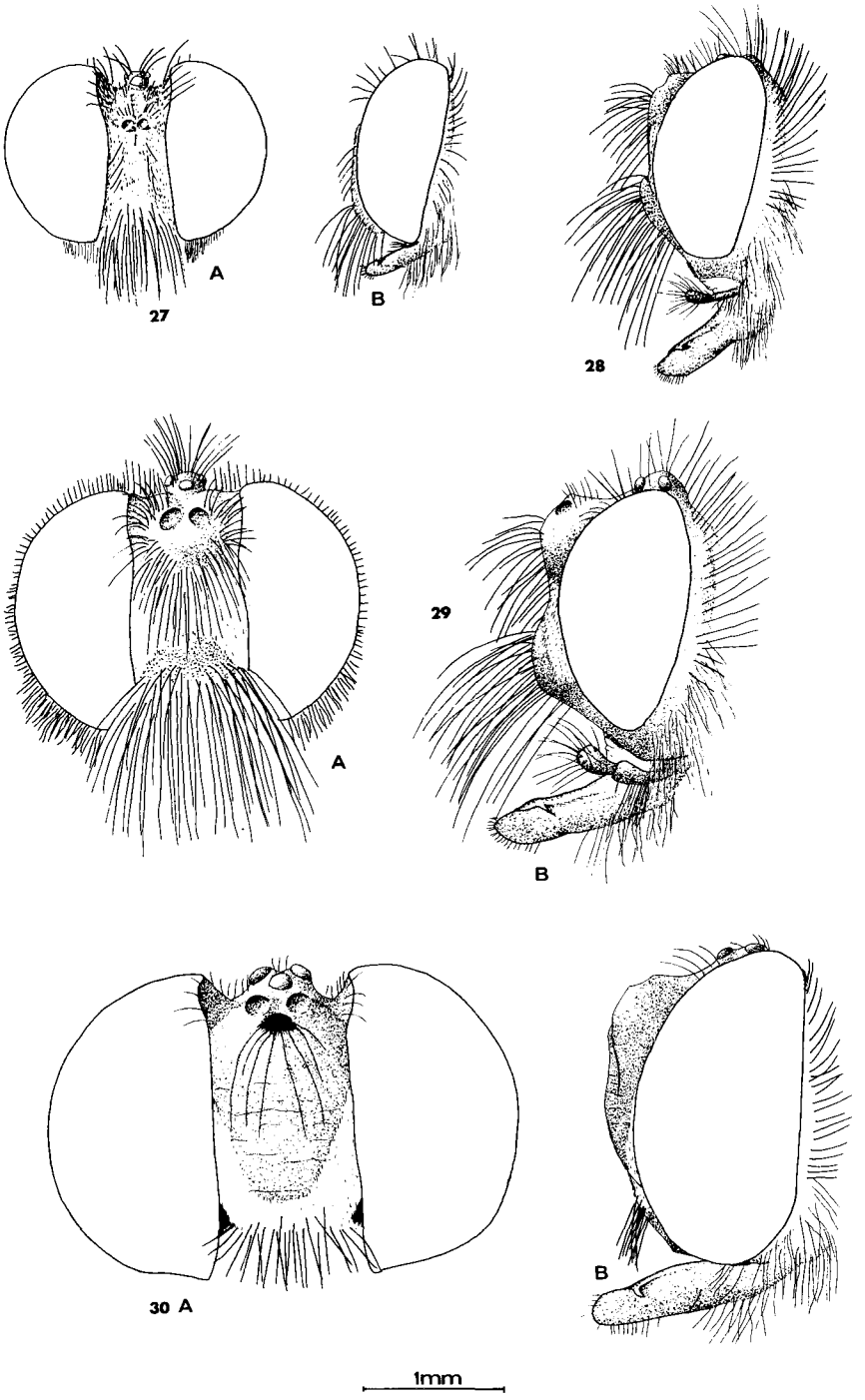

Fig. 27-30. Head; A. front aspect; B. lateral aspect; Fig. 27. *Bohartia isabella;* Fig. 28. *Dicolonus medium;* Fig. 29. *D. simplex;* Fig. 30. *Myelaphus lobicornis.*

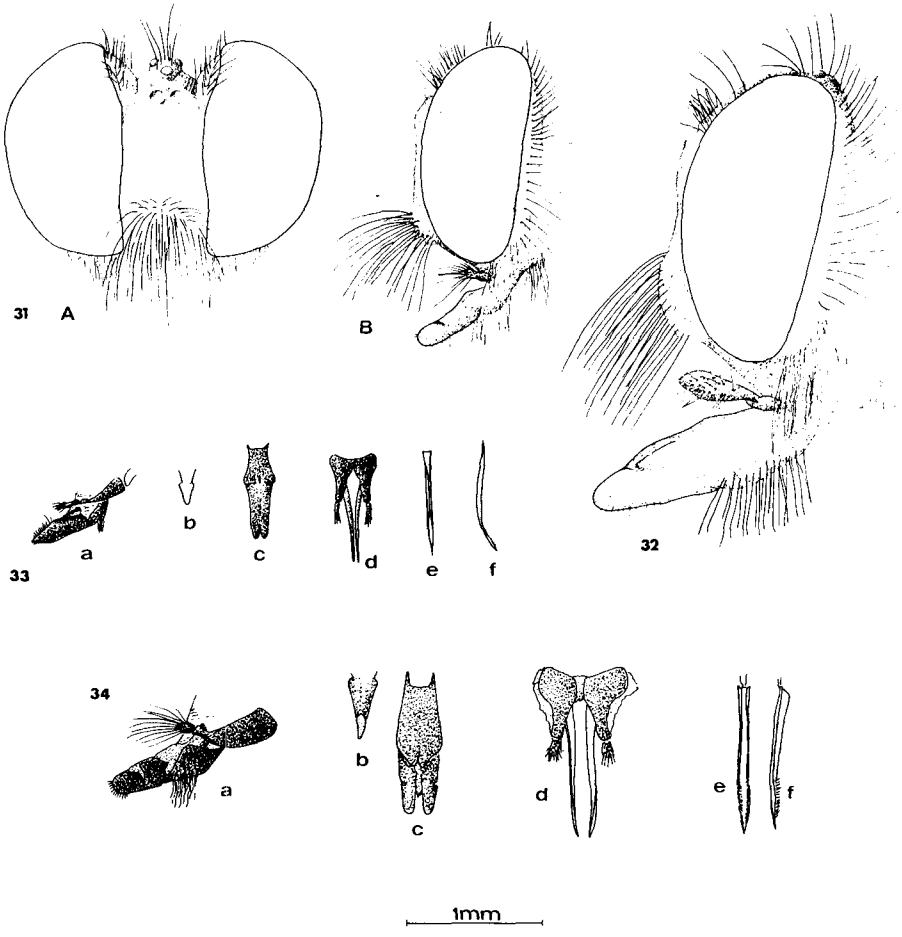

Fig. 31-32. Head; Fig. 31. *Eudioctria albius*; Fig. 32. *Echthodopa pubera.* Fig. 33-34. Mouthparts; Fig. 33. *Dioctria pusio*; Fig. 34. *Eudioctria albius*; a. proboscis, lateral aspect; b. labrum; c. labium, ventral aspect; d. maxilla, ventral aspect; e. hypopharynx, dorsal aspect; f. right lateral blade of hypopharynx, lateral aspect.

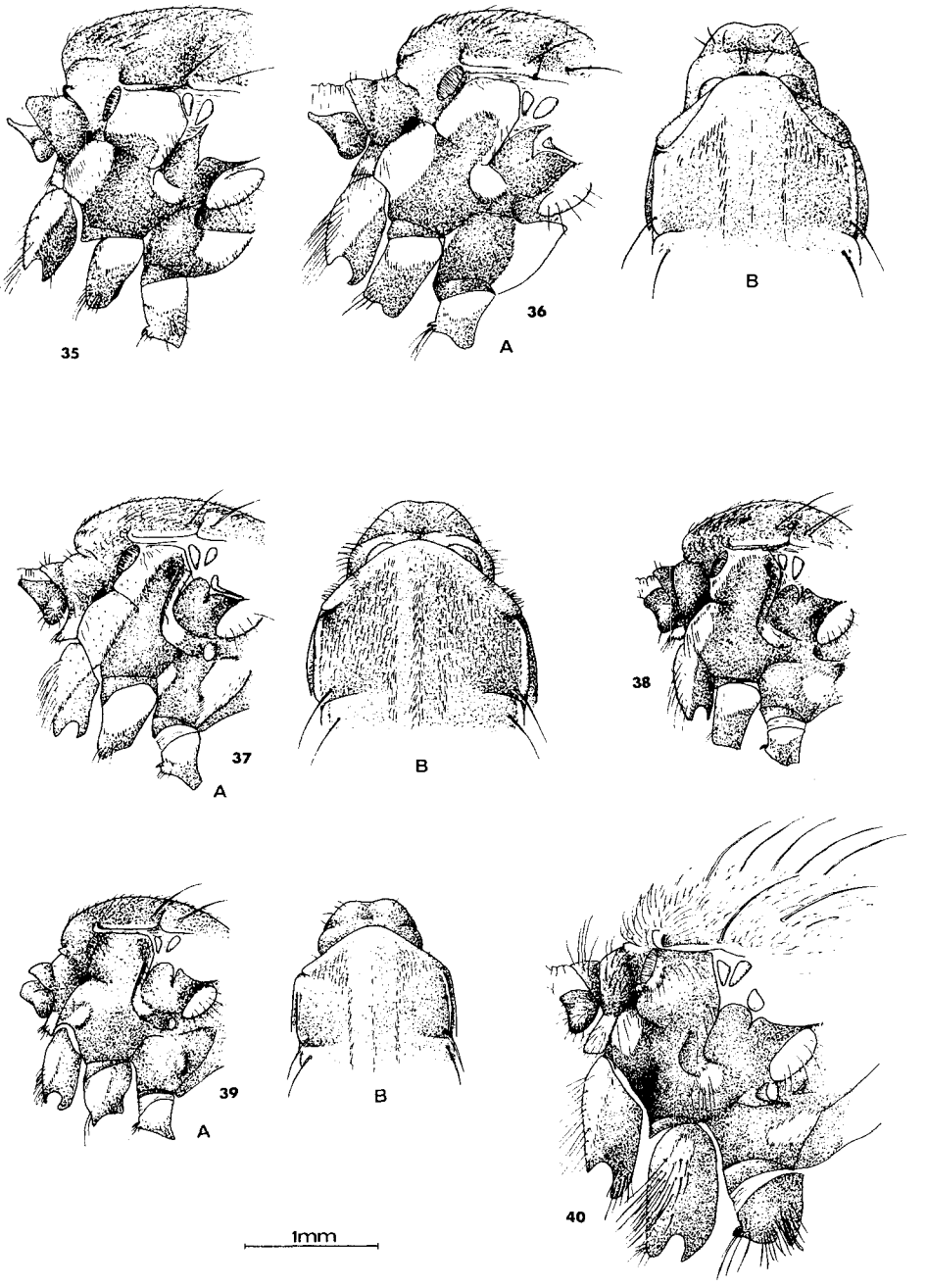

Fig. 35-40. Thorax, A. lateral aspect; B. dorsal aspect; Fig. 35. *Dioctria albicornis;* Fig. 36. *D. seminole*; Fig. 37. *D. pleuralis;* Fig. 38. *D. henshawi*; Fig. 39. *D. pusio;* Fig. 40. *Metadioctria rubida.*

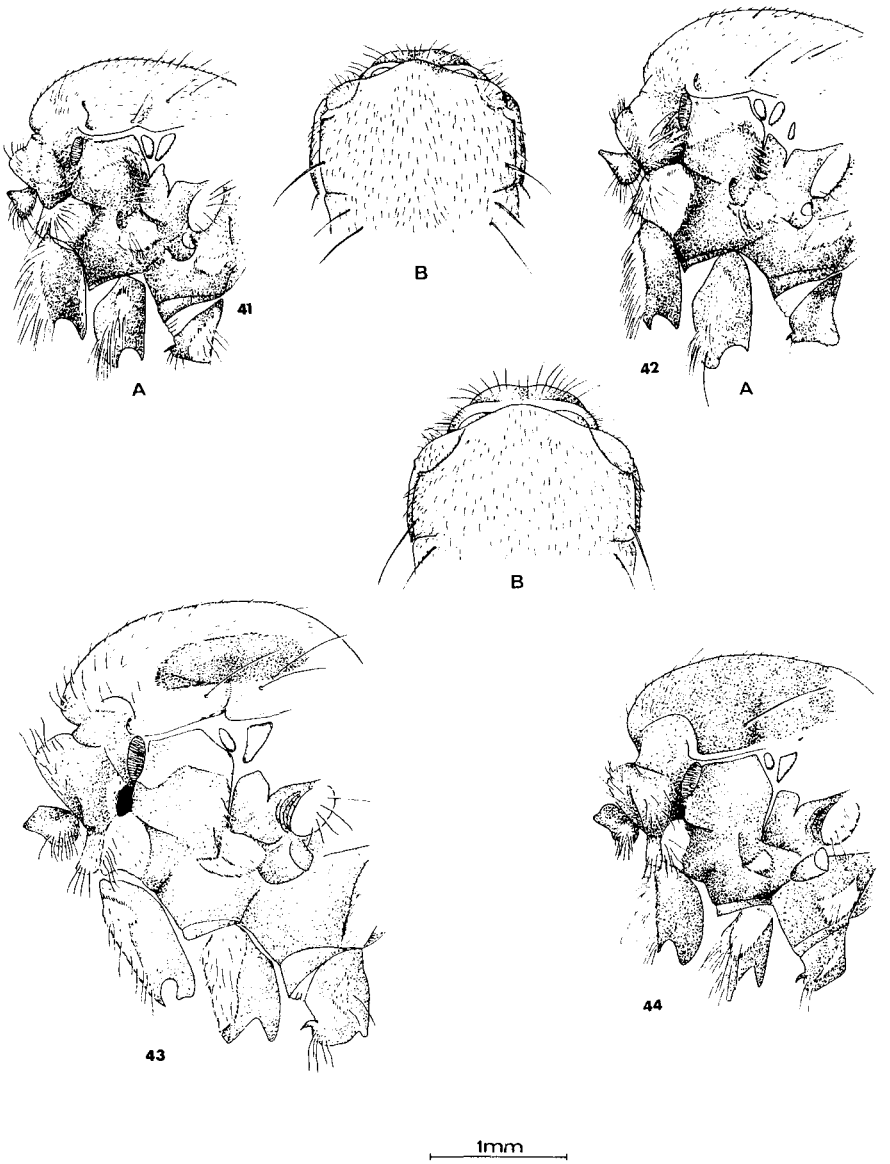

Fig. 41-44. Thorax, A. lateral aspect; B. dorsal aspect; Fig. 41. *Bohartia isabella;* Fig. 42. *B. martini*; Fig. 43. *Eudioctria albius*; Fig. 44. *E. tibialis.*

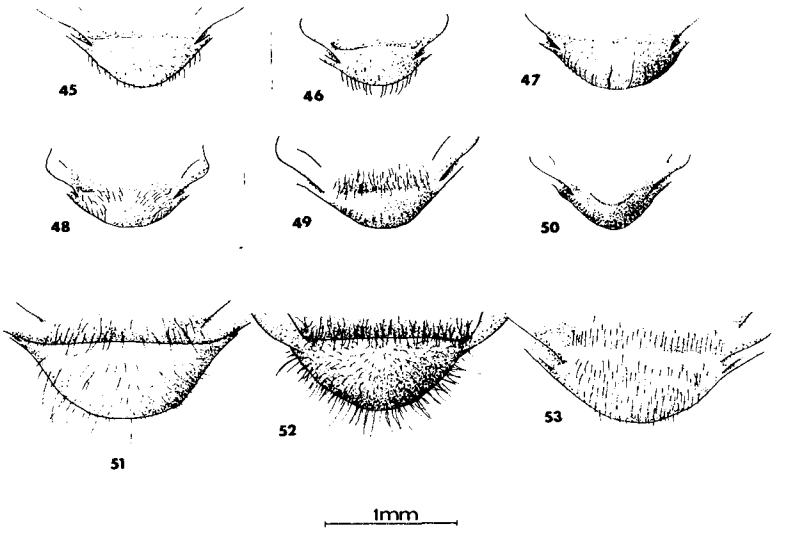

Fig. 45-53. Scutellum, dorsal aspect; Fig. 45. *Dioctria albicornis*; Fig. 46. *D. pusio*; Fig. 47. *Metadioctria rubida*; Fig. 48. *Bohartia isabella*; Fig. 49. *Eudioctria albius*; Fig. 50. *E. sackeni*; Fig. 51. *Echthodopa pubera*; Fig. 52. *Dicolonus simplex*; Fig. 53. *Myelaphus lobicornis.*

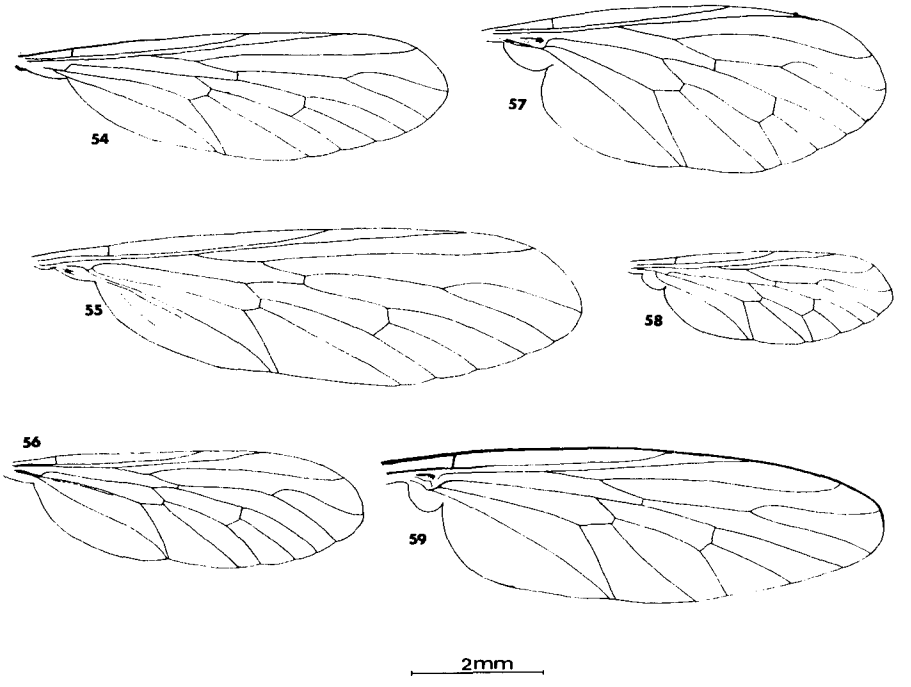

Fig. 54-59. Wing; Fig. 54. *Dioctria albicornis*; Fig. 55. *D. seminole*; Fig. 56. *D. pusio*; Fig. 57. *Metadioctria rubida*; Fig. 58. *Bohartia isabella*; Fig. 59. *Eudioctria albius.*

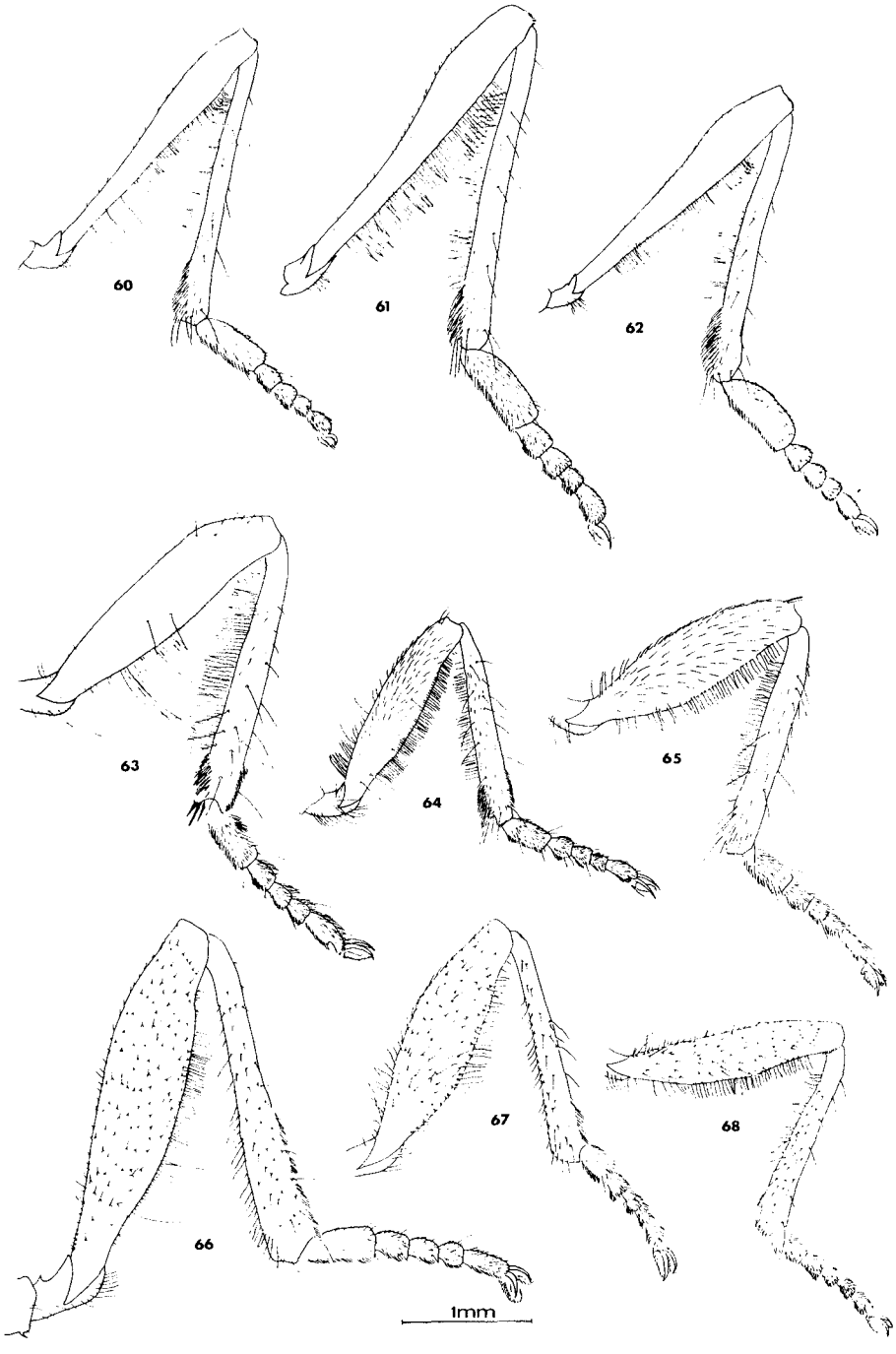

Fig. 60-68. Hind leg; Fig. 60. *Dioctria albicornis*; Fig. 61. *D. seminole*; Fig. 62. *D. pleuralis*; Fig. 63. *Metadioctria rubida*; Fig. 64. *Bohartia isabella*; Fig. 65. *B. martini*; Fig. 66. *Eudioctria albius*; Fig. 67. *E. unica*, male; Fig. 68. *E. unica*, female.

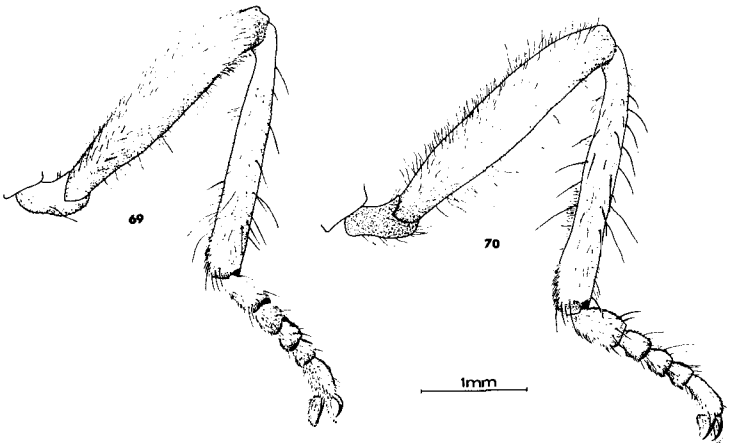

Fig. 69-70. Hind leg; Fig. 69. *Dicolonus medium*; Fig. 70. *D. nigricentrum.*

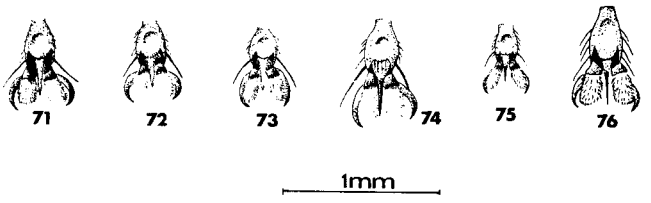

Fig. 71-76. Empodium; Fig. 71. *Dioctria albicornis;* Fig. 72. *D. seminole*; Fig. 73. *D. pleuralis*; Fig. 74. *Metadioctria rubida*; Fig. 75. *Bohartia isabella*; Fig.76. *Eudioctria albius.*

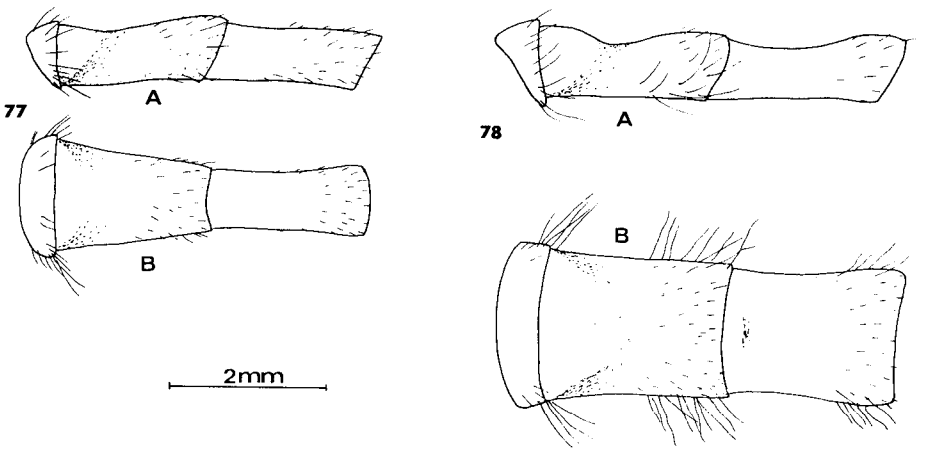

Fig. 77-78. First three segments of abdomen. A. lateral aspect; B. dorsal aspect; Fig. 77. *Dioctria albicornis*; Fig. 78. *D. seminole.*

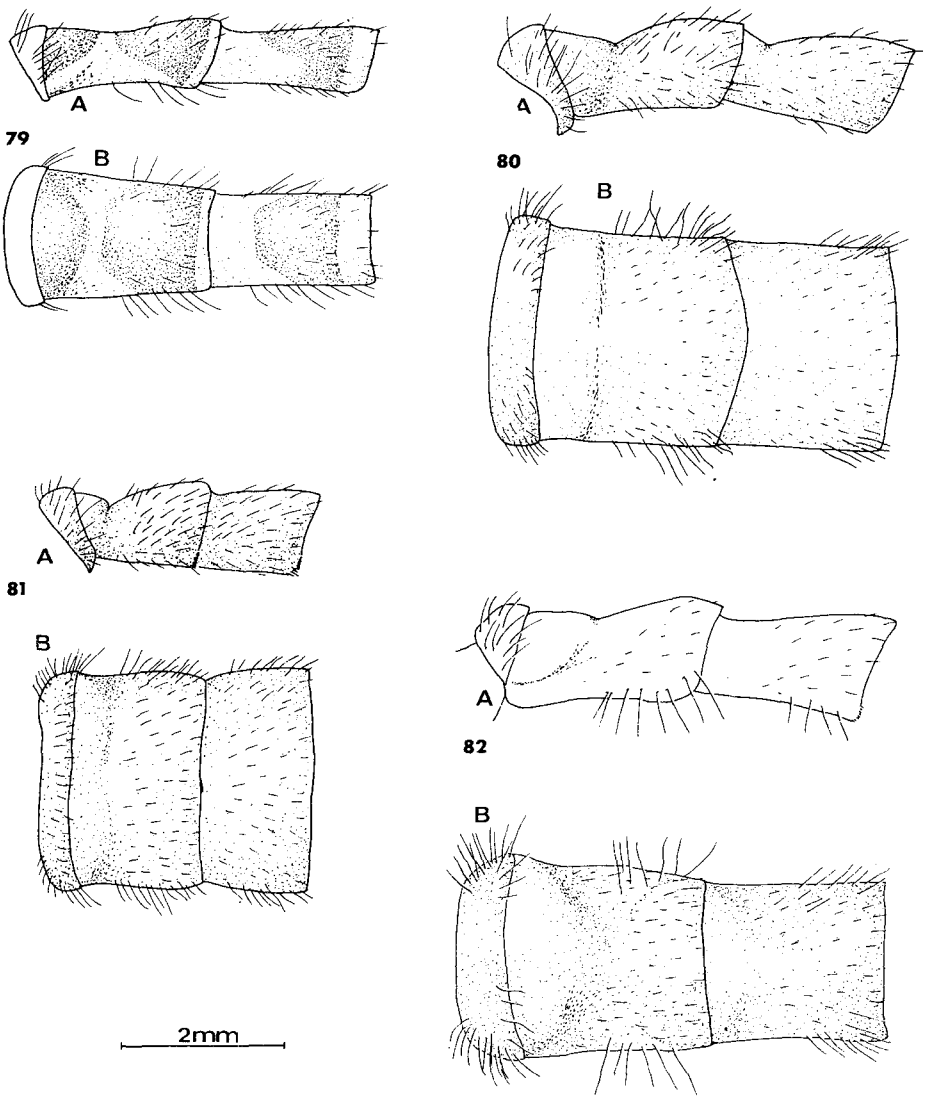

Fig. 79-82. First three segments of abdomen, A. lateral aspect; B. dorsal aspect; Fig. 79. *Dioctria pleuralis*; Fig. 80. *Metadioctria rubida*; Fig. 81. *Bohartia isabella*; Fig. 82. *Eudioctria albius.*

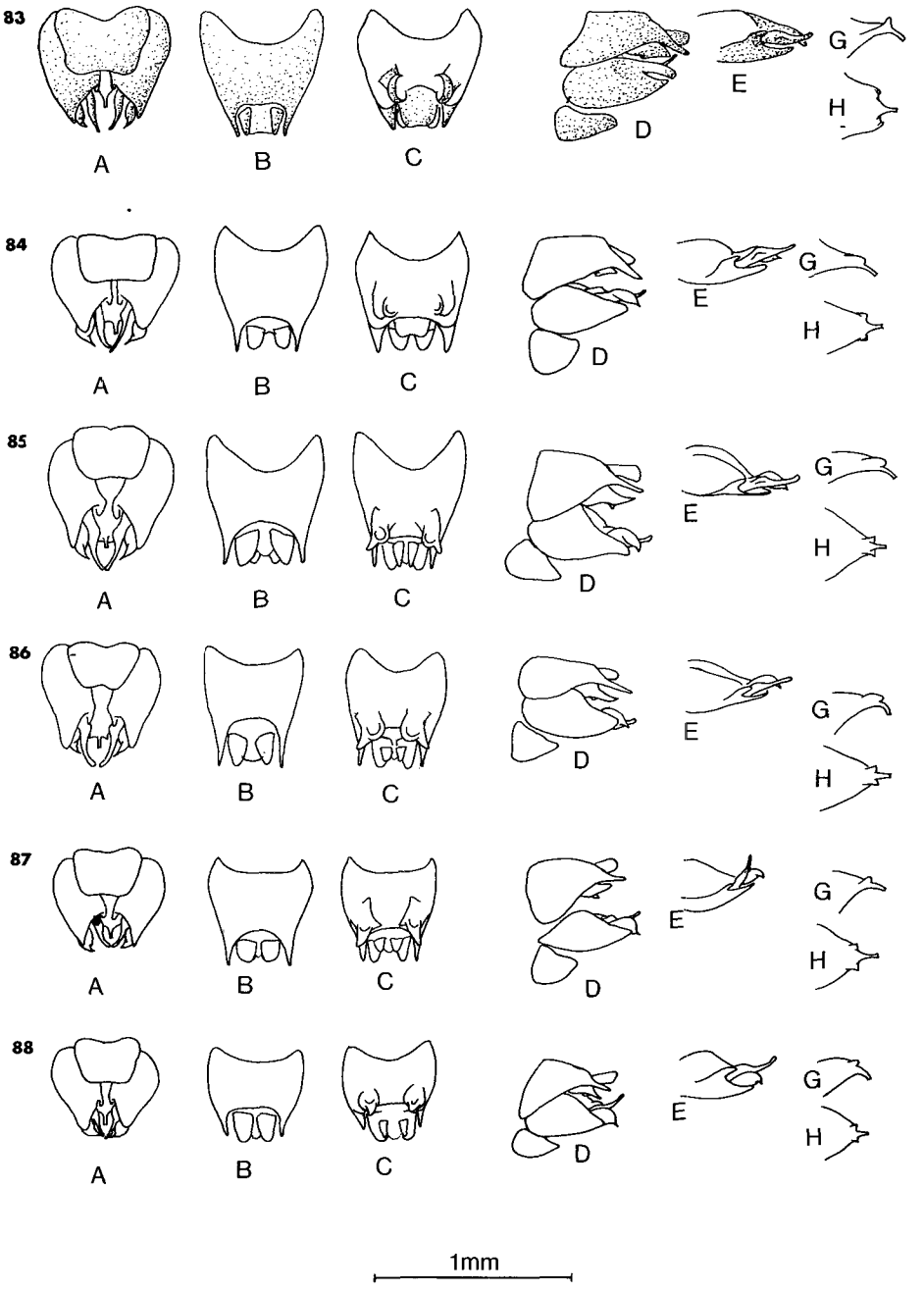

Fig. 83-88. Male genitalia, A. ventral aspect, epandrium omitted; B. epandrium, dorsal aspect, C. epandrium, ventral aspect; D. lateral aspect of genitalia; E. gonopode, mesal aspect; F. gonopode, dorsal aspect; G. aedeagus, lateral aspect; H. aedeagus, dorsal aspect; Fig. 83. *Dioctria albicornis*; Fig. 84. *D. wilcoxi*; Fig. 85. *D. pleuralis*; Fig. 86. *D. henshawi*; Fig. 87. *D. vera*; Fig. 88. *D. pusio.*

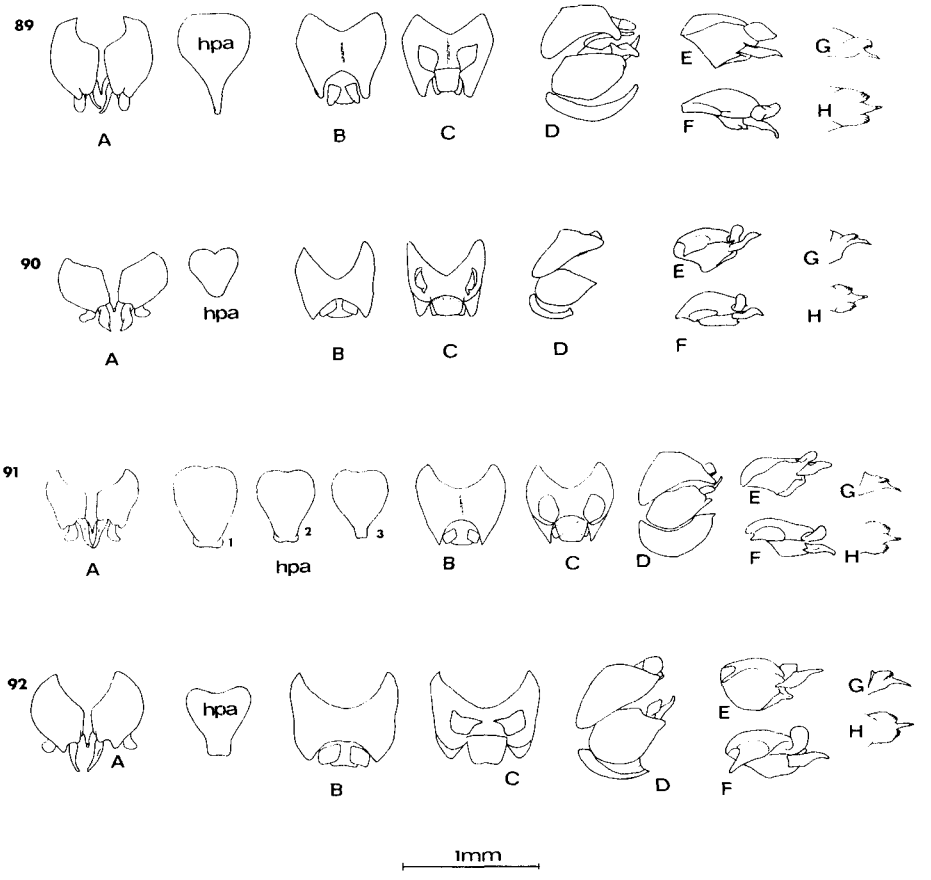

Fig. 89-92. Male genitalia; Fig. 89. *Metadioctria rubida;* Fig. 90. *Bohartia isabella*; Fig. 91. *B. martini*; Fig. 92. *B. bromleyi.*

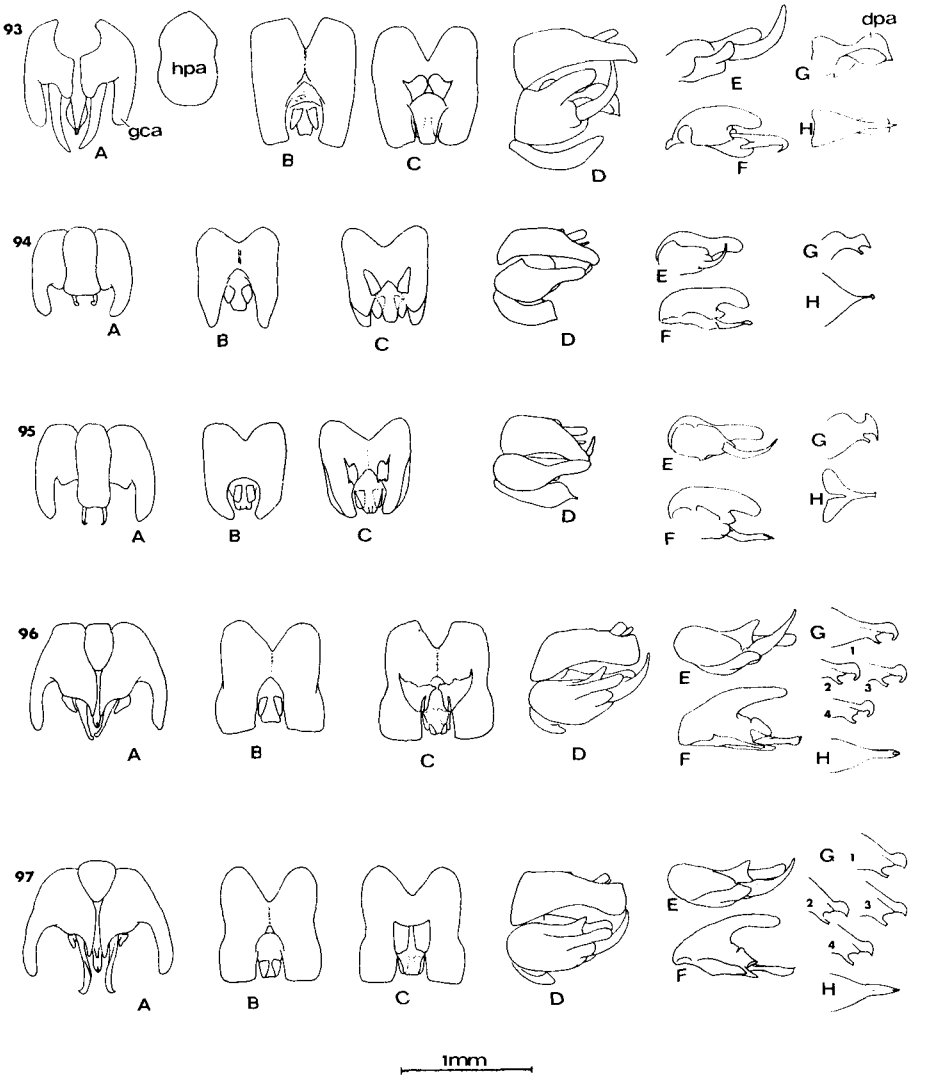

Fig. 93-97. Male genitalia; Fig. 93. *Eudioctria media*, gca – lateral arm of gonocoxite; dpa – dorsal process of aedeagus; Fig. 94. *E. monrovia*; Fig. 95. *E. dissimilis*; Fig. 96. *E. albius*; Fig. 97. *E. propinqua*.

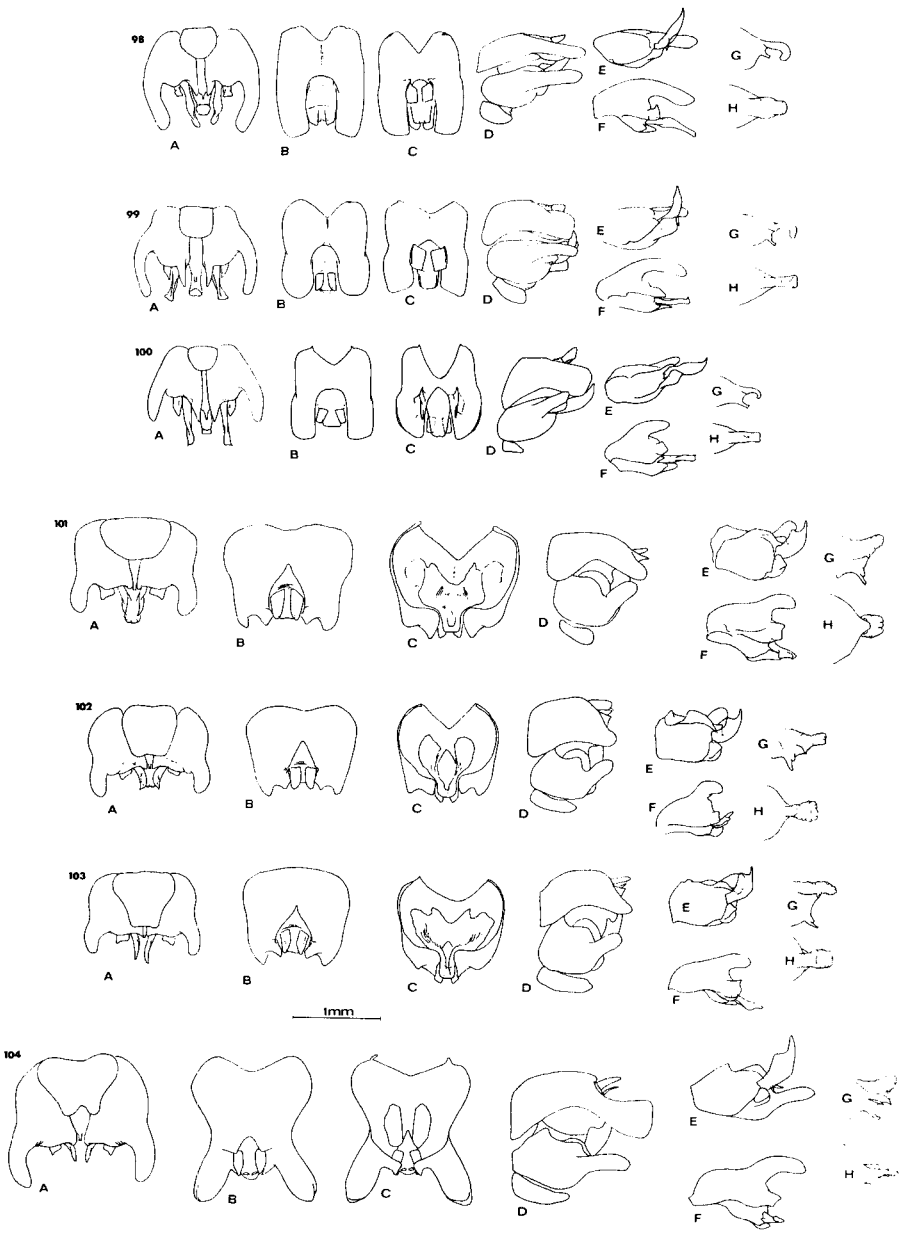

Fig. 98-104. Male genitalia; Fig. 98. *Eudioctria nitida;* Fig. 99. *E. denuda*; Fig. 100. *E. unica*; Fig. 101. *E. doanei*; Fig. 102. *E. doanei,* from Crescent City, California; Fig. 103. *E. doanei*, from Forest Hill, Placer Co., California; Fig. 104. *E. beameri.*

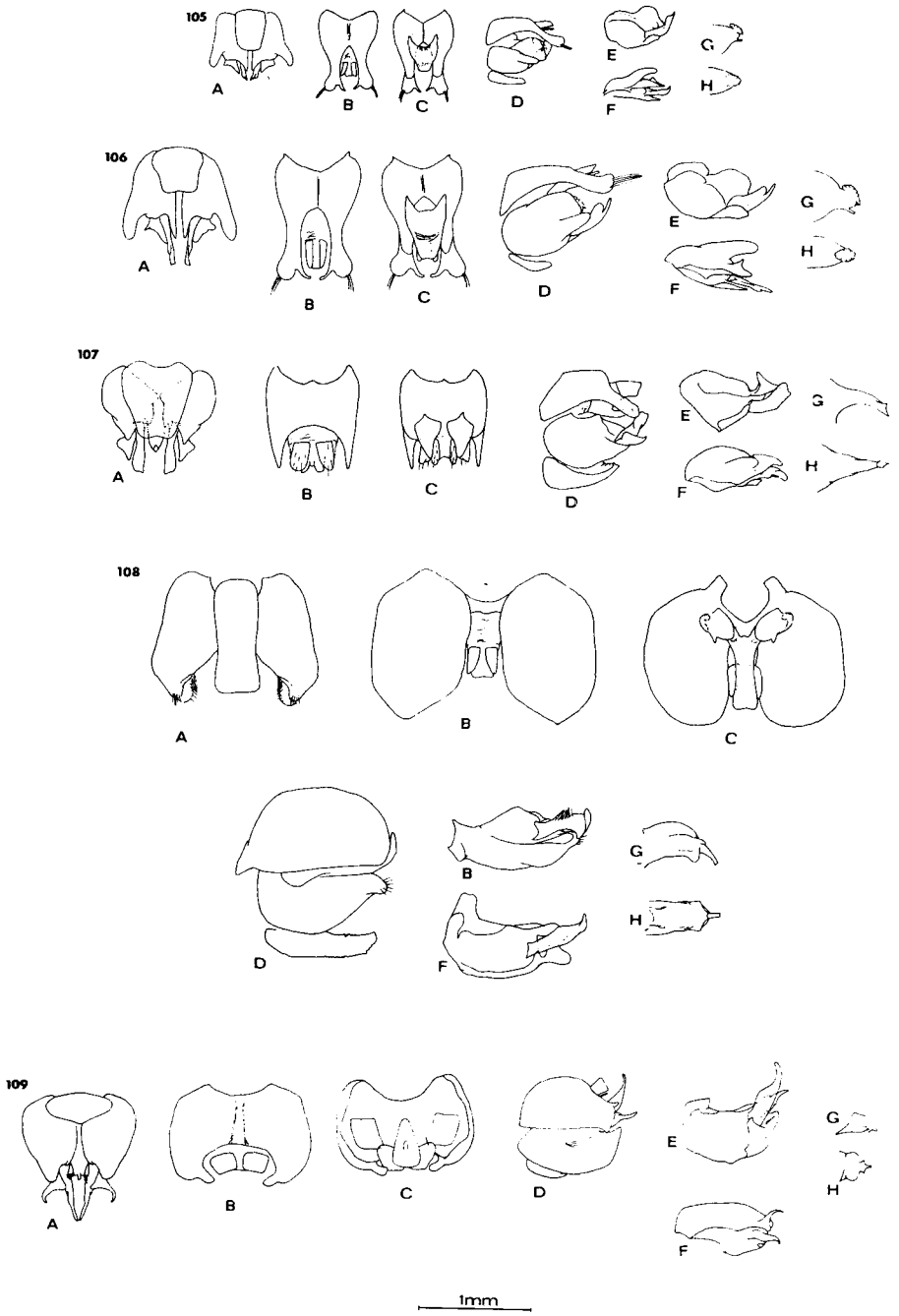

Fig. 105-109. Male genitalia; Fig. 105. *Eudioctria sackeni*; Fig. 106. *E. brevis;* Fig. 107. *Dicolonus simplex;* Fig. 108. *Echthodopa pubera*; Fig. 109. *Myelaphus lobicornis.*

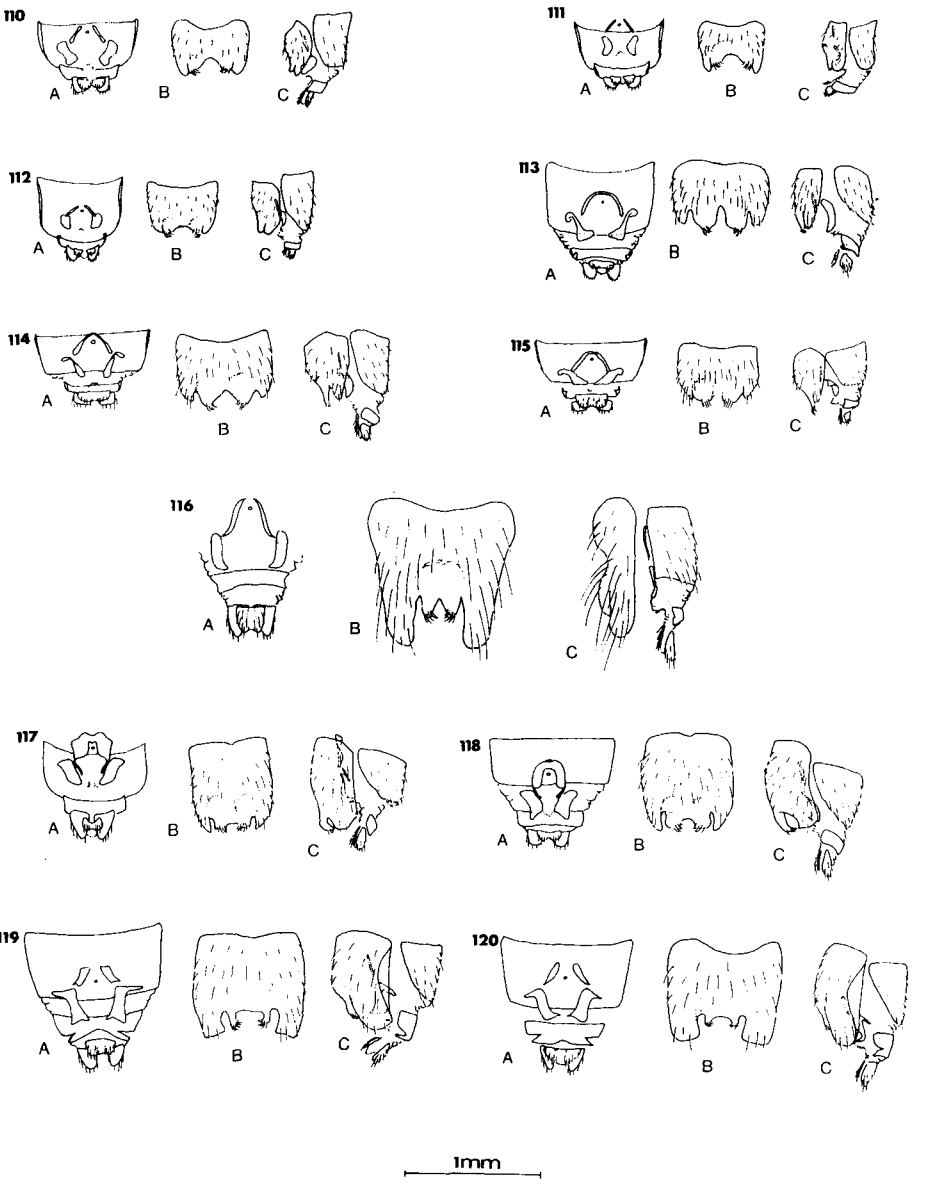

Fig. 110-120. Ovipositor, A. ventral aspect, hypogynium omitted; B. hypogynium, ventral aspect; C. lateral aspect of ovipositor; Fig. 110. *Dioctria wilcoxi*; Fig. 111. *D. vera*; Fig. 112. *D. pusio*; Fig. 113. *Metadioctria rubida*; Fig. 114. *Bohartia isabella:* Fig. 115. *B. martini*; Fig. 116. *Eudioctria media*; Fig. 117. *E. monrovia*; Fig. 118. *E. dissimilis*; Fig. 119. *E. albius*; Fig. 120. *E. propinqua.*

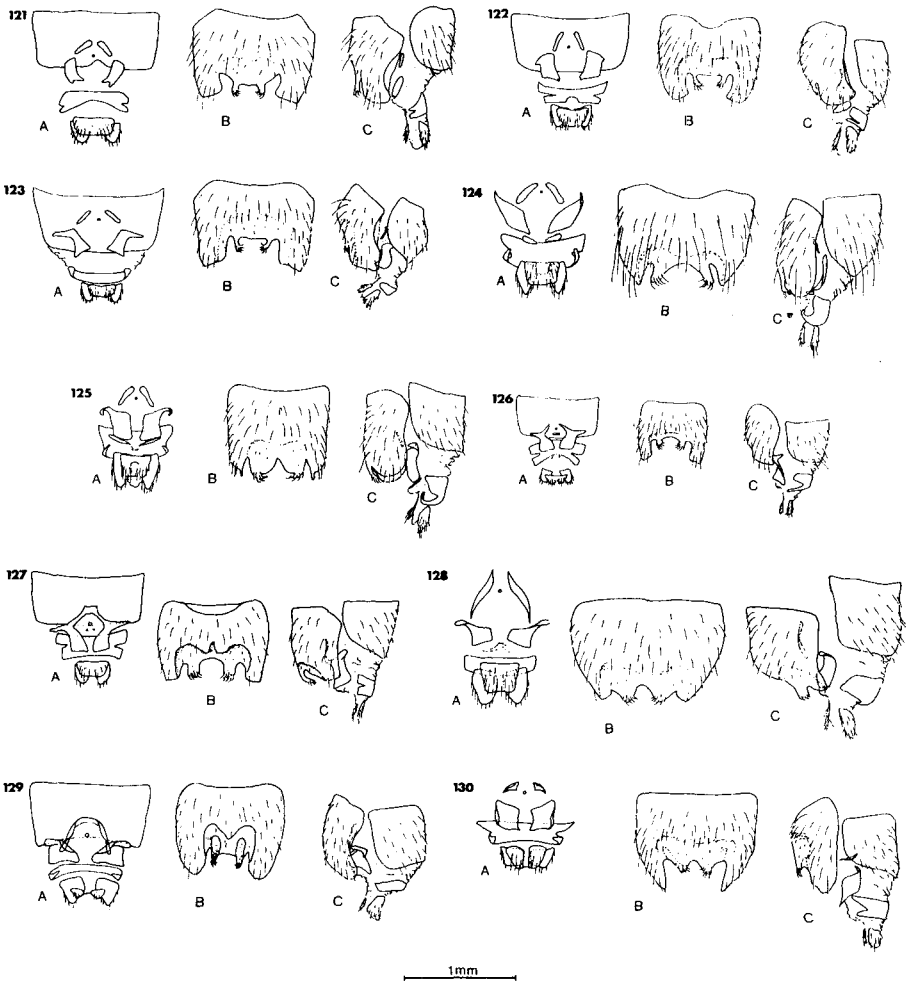

Fig. 121-130. Ovipositor; Fig. 121. *Eudioctria nitida;* Fig. 122. *E. denuda*; Fig. 123. *E. unica*; Fig. 124. *E. doanei*; Fig. 125. *E. beameri*; Fig. 126. *E. sackeni*; Fig. 127. *E. brevis*; Fig. 128. *Echthodopa pubera*; Fig. 129. *Dicolonus simplex*; Fig. 130. *Myelaphus lobicornis.*

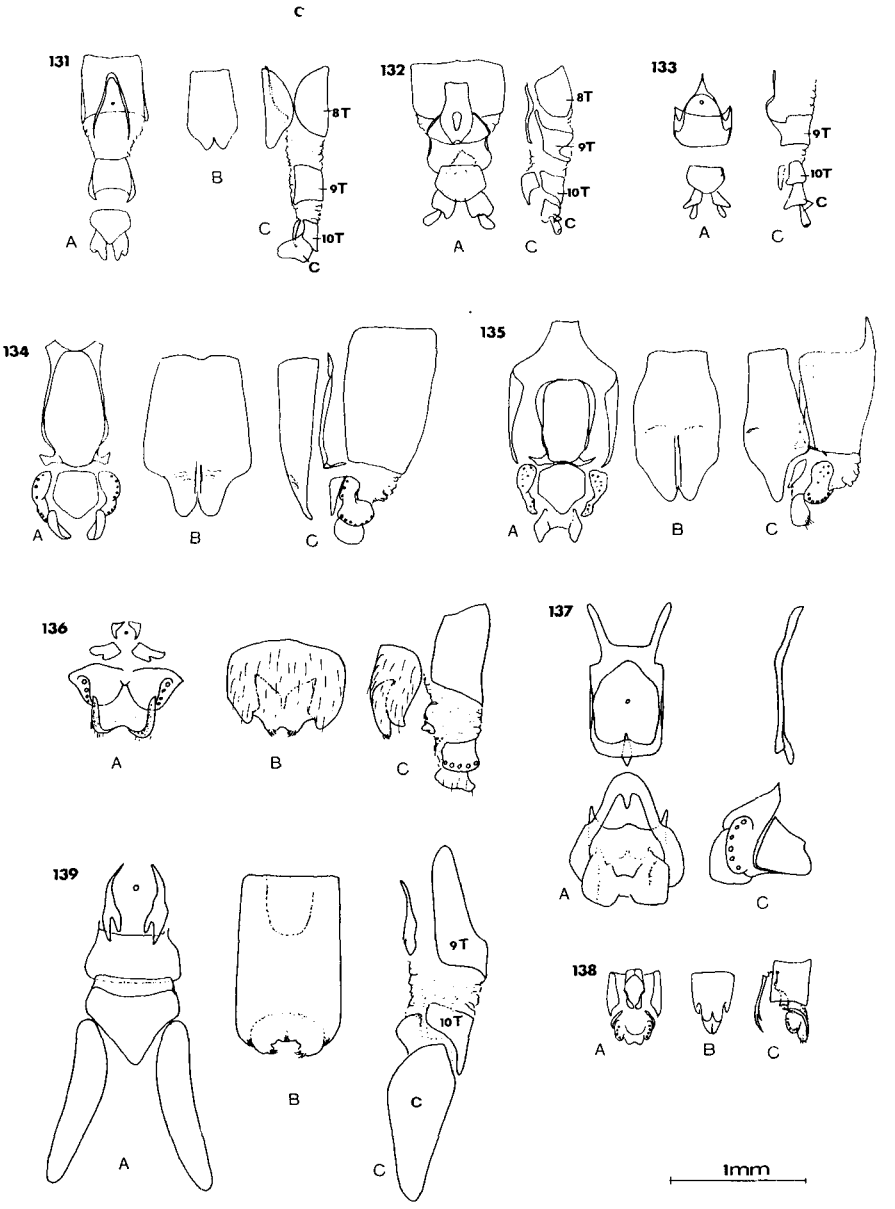

Fig. 131-139. Ovipositor; Fig. 131. *Rhagio orestes*; Fig. 132. *Symphoromyia* sp.; Fig. 133. *Chrysopilus* sp. Fig. 134. *Thereva flavicincta*; Fig. 135. *Metaphragma planiceps;* Fig. 136. *Stenopogon inquinatus*; Fig. 137. *Nemomydas pantherinus*; Fig. 138. *Aphoebantus obtectus*; Fig. 139. *Trichophthalma lundbecki.*