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PHYLOGENETIC INVESTIGATIONS IN ASILIDAE BASED ON
A SYSTEMATIC REVISION OF THE NEARCTIC DIOCTRIA
MEIGEN (S.L.) AND RELATED GENERA (DIPTERA).

by

SOENARTONO ADISOEMARTO, B. Sc., M. Sc.

A thesis submitted to the Faculty of Graduate
Studies in partial fulfillment of the require-
ments for the degree of Doctor of Philosophy.

Department of Biology
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May 1970

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ABSTRACT

1. Morphological studies have shown the existence of eight species of the Dioctriini and 35 species of the Echthodopini in North America. Each of these species is described. Keys for male and female are provided.
2. These morphological findings are used as a basis for grouping the species into higher taxa and for formulating an interpretation of their phylogeny.
3. The relationships of the Dioctriini with other asilids, especially with Leptogaster, are discussed.
4. The ranges of various species are plotted, and patterns of distribution analyzed in conjunction with their phylogeny.

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INTRODUCTION

The family Asilidae, with 6000 named species, is one of the largest groups of the suborder Brachycera, easily recognized by its behaviour as well as by the morphological characters of the adults. Adult asilids, or robber flies, are predators of other insects which they capture indiscriminately on the wing. The prey ranges from small soft-bodied flies and hard-bodied Hymenoptera to grasshoppers larger than the size of the predators but rarely consists of species other than insects. Spiders as the prey of the asilids have been reported by Bristowe (1924) and Bromley (1946). Cannibalism in the Asilidae has been reported in Diogmites angustipennis Loew (Alex 1936) and Dasypogon diadema Fab. (Poulton 1906), and tendency toward this habit has also been reported (Adisoemarto 1965). In addition to their role as predators of other insects, the robber flies serve as prey of other predatory insects, spiders, lizards, birds and, in one recorded instance, of the larva of a tiger beetle (Adisoemarto 1965).

The success in their predatory habit may be attributed to several morphological and physiological as well as behavioral factors. This success is in large measure attributable to their flying ability. These flies are agile creatures that can fly in a straight line. This behaviour, coupled with good vision, enables

the robber flies to catch their prey while on the wing.

One of the morphological structures responsible for their success in their predatory habit is the mouth-parts (Figs. 33, 34). The hypopharynx (e,f), two maxillary blades (d), and the labrum (b) are enclosed by the heavily chitinized, more or less tubular, labium (c), together forming a rigid proboscis. The labium consists of a basal prementum and a pair of apical labella. The labella are fused medially, free apically and laterally, folded so that the lateral edges meet to form the dorsum of the proboscis. The tip of each labellum is membranous and provided with sensory hairs. The sharp hypopharynx, which enables the robber flies to puncture the hard integument of the prey, is thrust through the opening at the tip of the proboscis. The hypopharynx consists of three pointed blades, a medioventral blade and two subapically serrate lateral blades. The maxillary blades which together with the hypopharynx are ensheathed by the labium are sharp and blade-like and lack apical teeth.

The main physiological factor of their success is the proteolytic enzyme or enzymes released into the prey by the salivary glands through the salivary ducts along a channel in the medioventral blade of the hypopharynx. These enzymes rapidly digest the protein of the prey in situ and in a relatively short time the robber fly is able to suck out the liquified contents

of the prey.

The habitats of the robber flies are variable, from sand dunes to river banks and lake beaches, from grasslands to coniferous forests. Open areas are necessary for the hunting activities of these flies. Some species of Eudioctria Wilcox and Martin in eastern North America occur in forests of red spruce mixed with poplar growing on well drained soil. The Nearctic species of Dioctria Meigen, found only in western North America, except seminole Bromley and baumhaueri Meigen (introduced from Europe), fly mainly along the edges of clearings in montane coniferous forests at moderate altitudes (5000-9000 feet). The vast geographic extent of this habitat, from British Columbia to southern Mexico, often isolated on mountain ranges, may be a contributing factor to speciation. Their Palaearctic counterparts are found in fields and at the edges of thickets of bushes and young trees that border mixed forests (Melin 1923).

Classification of the robber flies.

Among the original 16 species of Asilus described by Linnaeus (1758, 1767) ten have since been assigned to other genera of the Asilidae and one to another family.

The family Asilidae was first proposed by Leach in Samouelle (1819). Loew (1847) introduced subfamilial groupings, subdividing the Asilidae into three subfamilies, the Asilinae, the Dasypogoninae and the Laphriinae.

Schiner (1862) added Leptogastrinae by separating Leptogaster Meigen (1803) from the Dasypogoninae. No major changes were proposed until Hull (1962) erected the Megapodinae by raising Megapoda Macquart, and related genera which formerly were Dasypogoninae, to subfamily rank. These changes of rank were based on a relatively distinctive habitus without attempting to determine sister group affinities.

The Dasypogoninae have been subdivided into ten tribes (Hull 1962) of which five were considered closely related on account of the lack of spines on the ovipositor. These are the Chrysopogonini, the Damalini, the Dioctriini, the Laphystiini and the Phellini. Only three of these, the Damalini, the Dioctriini and the Laphystiini are represented in North America, and of these three, only the Dioctriini are considered in this thesis.

According to Hull (1962) the tribe Dioctriini is represented in the Nearctic region by Dicolonus Loew, Dioctria Meigen, Echthodopa Loew and Myelaphus Bigot, but not Bohartia Hull, which Hull (1962) assigned to Laphystiini. Martin and Wilcox (1965) transferred it to Dioctria. However, further examination of all the species of these four genera and analysis of their morphological characters has shown that the classification of the Dioctriini has to be revised. Based on one of the principles of phylogenetic systematics (Hennig 1966),

organisms should be grouped into a monophyletic group by a set of characters peculiar to the members of that group only (Dendr. 1A). Such characters are called derived or apomorphic and the sharing of these characters is termed synapomorphy. The unmodified condition from which an apomorphic character has been derived is termed plesiomorphic and the sharing of plesiomorphic characters is called symplesiomorphy. In contrast, a group is called paraphyletic when its members do not have an ancestor common solely to them (Dendr. 1B). Similarity based on convergence, when misinterpreted to indicate relationship, is called polyphyly (Dendr. 1C).

Another important principle in phylogentic systematics is that of ranking sister groups. A monophyletic group should be classified as a single taxon and given equal rank to that of its sister group; the two groups in turn together form a monophyletic taxon of the next highest rank. Therefore an interpretation of the family tree of a given higher taxon can be worked out from a study of the living species by applying the principle of relating sister species and sister species groups, by their apomorphic characters, into progressively larger monophyletic units.

Using the approach outlined above, an attempt is made in this paper to study, in detail, the morphology of and the interrelationships among, all of the species of Dicolonus, Dioctria (sensu Martin and Wilcox 1965), Echthodopa and Myelaphus occurring in North America.

Dendrogram i

MATERIALS AND METHODS

During the preparation of this paper a total of about 4000 male and female specimens of the genus Dioctria (sensu Martin and Wilcox 1965) and related genera, Dicolonus, Echthodopa and Myelaphus, were studied. These were obtained from ten institutions and two private collections as well as from collecting trips made by the author in Ontario, Quebec, Maine and Nova Scotia. Specimens relevant to this study were encountered in the vicinity of Halifax, N.S. and in Baxter State Park, Maine. These are now deposited in the Canadian National Collection. The sources of the other material examined are as follows: the American Museum of Natural History (AMNH), New York City, N.Y.; the Arizona State University (ASU), Tempe, Ariz.; the California Academy of Sciences (CAS), San Francisco, Calif.; the California Insect Survey (CIS), University of California, Berkeley, Calif.; the Canadian National Collection (CNC), Entomology Research Institute, Ottawa, Ont.; Cornell University (CU), Ithaca, N.Y.; the University of California, Davis (UCD), Calif.; the University of California, Riverside (UCR), Calif.; the University of Idaho (UI), Moscow, Ida.; the 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 later in the text under the discussion of each species to indicate deposition of the specimens.

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. The drawings were made with the aid of a camera lucida.

After assembling, dissecting and studying all the relevant material, the next step in this study was grouping the specimens into species. Identification to the species level was done with the aid of available keys to the species and by comparison with the original descriptions and, whenever possible, to type specimens.

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. This process of determining sister species and species groups was greatly facilitated by constructing a chart for each showing all the characters that could be found in every species (Charts 1 - 6).

The presentation of the phylogenetic analysis has been simplified by using dichotomous tables (Tables 1 - 9). 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 can be used to show the interpretation of the direction of evolutionary changes, i.e., from left to right. However, each lineage usually develops its own apomorphic characters and thus it is not clear in every case which line of the two has diverged more.

Dendrograms were constructed to indicate the sister group relationships of the species, species groups and higher taxa by repeatedly linking monophyletic units together with their sister groups.

Unfortunately, one cannot know how many species have become extinct or have not yet been discovered, and thus cannot say how many species have arisen from any given point in the dendrogram. Nevertheless fossil information, though helpful, is not necessary, for phylogenetic inference can be based on properties of the living forms. In developing a discussion of the phylogeny as graphically shown by a dendrogram, one can either progress from the hypothetical ancestor to the extant species or the opposite. Perhaps it is more realistic to discuss the phylogeny from the species level to the higher categories thus reflecting the process that was actually followed.

After the phylogeny, represented by the dendrograms, was established, the genera were then classified into higher taxa, i.e., tribes and subfamilies, in such a way that they could be interpolated among the other existing subfamilies (see Section on Systematic Relationships).

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. 3) the common ancestor of this group is given the number 6. Each of the two resulting lineages is numbered 6.1 and 6.2. The branch to the right, leading in this case to the subgenus Dioctria, is believed to have the greatest number of apomorphic characters. The left branch, 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., 6A, 6B, etc. and the two lineages arising from 6A are numbered 6A.1 and 6A.2, from 6B, 6B.1 and 6B.2. By means of this numbering, the characteristics of each lineage can be more readily located in the accompanying dichotomous table.

MORPHOLOGY AND TERMINOLOGY

Diagnostic characters of the groups studied are not confined to certain parts but are distributed over the body (basic and superficial).

Head (Figs. 1, 21-32). The excavated dorsal area of the head is the frontoververtex (Fig. 1A, fv); the boundary between the front and the vertex cannot be distinguished. It has also been called postantennal region of the frons, or post-frons (Crampton 1942). As a consequence of the excavation, the frontoververtex is slightly elevated on the sides. A pair of grooves, or furrows, of various depth extend from the antennal bases to converge posteriorly on the occiput, or the posterior part of the head. The area between the converging furrows on the occiput, here called vertical extension, may be posterior extension of the vertex, or the part of the occiput itself.

The antennal bases (Fig. 1B, ant.b), i.e., the area surrounding the points of attachment of the antennae on the head, vary in convexity, from completely flat (Figs. 21, 22, 27) to highly elevated as a tubercle-like structure (Figs. 23, 26, 28, 29). This area indicates the anterior boundary of the frontoververtex. Anteroventral to this boundary is the face (Fig. 1A, fc) (Walton 1909). It has also been called frontoclypeus (Peterson 1916) or

preantennal region of the frons, or prefrons (Crampton 1942). A convexity, the facial gibbosity, may be present on the lower part of the face. This area is provided with a patch of bristles, the mystax (Fig. 1A, mx), arranged as a row along the lower margin of the face (Figs. 21-25) or as a cluster on the gibbosity (Figs. 26-32). The hairs or bristles of the mystax vary in color, from black or yellow to white or mixed.

Antenna (Figs. 7-20). The antenna is three segmented, the third segment bearing a one- or two-jointed apical appendage or style which carries a basal spine-like structure. The antennal segments and the style vary in shape, size and pile pattern. The first segment is cylindrical, varying in length. The pile on this segment varies in texture, color, pattern and abundance. The second segment is somewhat compressed laterally, widening dorsoventrally toward the apex. This second segment is usually the shortest, except in Dioctria albicornis Wilcox and Martin (Fig. 7). Pile on this segment is present only on the apex, on the dorsal and ventral surfaces. The third segment is elongate, and variable in thickness; subcylindrical and slightly tapered apically, broadened in the middle, or compressed laterally. A short hair is sometimes present on the middorsal surface of this segment. The style varies in shape and size, short subtruncate (Figs. 12-14), spoon-

shaped (Figs. 15-18, 20), scaphiform (Fig. 11) or flattened laterally (Fig. 19).

Mouthparts (Figs. 33, 34). Description of the mouthparts of the Asilidae have been presented by Melin (1923) and Adisoemarto (1965). The labium is either somewhat pointed (Fig. 33) with the pile on the apical dorsal edge as well as sparsely on the tip of the prementum or blunt apically with pile on the apical ventral surface and abundantly on the prementum (Fig. 34). A notch, here believed to be homologous to a similar notch in the thickened upper rim of the labellum of the Brachycera, is usually present on the subapex of the labellum (Fig. 34), but absent in some species (Fig. 33). The labial pile is always pale yellowish or whitish. The remaining parts, i.e., hypopharynx and maxillary blades, are less useful as diagnostic characters.

Thorax (Figs. 2, 35-44). The thoracic sclerites vary in shape, size, color and in the color and pattern of pollinosity and pile. The lateral cervical sclerite (Fig. 2, lcs) is either bare or pilose. The prothorax is well developed; the anteprenotum (apn) traversed by a furrow, bare, pollinose, or pilose and the postpronotum or the humerus (ppn), elongate and slanting (Figs. 35, 36) or short and upright (Figs. 37-44), with the pile varying from short and sparse to long and abundant (Fig. 40).

The mesothoracic sclerites vary in shape and ornamentation. The mesopleuron (Fig. 2, msp) usually has a depression on the posterodorsal corner although it is absent in some species. In still others, a ridge is present near the posterior margin of the mesopleuron (Figs. 2, mpr; 37-39). The sternopleuron (stp) usually has a furrow running upward from a point between the front-and the mid-coxal attachments (Figs. 40-44). Superficial interspecific variation occurs in integumental coloration and in the patterns and coloration of pollinosity and pile.

The scutellum is either bare (Figs. 49, 50), with short fine hairs (Figs. 45, 46), with appressed pile (Fig. 52), with stiff long hairs on the edge (Fig. 47) or densely pilose on both the edge and the dorsal surface (Figs. 48, 51, 53). In some species the dorsal surface of the scutellum is partly or largely pollinose (Fig. 50).

Wing (Figs. 3, 54-59). The wing is either hyaline or slightly infuscated, paler along the veins or with white or orange coloration on the basal third. The size varies but, in general, there are two types: one is narrower, with the fourth branch of the radial vein (R_4) ending at or behind the wing tip and the alula absent (Figs. 54-56), the other is wider with R_4 ending before the wing tip usually with the alula

(Fig. 3, al) well developed (Figs. 57-59).

Legs (Figs. 4, 60-70). The hind femur (Fig. 4, fm) is slender and club-shaped (Figs. 60-62) and or stouter thickest subbasally or medially. The hind tibia (tb) is club-shaped (Figs. 60-62) or only gradually thickened apically (Figs. 63-70). In some species the hind legs are tuberculate (Figs. 66-68). The hind basitarsus is conspicuously enlarged and longer than the succeeding three segments in some species (Figs. 60-62). In these species, the hind empodium is comparatively shorter and completely covered with pollinosity (Figs. 71-73) while in others the empodium is slender, longer and pollinose only basally (Figs. 74-76). The pile on the legs varies from sparse and hair-like to abundant and bristle-like. In some species the femora have two sets of hairs, both erect and appressed (Fig. 64). The legs also vary in coloration.

Pregenital segments of the abdomen (Figs. 77-82). There are eight segments in the pregenital part of the abdomen of males but in females the eighth sternum is part of the ovipositor. The first segment is always short with pile on the posterior corner. The second segment is parallel-sided or narrower posteriorly with a distinct subbasal groove turning forward laterally. The third segment is parallel-side or slightly widened posteriorly. Subsequent segments gradually shorten and widen becoming widest at the apex of the fifth segment.

The eighth tergite of both sexes is concealed under the seventh. The eighth sternite of the male is absent. In some species, the female abdominal segments are relatively wider than those of the male.

Male genitalia (Figs. 5, 83-109). The ninth tergite or epandrium (Fig. 5, epa) may be trapezoidal with short pointed arms (Figs, 83-92, 107), deeply cleft posteriorly (Figs. 93-104), bifurcate (Figs. 105,106) or split into two halves (Fig. 109). On the ventral surface of the epandrium there is a pair of sclerites, the surstyli (ss), also called edita (Crampton 1942, van Emden and Hennig 1956), well developed in some species (Figs. 83-88) or flat (Figs. 89-109) and sometimes fused mesally (Figs. 105, 106). The ninth sternite or hypandrium (hpa) is of various shapes, trapezoidal (Figs. 83-88), heart-shaped (Figs. 90-92) or elongate (Figs. 94,95, 109). Articulated between the epandrium and the hypandrium are a pair of structures, the gonopods, each of which consists of two main elements, a basal gonocoxite (gc) and a distal gonostylus (gs). There are additional unarticulated processes on the gonocoxite, one of these is the lateral process (lp) (Karl 1959) originating on the inner surface of the gonocoxite lateral to the base of the gonostylus, another is the medioventral process (mvp) on the ventral inner edge of the gonocoxite mesal to the base of gonostylus. In some species there is a lateral outgrowth

on the outer surface of the gonocoxite, here designated as the lateral arm of the gonocoxite (Fig. 93, gca).

The lateral process (lp) varies from club-shaped (Figs. 83-91) or T-shaped (Figs. 107, 108) to flat or scoop-like (Figs. 96-97) or is absent in Eudioctria media Banks (Fig. 93). The medioventral process varies from small and finger-like (Fig. 83-88) to broad (Figs. 98-100) but is absent in Eudioctria monrovia Wilcox and Martin and E. dissimilis new species (Figs. 94, 95).

The aedeagus (Fig. 5, ae) is more or less funnel-shaped at the base, narrowing to a tube-like apex. A pair of dorsolateral short processes (adp) are present on the aedeagus of some species, they may be simple (Figs. 83-88) or lamellate (Figs. 89-92). In some other species the apex of the aedeagus is directed more or less ventrally while the dorsal surface has developed a process of various shapes, sclerotized (Figs. 93-100) or membranous (Figs. 101-106), here called the dorsal process of the aedeagus (Fig. 93, dpa).

Ovipositor (Figs. 110-139). The ovipositor is made up of the eighth, ninth and tenth abdominal segments. The eighth tergum or epigynium (Fig. 6, epg) (Crampton 1942) is reduced in size but not modified in shape. Ventral to this sclerite there is a structure called the hypogynium (hpg) with a pair of posterior valves or lobes called the hypogynial valves (hv).

interpreted as the anterior gonapophyses in the Tabanidae (Mackerras 1955). The hypogynium, including the valves, was considered as the eighth sternite only (Crampton 1942, van Emden and Hennig 1956). Cole and Wilcox (1938), in a revision of Lasiopogon Loew (Asilidae) concluded, probably incorrectly, that the valves were the ninth sternite.

Between the eighth tergite and the hypogynium there is a pouch-like space called the vagina (Reichardt 1929). On the roof of this pouch there is a pair of sclerites flanking the spermathecal opening (Fig. 5, gf), here believed to be homologous to the genital fork of the Nematocera and Rhagionidae (Fig. 133). These sclerites may be fused at their anterior ends to form a single inverted V- or U-shaped sclerite (Figs. 114-118, 127). Posterior to this structure there is another pair of sclerites that have previously been considered the ninth sternite (Reichardt 1929, Crampton 1942, van Emden and Hennig 1956). However, these sclerites are interpreted differently here.

In the Tabaniformia, such as Rhagio Fab. (Fig. 131) and Symphoromyia Frauenfeld (Rhagionidae) (Fig. 132), and non asilid groups of the Asiliformia, such as Aphoebantus Loew (Bombyliidae) (Fig. 138), and Nemomydas Curran (Mydidae) (Fig. 137), there is no such pair of sclerites behind the genital fork. In the Asilidae and the other families of the Asiliformia in which the pair of

sclerites behind the genital fork is present (Figs. 134-136), there is only one tergite behind the eighth tergite, separated from it by an extensive membranous area, while in the groups where these sclerites are absent there are two tergites, one behind the other, posterior to the eighth tergite and no such extensive membranous area. These tergites are here interpreted as the ninth and the tenth. In the rhagionids, there is a tendency for the ninth tergite to split into two lateral halves (Fig. 132). This tergite is always split in the tabanids (Mackerras 1955).

It is interpreted here that the pair of sclerites posterior to the genital fork are the lateral portions of the ninth tergite which have become split into two halves and have moved toward the ventral position. The sclerite posterior to the eighth tergite, in the Asilidae, is thus the tenth tergite.

TAXONOMIC TREATMENT

By applying the methods outlined in the previous section, the forty-three species of North American Dioctriini (sensu Hull 1962) described in this treatment can be grouped into seven genera as follows:

Bohartia, Dicolonus, Dioctria, Echthodopa, Eudioctria, Metadioctria, and Myelaphus.

Before reaching this conclusion, however, it is necessary to describe, for each species the morphological characters that form the evidence for subsequent phylogenetic discussions. For convenience, the species are grouped in this section in the genera to which they ultimately can be shown to belong.

Key to the North American genera of
Dioctriini (sensu Hull 1962)

1. Labium without subapical notch (Fig. 33 a); pile on prementum sparse, restricted to tip; ocellar tubercle without bristles on dorsal surface; hind femur club-shaped, abruptly enlarged apically, hind metatarsus conspicuously enlarged, at least as long as subsequent three tarsal segments (Figs. 60-62); R_4 ending behind wing tip (Figs. 54-56)..... Dioctria Meigen

- Labium with subapical notch (Fig. 34 a); pile on prementum abundant, at least occupying apical half of prementum; ocellar bristles arranged in curved rows; hind femur thickest subbasally, at middle, or only gradually enlarged apically; hind metatarsus shorter than three subsequent tarsal segments (Figs. 63-70); R₄ ending before wing tip (Figs. 57-59) 2
2. Antennal style two-segmented (Fig. 19); face glabrous, pollinose only on lower margin (Fig. 30 A); mystax a narrow band along lower margin of face Myelaphus Bigot
- Antennal style one-segmented (Figs. 12-18, 20); face largely or entirely pollinose; mystax a cluster of bristles (Figs. 26-29, 31, and 32) 3
3. Upper face below antennal bases with abundant long stiff hairs, extending downward along lateral margins (Figs. 28 and 29); gibbosity on lower part of face with triangular black marking Dicolonus Loew
- Upper face without hairs or with a single row along the lateral margin (Figs. 26 and 27); face entirely pollinose..... 4
4. Upper face destitute of hairs (figs. 31 and 32) 5
- Upper face with a row of hairs on each side ... 6

5. Mesopleuron largely covered with smooth recumbent hairs; pollinosity on upper hind corner of sternopleuron extending forward to reach the pollinosity of front corner; scutellum pilose (Fig. 51) Echthodopa Loew
- Mesopleuron pilose only marginally; pollinosity on sternopleuron as two separate patches; scutellum bare (Figs. 49 and 50
..... Eudioctria Wilcox and Martin
6. Frontoververtex and occiput pollinose; mesonotal pile short and appressed; pteropleuron pilose
..... Bohartia Hull
- Frontoververtex and occiput without pollinosity; mesonotal pile long, abundant and suberect; pteropleuron bare
..... Metadioctria Wilcox and Martin

Genus Bohartia Hull

Bohartia Hull 1958: 317. Type of genus: Bohartia bromleyi Hull (loc. cit.), by monotypy.

This genus was considered an aberrant member of the Laphystiini (Hull 1958, 1962) but Martin and Wilcox (1965) transferred it to Dioctria (s. l.) as an additional subgenus. However, in this treatment Bohartia is considered as a separate genus for reasons outlined in the following section.

Head largely pollinose, only ocellar tubercle and surrounding area bare; occiput and vertical extension pollinose; antennal bases flat; upper face below antennal bases with a row of hairs on each side; mystax a cluster of hairs; labium with a pair of notches near apex; pile on prementum abundant, occupying anterior half; postpronotum and mesonotum entirely pollinose; scutellum pollinose, bare on posterior edge; mesonotal pile appressed, short, distributed evenly; bristles present on supralar region and posterior callus; scutellum with two patches of suberect pile on marginal bristles; anterior half of pteropleuron pilose; wing hyaline; alula well developed; anterior branch of third vein (R_4) ending before wing tip; first two abdominal segments parallel sided, third segment slightly broader posteriorly; male genitalia quite uniform throughout the genus (Figs. 90-92), differing only in the shape of the hypandrium and surstylus; epandrium trapezoidal with a 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, forming a U-shaped structure (Figs. 114 and 115, A).

Key to the species of *Bohartia*

1. All femora entirely light reddish brown
..... nitor n. sp.
Femora partly or entirely black 2

2. Femora only partly black, at least hind pair
 largely or entirely light reddish brown ..
 3
 Femora entirely black, at most hind pair
 brownish on extreme bases or apices 4
3. At least apical half of each tibia black;
 tarsi black; dorsal apex of front femur
 black; ocellar bristles black mixed with
 a few white bristles munda n sp.
 All tibiae and hind tarsi reddish brown or
 brownish orange; entire apical fourth of
 front femur, entire apical third and ex-
 treme base of middle femur brownish or
 light reddish brown; ocellar bristles en-
 tirely black senecta n sp.
4. Occipital bristles entirely black; second
 antennal segment with at least two dis-
 tinct dark reddish or dark brown bris-
 tles on ventral surface bromleyi Hull
 Bristles on upper occiput partly or entirely
 white; pile on ventral surface of second
 antennal segment whitish 5
5. Bristles on head and thorax entirely white ..
 tenuis n sp.
 Bristles on head black and white; mesonotal
 bristles black 6

6. Abdomen and legs entirely black; pollinosity on postsutural anteprenotum only on dorsal fourth to third..... isabella n. sp.

Abdomen with reddish markings; tibiae reddish dorsally, at least on base martini n. sp.

Bohartia bromleyi Hull

Bohartia bromleyi Hull 1958: 318-320

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

Male: length 8-9 mm.; entirely black; bristles on frontovertex, on ocellar tubercle and along upper margin of occiput black; mystax whitish yellow mixed with a few black bristles; second antennal segment with reddish bristles, two distinct strong bristles present on ventral surface (Fig. 14); first antennal segment with whitish pile; anteprenotum pollinose only on dorsal one third; mesonotal bristles and bristles on scutellar edge black; genitalia with elongate trapezoidal hypandrium (Fig. 92 A) and broad surstylus (Fig. 92 C).

Female: same as male.

Distribution: this species has been recorded only from Charleston Mt. Park, Nevada, at 9000' (Map 19).

Specimens examined: 2♂♂, 2♀♀.

Bohartia isabella new species

A species with entirely black integument and with pile mostly pale yellowish or whitish. It can be distinguished from bromleyi by the color of the bristles on the occiput and antennae.

Male: Length $5\frac{1}{2}$ -6 mm; entirely black; yellowish tomentose and pollinose; frontal and ocellar bristles entirely black; occipital bristles mixed white and black; antennal pile entirely white; mystax mostly white, a few black bristles on upper part; the rest of pile on head white; thorax covered with yellowish pollinosity; postsutural anteprenotum pollinose only on dorsal one fourth to one third, sometimes extended downward on anterior margin; front margin of pollinosity on posterodorsal corner of sternopleuron straight; prothoracic bristles entirely white; mesonotum evenly covered with short recumbent white pile; mesonotal and scutellar bristles black, pile on scutellar disc white; legs entirely black, bristles and other pile entirely 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- $6\frac{1}{2}$ mm; same as male; pile on ovipositor white.

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

♀, same data. Paratypes: Calif.: 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 Co., 13.V. 1962 (A.S. Menke) - UCD; 1♀, Pointe 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, Calif., west and northwest of Death Valley (Map 20).

Bohartia martini new species.

This species is 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.

Male: length 6-7½ mm; head as in isabella, but at least two bristles on ventral, and most bristles on dorsal, surface of second antennal segment reddish, or black; postsutural antepnotum pollinose at least on dorsal half; pollinosity on posterodorsal corner of sternopleuron slightly extended forward on lower part;

mesonotal 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, eighth segment black; male genitalia black with black bristles; hypandrium varies, but always bulging ventrally near base (Fig. 91 D).

Female: length $6\frac{1}{2}$ -8mm; same as male; ovipositor (Fig. 115) reddish brown, bristles on hypogynium black.

Holotype: ♂, Hy. 395, June Lane Jct., Calif., 20.VI. 1954 (Dorothy Martin) - CHM; Allotype: ♀, same data. Paratypes: Calif.: 4♂♂, 3♀♀, same data; 23♂♂, 3♀♀, same data (C.H. Martin) - CHM; 3♂♂, 4 mi. SW Tom's Place, Mono Co., L3.VII. 1961 (G.I. Stange) - CIS; 1♂, 7 mi. E Bodie, Mono Co., 2.VII. 1964 (P. Rude) - CIS; 1♂, Leevining, 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♂, 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; Ariz.:
 1♂, 8 mi. S. Cay Creek, Maricopa Co., 22.VI. 1962
 (D.M. Zohner) - ASU; Nev.: 1♂, Kingsbury Gd, Douglas
 Co., 19.VI. 1964 (F.D. Parker) - UCD; 1♂, Grovada, 6.VI.
 (G.E. Bohart) - USU; Wash.: 1♂, Odessa, 27.VI. 1960
 (E.I. Schlinger) - UCR; Wyo.: 1♂, Mesa Conserv. Area,
 S. of Pinedale, 17-18.VII. 1968 (R.J. Lavigne) - CHM;
 Ida.: 16♂♂, 10♀♀, 6 mi. NE. Malta, Cassia Co., 22.VI.
 1965 (R.L. Westcott) - UI. (Map 21).

Bohartia munda new species

This species is similar to isabella but readily distinguished by the color pattern of the legs; it is also similar to martini with regard to the color of the pile on the head, but differs from it on the color pattern of the abdomen and of the legs.

Male: length $6\frac{1}{2}$ mm.; head as in *martini*; thoracic pollen pattern as in *isabella*; mesonotal pile short, sparse, appressed; coxae black, trochanters light reddish brown; front femur black with reddish brown markings on extreme base and ventral apical one fourth, apical one fourth of mid femur entirely light reddish brown, hind femur entirely light reddish brown; tibiae brownish basally, gradually darkened to black apically; tarsi and claws black; pile on legs pale yellow; abdomen black, with pale yellowish pile; male genitalia black with black pile. Genitalia not dissected or figured.

Female: length $6\frac{1}{2}$ -7 mm.; otherwise same as male; two paratype female specimens with hind femur black on extreme base and entirely black tibiae; pile on hypogynium black.

Holotype: ♂, in copula with allotype, Bear Valley, Calif., 27.VI.1948 (J. Wilcox) - J.W. 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 Co., Calif., 22.V.1957 (E.I. Schlinger) - UCD (Map 20).

Bohartia nitor new species

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

Female: length $7\frac{1}{2}$ mm; head black, yellowish white pollinose; pile entirely pale yellow; (third antennal segments missing); thorax black with pattern of pollinosity as in isabella; mesonotal 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, appressed on tergum, recumbent on sternum.

Holotype: ♀, Tracy, Calif., 2.VI. 1920 (E.P. VanDuzee) - JW. (Map 19).

Bohartia senecta new species

This is also a black species with reddish brown legs, somewhat like munda but differing from it in the black bristles on the head and in the entirely reddish brown tibiae.

Male: length 7 mm; mystax yellow mixed with a 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 fourth of front and apical third of mid femora entirely reddish brown; hind femur reddish brown with subbasal black band; tibiae entirely reddish brown; tarsi reddish brown, gradually darkening 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.

Holotype: ♂, 15 mi.N. Colonia Guerrero, Baja California, Mexico, 9.V.1949 (R.C. Dickson) - UCR (Map 29).

Bohartia tenuis new species

This species is somewhat like martini but easily distinguished by the color of the pile on the head and thorax.

Male: length 6 mm; pile on head and antennae entirely white, on ocellar tubercle slightly reddish; thoracic pollen pattern as in martini; thoracic pile appressed, entirely white; legs almost entirely black, joints between femora and tibiae brownish; claws black; pile on legs white; first abdominal segment black, second segment black basally, reddish apically, third to seventh segments reddish brown, eighth segment black; abdominal pile yellowish; genitalia black with brownish orange pile. Genitalia not dissected or figured.

Female: length 7 mm; otherwise same as male except for sexual differences.

Holotype: ♂, Tempe, Arizona, 17.V.1926 (A.A. Nichol) - JW. Allotype: ♀, Florence Jct., Ariz., 18.IV. 1935 (F.H. Parker) - USNM. (Map 21).

Genus Dicolonus Loew

Dicolonus Loew 1866: 32. Type of genus: Dicolonus simplex Loew (loc. cit.) , by monotypy.

Dicolonus Loew: Back 1909:246.

This genus is uniform; the species assigned here can be distinguished only by the variation of the length, texture and color of the pile.

Head densely pilose on ocellar tubercle, around antennal bases, and on upper face below antennal bases; face pollinose with a triangular bare marking on gibbosity; occiput pollinose; frontovertex and vertical extension bare; pollinosity absent in thorax; prothoracic sclerites, mesonotum, scutellum, anterior and posterodorsal corners of sternopleuron densely pilose; abdomen parallel sided, uniformly and densely pilose; male genitalia uniform (Fig.107); epandrium trapezoidal with a pair of posterior arms; lateral process of gonocoxite T-shaped; aedeagus without processes; genital fork of ovipositor divided into two sclerites (Fig. 129A).

Key to the species Dicolonus

1. Pile on edge and surface of scutellum short, hardly exceeding thickness of scutellum; mesonotal pile short, recumbent 2
- 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. Pile on centre of mesonotum reddish brown, surrounded by orange pile on margins; occipital bristles when viewed laterally orange mixed with black along margin sparsipilosum Back

- Pile on centre of mesonotum uniformly orange yellow
 occipital pile entirely orange yellow
 pulchrum n. sp.
3. End of each hair curled simplex Loew
 Hairs of pile straight 4
4. Frontal and ocellar bristles at most as long as
 first antennal segment; mesonotum without
 black bristles along dorsocentral region;
 pile on front and dorsal surfaces of hind
 femur appressed (Fig. 69)..... medium n. sp.
- Frontal and ocellar bristles one and a half
 times as long as first antennal segment;
 black bristles present along dorsocentral
 region, also present on supraalar region;
 pile on hind femur uniformly erect or semi-
 erect (Fig. 70)..... nigricentrum n. sp.

Dicolonus medium new species

The length of the pile, especially on the mesonotum, is intermediate between that of sparsipilosum and simplex.

Male: length $9\frac{1}{2}$ 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; mesonotal pile suberected, as long as or slightly longer than diameter

of first antennal segment, slightly brownish on central area; a row of orange bristles present on dorsocentral region, a few orange bristles also present on supraalar region; scutellar bristles longer than length of scutellum; remaining thoracic pile pattern as in sparsipilosum but longer and suberected; abdomen with long and erect pile, forming fringes along lateral margins when viewed from above.

Female: length 10 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. Paratype: 1♂, Charleston Mt. Park, Nevada, 9000', 21.VI.1940 (R.M. Bohart) - USNM. (Map 23).

Dicolonus nigracentrum new species

This species is very similar to medium but can be distinguished by the longer bristles on the head and the distinct black bristles on the mesonotum.

Male: length 10-12 mm; head as in medium, but frontal bristles one and a half times as long as first antennal segment; longest pile on upper face below antennal bases as long as frontal bristles; thorax as in medium, but pile on mesonotum reddish brown on central area; dorsocentral bristles black, distinctly longer than the remaining pile; scutellar pile orange, longer than length of scutellum; legs with suberect pile on hind femur (Fig. 70).

Female: length 12-14 mm; mesonotal pile orange yellow, dorsocentral and supraalar bristles black; otherwise same as male.

Holotype: ♂, Pullman, Wash., 4.VI.1907 - USNM. Allotype: ♀, same data - USNM. Paratypes: 1♂, 1♀, Rock Lake, Wash., - USNM; 1♀, Potlatch, Ida., 29.VI.1907 - USNM; 1♂, Twisp, Wash., 12.VII. 1960 (F.C. Harmston) - USNM - USNM; 1♀, Keremeos, B.C., 29.VI.1923 (C.B. Garrett) - CNC. (Map 23).

Dicolonus pulchrum new species

This species is similar to sparsipilosum but can be distinguished by the following characteristics:

Male: length $9\frac{1}{2}$ mm.; frontal bristle black, slightly shorter than first antennal segment; ocellar bristles black, one third as long as frontal bristles; occipital bristles orange; mesonotal pile orange, dense, covering mesonotum as a velvety orange layer, obscuring ground color of mesonotum; dorsocentral bristles absent; posterior edge of scutellum without long bristles, but with only short pile not exceeding thickness of scutellum.

Female: length $10\frac{1}{2}$ mm., otherwise same as male.

Holotype: ♂, Tallac, Lake Tahoe, Calif., 25.VII. 1915 (E.P. VanDuzee) - USNM. Allotype: ♀, same locality, 17.VII.1915 (E.P. VanDuzee) - USNM. Paratype: 1♀, Yosemite, 3880-4000', Calif., 19.VI.1921 - USNM. (Map 23).

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.

Male: length 13-14 mm.; pile in general long, dense and erect, each hair curled at tip; frontal bristles black, one and half 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; mesonotal 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 12-15 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 22).

Specimens examined: 10♂♂, 13♀♀.

Dicolonus sparsipilosum Back

Dicolonus sparsipilosum Back 1909: 247.

Male: length $8\frac{1}{2}$ - $9\frac{1}{2}$ 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 along margin of occiput; mesonotal pile orange on anterior margin of mesonotum, reddish brown on remainder of mesonotum, short and sparse, exposing ground color of mesonotum; dorsocentral bristles absent; scutellar pile orange, short and sparse, on posterior edge of scutellum not exceeding thickness of scutellum.

Female: length 9-10 mm.; otherwise same as male.

Distribution: Western slopes of the Rocky Mountains from Montana to Colorado (Map 23).

Specimens examined: 6♂♂, 4♀♀

Genus Dioctria Meigen

Dioctria Meigen 1803: 270. Type of genus: Asilus

oelandicus Linnaeus 1758, designated by Latreille 1810 (see also Coquillett 1910).

Labellum without subapical notch (Fig. 33), with short yellowish hairs mostly on dorsal edge; side of frontovertex with sparse weak bristles; ocellar tubercle without bristles on dorsal surface, short sparse bristles present on posterior surface; front femur cylindrical, gradually enlarged apically with yellowish pile appressed on dorsal and erect on ventral surface; mid femur slightly longer than front femur, more distinctly enlarged apically; hind femur one and one fourth times as long as mid femur, club-shaped (Figs. 60-62); front

and mid tibiae cylindrical, with short pile, sometimes bare dorsally; hind tibia club-shaped, distinctly enlarged at apex, with ventral hairs distinctly erect; hind metatarsus distinctly enlarged, as long as or longer than three subsequent segments; empodium short, almost completely covered with pollinosity (Figs. 71-73); wings hyaline except in oelandieus (figs. 54-56), with R_4 ending at or below wing tip; alula poorly developed; abdominal segments, except first segment, subequal, narrowest at base of third (Figs. 77-79).

The species assigned to this genus can be grouped into two subgenera, Dioctria and Nannodioctria Wilcox and Martin, based on the characteristics of the antennae, the antennal bases, and the thoracic sclerites.

Subgenus Nannodioctria Wilcox and Martin

Dioctria, subgenus Neodioctria Wilcox and Martin 1941:7.

Type of subgenus albicornis (loc. cit.), by original designation. Preoccupied by Ricardo 1918: 58.

Dioctria, subgenus Nannodioctria Wilcox and Martin 1942:

35, as new name for Neodioctria Wilcox and Martin nec Ricardo.

Antennal style short, one fifth as long as third antennal segment, subtruncate or spoon-shaped; third segment thickened in the 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 postpronotum, posterior half of pteropleuron, posterodorsal corner of sternopleuron and upper margin of hypopleuron; prothoracic sclerites comparatively elongate (Figs. 35 and 36); postpronotum broad, slanting.

Wilcox and Martin (1941) included only albicornis in this subgenus, but two more species, seminole Bromley and australis n. sp. can be shown to belong.

Key to the species of subgenus Nannodictoria

1. First two antennal segments and basal third of third segment pale yellow; pollinosity on mesal area of frontovertex reaching ocellar tubercle; prothoracic and mesothoracic sclerites largely yellowish brown; mesonotum yellowish brown on sides albicornis Wilcox and Martin
- All antennal segment black or dark colored; frontovertex entirely bare; prothoracic and mesothoracic sclerites largely or entirely black; mesonotum entirely black, bare or pollinose 2
2. Mesonotum bare; first antennal segment four times as long as its diameter (Fig. 8) seminole Bromley

Mesonotum pollinose; first antennal segment only
 twice as long as its diameter (Fig. 9)
 australis n. sp.

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 the color of the antennal segments, the shape of the antennal style, the shape of the face, and the pattern of pollinosity on the frontovertex.

Male: length $8\frac{1}{2}$ -9 mm; first antennal segment shorter than second; third segment thickest at middle (Fig. 7); first two and basal third 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. 21 A); pollinosity on mesothoracic pleuron present on anterior margins of sternopleuron and mesopleuron, continuous along upper margin of mesopleuron, on posterodorsal corner of sternopleuron, and on posterior half of hypopleuron (Fig. 35 A); mesonotum pollinose only on lateral margin; legs orange yellow, apical fourth of each tibia black; a black streak

present on dorsal surface of hind femur; tarsi brownish becoming black apically; abdomen black with orange yellow band on each intersegment; epandrium (Fig. 83 B) trapezoidal with a pair of posterior arms; surstylus thick with flanged ventral surface (Fig. 83 C); 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 a semicircular narrow band.

Female: length 9-11 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.

Male: length 11 mm.; antennal style spoon-shaped, one fifth 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 anteprenotum largely black, orange along suture; postprenotum brownish; bristles on lateral cervical sclerite and along presutural anteprenotum orange; mesothorax black with brownish patches on posterodorsal corner of sternopleuron, upper margin of hypopleuron and posterior half of pteropleuron; mesonotum black, largely orange yellow pollinose, with a 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 same as in other two species; 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; wing hyaline, one

and three fourths the length of abdomen; alula poorly developed; wing veins dark brown; abdomen entirely black; genitalia orange with triangular black marking on base of epandrium. Length: 11 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, the shape of the antennal style (Fig. 8), the shape of the antennal bases (Fig. 22), the occipital pollen pattern, the shape of the postpronotum (Fig. 36) and the absence of a mesopleural ridge, suggest a closer affinity to Nanno-dioctria than to Dioctria.

Female: length $10\frac{1}{2}$ mm.; antennal segments black, first segment elongate, one and two thirds 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 albicornis; abdomen black with orange intersegmented bands.

Only the female holotype, from Tallahassee, Florida, is known (Map 1).

Subgenus Dioctria Meigen

In North America members of this subgenus are more uniform than those of Nannodioctria. The Eurasian species of Dioctria can be grouped in this subgenus as well, but they are morphologically more variable, and differ from the North American species in the patterns of pollinosity on the mesonotum, in the abdominal color pattern and in the shape of the gonostylus which curves laterally instead of mesally.

Antennae uniform (Figs. 10, 11); antennal style long, one third to one half as long as third segment, more or less scaphiform; third segment subcylindrical; second segment shorter than first segment;

- corner of sternopleuron, and upper half of
hypopleuron wilcoxi n. sp.
- Postsutural antepnotum entirely devoid of
pollinosity; postpronotum black; meso-
thoracic pleura largely or entirely
black 3
3. Upper half of postpronotum distinctly pollinose..
..... pleuralis Banks
4. Mesopleural pollinosity always present in
front, forming single uninterrupted band
with sternopleural pollinosity; sides of
antennal bases pollinose vera Back
- Mesopleural pollinosity present or absent in
front, if present, sternopleural polli-
nosity not reaching upper margin, leaving
gap; sides of antennal bases bare 5
5. Mesopleural pollinosity present in front; face
always completely pollinose
..... henshawi Johnson
- Mesopleuron devoid of pollinosity; bare streak
present on upper face below antennal
bases pusio Osten Sacken

Dioctria (Dioctria) henshawi Johnson

Dioctria flavipes Banks 1917: 119, nec Meigen 1804.

Dioctria vertebrata Cole 1919: 230.

Dioctria (Dioctria) henshawi Johnson: Wilcox and Martin
1941: 5.

Male: length 7-8 mm.; antennal bases bare on sides (Fig. 24); postpronotum bare; pollinosity on anterior margin of mesothoracic pleuron interrupted by bare areas on lower margin of mesopleuron and upper margin of sternopleuron (Fig. 38); surstylus with lateral projection (Fig. 86 C).

Female: length 7-8½ mm.; otherwise same as 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.

This species is readily recognized by the presence of pollinosity on the upper part of postpronotum and by the dense appressed pile covering the lateral part of the mesonotum behind the post pronotum.

Male: length 8-10 mm.; antennal bases pollinose on sides (Fig. 23 B); upper half of postpronotum pollinose; pollinosity on anterior margin of mesothoracic pleuron continuous as single band (Fig. 37 A); pile on mesonotum extending from behind postpronotum to mesonotal suture (Fig. 37 B); surstylus on ventral

surface of epandrium with lateral projection (Fig. 85 C).

Female: length 9-11½ mm.; otherwise same as 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, Calif. 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, Calif., possess postpronotal pollinosity like that of the Santa Cruz Is. specimens, but with intersegmental orange bands present on the abdomen. This is interpreted as intraspecific variation only.

The coloration of the legs in pleuralis is similar to that in 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 Co., including Santa Cruz Is., to San Diego Co. It is also recorded 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 (s.s.) this one is the least pollinose, appearing as a bare shiny species.

Male: length 7-8 mm.; sides of antennal bases bare (Fig. 25 B); upper face below antennal bases sometimes with median bare streak; mesopleuron entirely bare (Fig. 39 A); legs largely orange, hind femur without dorsal black streak, hind tibia dark brown or black; tarsi dark brown becoming black apically; abdomen largely brownish orange, first segment and middle basal half of second segment black; surstylus with lateral projection (Fig. 88 C).

Female: length 8-9 mm.; otherwise same as male.

Distribution: Southern British Columbia to California and central Colorado, along the Cascade and Coast Ranges to the Sierra Nevada (Map 5).

Specimens examined: 57♂♂, 50♀♀.

Dioctria (Dioctria) vera Back

Dioctria vera Back 1909: 256.

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

This species is easily confused with pleuralis, but can be distinguished from it by the pattern of pollinosity and pilosity on the thoracic sclerites.

Male: length 8-9 mm.; antennal bases pollinose on sides; postpronotum bare; pollinosity on anterior margin of mesothoracic pleuron continuous as single band; pile on mesonotum restricted behind postpronotum and along dorsocentral region; surstylus with lateral projection (Fig. 87 C).

Female: length 8-10 mm.; otherwise same as male.

As in 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 black hind femur, and black hind tibia and tarsus.

Distribution: widely distributed in the Southwestern U.S., especially along the Coast Range, the Sierra Nevada and the Southern part of the Rocky Mountains 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

Male: Head typical of subgenus Dioctria, but pollinosity of frontovertex slightly more extensive, 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 brownish; pollinosity on sides of postsutural antepronotum yellowish orange; mesonotum behind postpronotum pollinose; sternopleural and mesopleural pollinosity continuous; anterior two pairs of legs and hind coxa orange yellow; hind femur black, hind tibia and tarsus black; basal half of claws brownish, the rest 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. 24 C).

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

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

Holotype: ♂, Strawberry, Tuolumne Co., Calif., 20.VII.1951 (W.C. Bentinck) - CIS. Allotype: ♀, same locality, 15.VIII.1960 (C.A. Toschi) - CIS. Paratypes: Calif.: 1♂, same locality, 14.VII.1951 (Don Burdick) - CIS; 1♂, Pinecrest, Tuolumne Co., 11.VIII.1948 (P.H. Arnaud, Jr) - JW; 1♀, Strawberry, Tuolumne Co., 29.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) - J.W.

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 is introduced from Europe (Johnson 1918) and has become common to eastern North America.

Male: 10-13 mm.; face whitish yellow pollinose, below antennal bases bare; mystax whitish, bristles on antennal segments dark brown; other pile on head yellowish; prothoracic sclerites without pollinosity; mesonotum largely pollinose with two bare streaks on dorso-central region and a bare spot on each submargin; pollinosity on mesothoracic pleuron present along anterior margin of sternopleuron, continued to anterior, dorsal and posterior margins of mesopleuron, on posterodorsal corner and posterior margin of sternopleuron, on hypopleuron and posterior half of pteropleuron; sides of coxae, dorsum of each femur, tip of each tibia and tarsi black, remaining legs orange yellow; hind femur varied from completely orange yellow to completely black; hind tibia varied from largely orange yellow with black tip to largely black with orange yellow base; wing hyaline; abdomen black; genitalia black, surstylus without

lateral projection; gonostylus curved laterally.

Female: same as male.

Distribution: Long Island, interior of New York State, north to Bells Corners, near Ottawa, west to Southwestern Michigan (Oakland Co.)

Specimens examined: approximately 300 of each sex.

Genus Echthodopa Loew

Echthodopa Loew 1866: 15. Type of genus: Echthodopa pubera Loew (loc. cit.), by monotypy.

Echthopoda Loew 1872 : 62, emendation of Echthodopa.

Three species have been assigned to this genus. The intersegment between the second and the third abdominal segments is constricted making this genus resemble the genus Eudioctria. However, many other characters distinguish Echthodopa from Eudioctria.

Antennal style spoon-shaped, third segment of antenna subcylindrical and elongate, first segment one and one third times as long as second with hairs on ventral surface not uniform in length (Fig. 20); frontovertex without pollinosity, bristles present along margins, a pair of patches of bristles present near antennal bases; ocellar bristles arranged as 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 anteprenotum; 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 two third of each tibia orange, remaining 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 ending before wing tip; abdomen black, narrowest at intersegment between second and third segment; second abdominal segment with transverse subbasal groove turning forward on sides; abdominal pile orange yellow, longest on sides of second segment; male genitalia almost uniform (Fig. 109), with hypandrium either parallel sided (Fig. 109 A) or constricted subapically; epandrium split into two lateral halves, without epandrial arms (Fig. 109 B, C); aedeagus with dorsal bulge (Fig. 109 G, H); ovipositor with genital fork split at anterior end (Fig. 128 A).

There has been confusion about the correct spelling of this genus. According to the International Codes of the Zoological Nomenclature (Articles 17 (6), 18, 32 (a) ii, and 32 (c) the valid name is Echthodopa.

This group is represented in both eastern and western North America.

Key to the species of Echthodopa

1. Mystax black carolinensis Bromley
 Mystax orange or yellow 2
2. Bristles on the male and female genitalia
 black; hypandrium constricted subapically ..
 formosa Loew
 Bristles on the male and female genitalia orange
 yellow; hypandrium parallel sided (Fig. 109)...
 pubera Loew

Echthodopa carolinensis Bromley

Echthodopa carolinensis Bromley 1951: 9.

Male: length 211 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 16).

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

Echthodopa formosa Loew

Echthodopa formosa Loew 1872: 62.

Echthodopa formosa Loew Back 1909: 248.

Male: length 18-19 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: from Massachusetts to North Carolina (Map 16).

Specimens examined: 6♂♂, 6♀♀.

Echthodopa pubera Loew

Echthodopa pubera Loew 1866: 15.

Male: length 17-19 mm.; pile uniformly pale yellowish; hypandrium parallel sided (Fig.109 A).

Female: same as male.

Distribution: rather widely distributed in two disjunct areas, from Washington and Idaho to Wisconsin Michigan, south to Texas (Map 17).

Specimens examined: 36♂♂, 56♀♀.

Genus Eudioctria Wilcox and Martin

Dioctria, subgenus Eudioctria Wilcox and Martin 1941: 8.

Type of subgenus: Dioctria albius Walker; by original designation.

This genus is quite uniform especially in such structural characters as the shape of the antennal segments, the facial gibbosity, the thoracic sclerites, the wings, and the abdominal segments. The color and pattern of the pollinosity vary even intraspecifically in some species.

Antennal style spoon-shaped, short, one fifth as long as third segment (Figs. 15-17); third segment thickened in the middle; second segment of equal length as first; first segment twice as long as its diameter; bristles on ocellar tubercle arranged as curved rows; antennal bases slightly elevated, with cluster of bristles on each side; face slightly concave in the middle, gibbosity distinct; bristles of mystax arranged in a cluster (Fig. 31); prementum densely pilose; labellum notched subapically (Fig. 34); occipital bristles long, dense, absent on vertical extension; frontovertex and occiput largely pollinose; lateral cervical sclerites densely pilose; antepronotum pilose along front margin and on sides; mesonotum entirely pollinose or pollinose with bare markings; mesonotal pile present on margins, on dorso-central and acrostichal regions; mesothoracic pleuron pollinose on upper and front margins of mesopleuron, front margin and upper hind corner of sternopleuron and posterior half of hypopleuron; 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 a tubercle (Figs. 66-68); anterior two pairs of tibiae subcylindrical with sparse long pile, distinctly erect on ventral surfaces; hind tibia tuberculate, with sparse erect pile and a row of bristles on

dorsal, front and ventral surface respectively; hind femur 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 basally; R_4 ends before wing tip (Fig. 59); alula distinct; abdominal segments invariably black, with base of third segment narrowest (Fig. 82); male genitalia variable (Figs. 93-106); epandrium long with posterior margin deeply cleft; posterior part of epandrium short and stumpy (Figs. 101-103), club-shaped (Figs. 104-106) or broad and flat (Figs. 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 membranous; ovipositor (Figs. 116-127) with hypogynium convex ventrally and narrow hypogynial valves; genital fork of separate sclerites (Figs. 119-125) or these fused to each other at their anterior ends (Figs. 117 and 118); portions of ninth tergite quadrangular; tenth tergite band-like, with or without lateral indentation.

Based on the structure of the male genitalia the members of this genus can be grouped into six species groups:

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

Key to the species of Eudioctria

1. Western species, found west of Great Plains 2
 Eastern species (incl. Texas)..... 10
2. At least basal half of scutellum tomentose 3
 Scutellum bare 4
3. Postpronotum (humeral) pollinose media Banks
 Postpronotum bare..... sackeni Williston
4. Postpronotum entirely bare 5
 Postpronotum pollinose 6
5. Mesonotum pollinose with sublateral bare spots ...
 monrovia Wilcox and Martin
 Mesonotum largely bare, only spots behind post-
 pronotum pollinose dissimilis n. sp.
6. Posterior edge of mesopleuron bare; bristles on
 antennae, on frontovertex, on ocellar tubercle
 and on upper occiput black 7

- Posterior edge of mesopleuron pollinose; bristles
on antennae, on ocellar tubercle and on upper
occiput orange 9
7. Gibbosity orange pollinose 8
Gibbosity with black marking unica n. sp.
8. Mesonotum entirely pollinose nitida Williston
Mesonotum with sublateral bare spots.....
..... denuda Wilcox and Martin
9. Tibiae entirely black... beameri Wilcox and Martin
Tibiae largely orange doanei Melander
10. Upper postpronotum largely bare; sides of ante-
pronotum bare or pollinose, if pollinose, dorso-
central region of mesonotum bare anteriorly ..
..... 11
Upper postpronotum pollinose; sides of ante-
pronotum distinctly pollinose 13
11. Sides of anteppronotum pollinose; mesonotum pol-
linose with bare markings along dorsocentral
region disjuncta n. sp.
Sides of anteppronotum bare; mesonotum either
completely bare or uniformly pollinose 12
12. Mesonotum and other mesothoracic sclerites al-
most completely bare tibialis Banks
Mesonotum pollinose brevis Banks
13. Mesonotum completely pollinose; posterior edge
of mesopleuron pollinose
..... propinqua bromley

Mesonotum with sublateral bare markings; lower
 half of posterior edge of mesopleuron not
 pollinose albius Walker

The albius group

Males of each species in this group show intra-specific variation in color. Each variety differs by a combination of two characters, the face and the wing base, each with two alternatives, making four possible combinations. All four combinations or forms have been found in propinqua but one form of albius, a white-faced, orange-winged male which should exist theoretically has yet to be discovered. The female of each species does not show such intraspecific variation in color.

The two species assigned to this group are similar to each other but can be distinguished by the shape of the aedeagus (Fig. 96 and 97) and the pattern of pollinosity on the mesonotum.

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.

In the male the face is either silvery white or golden yellow, and the wing is either uniformly infuscated (with slight whitish tinge on the base) or infuscated on apical half and orange on basal half. The specimens with orange wing base always have orange bases of tibia and orange pile. Those with uniformly infuscated wing have 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 possible four combinations have been described (Wilcox and Martin 1941) as follows:

form albius (white-faced, dark-winged), f. aurifacies (orange-faced, dark-winged), and f. xanthopennis (orange-faced, orange-winged).

The following are the characters shared by all forms:

Length 10-12 mm.; frontovertex and occiput (except vertical extension) yellowish pollinose; pile on mouthparts and lower part of occiput whitish yellow; side of antepronotum with orange pollinosity on posterior half; mesonotum orange yellow pollinose with a submarginal bare spot on each side; on mesothoracic pleuron yellowish pollinosity present on anterior corner and posterodorsal corner of sternopleuron, on dorsal half of mesopleuron, and on posterior half of hypopleuron; pile on mesothoracic pleuron, on legs and abdomen orange

yellow; genitalia with broad posterolateral part of epandrium (Fig. 96 B), aedeagus with dorsal process formed into a hook with blunt tip (Fig. 96 G).

There are four types of aedeagus (Fig. 96 G 1, 2, 3, 4) independent of the color variation. Each of these color forms has all four types of aedeagus. All other parts of the male genitalia are essentially uniform within the species.

Female: length 10-13 mm.; uniformly black; face orange yellow; mystax black, bristles on fronto-vertex, on antenna, on ocellar tubercle, on upper occiput and on mesonotum black; ovipositor with genital fork of two lateral sclerites (Fig. 119 A); hypogynial valves slender, wide apart (Fig. 119 B).

Distribution: all three forms are indiscriminately found along the Appalachians from Vermont to Georgia west to Wisconsin (Map 11).

Specimens examined: 77♂♂ f. albius, 11♂♂ f. aurifacies, 5♂♂ f. xanthopennis, and 137♀♀.

Eudioctria propinqua Bromley

Dioctria propinqua Bromley 1924: 125.

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

Color combinations homologous to those in albius occur in this species. All four possible combinations are known here. The aedeagus also varies into

four types (Fig. 97 G), independently from the color variation.

This species is similar to albius, but distinguished by the pattern of pollinosity on the thoracic sclerites: in this species the mesonotum is without submarginal bare spots and the hind margin of the mesopleuron is pollinose.

The occurrence of the white-faced forms in this species caused confusion of this species with albius.

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. 120 A), slightly different from that of albius.

Distribution: along the Appalachians from Maine, Nova Scotia, and Southeastern Quebec to Georgia, west to Southern Ontario (Georgian Bay, Lake Huron) (Map 10).

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 (Figs. 101-104, G, H), as well as a pair of sclerites situated behind the portions of the ninth tergite of the ovipositor (Figs. 124 and 125, A).

Eudioctria beameri Wilcox and Martin

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

Male: length 13-16 mm.; pile orange yellow, mystax black sometimes with a few orange bristles on lower part; antepronotum without pollinosity; dorsal half of postpronotum pollinose; mesonotum entirely pollinose; mesothoracic pleuron with pollinosity present on anterior and posterodorsal corner of sternopleuron, on dorsal half and posterior margin of mesopleuron and on posterior half of hypopleuron; legs entirely black; epandrium with postlateral projection (Fig. 104 B, C); aedeagus with dorsal membranous bulb-like structure (Fig. 104 G, H).

Female: length 13-17 mm.; ovipositor with a pair of sclerites posterior to genital fork (Fig. 105 A); genital fork of two separate sclerites; posterior edge of lateral valve of hypogynium brim-like (Fig. 125 B, C); otherwise same as male.

Distribution: in the vicinity of the Sequoia National Park and the Southern Sierra Nevada, California (Map 12).

Specimens examined: 6♂♂, 11♀♀.

Eudioctria doanei Melander

Dioctria doanei Melander 1923: 214.

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

This species has the color and patterns of pile and pollinosity similar to those of beameri, but distinguished by the following characteristics:

Male: length 14-16 mm.; face silvery white, but some specimens have orange face (Wilcox and Martin 1941); front and midtibiae orange yellow with black apices, hind femur orange yellow on basal two third, remaining one third black; postlateral projection on epandrium short, stumpy (Fig. 101 B, C).

Female: length 12-16 mm.; face orange yellow, but some specimens have silvery white face; ovipositor differs from that of beameri in shape of genital fork (Fig. 124 A); lateral valve of hypogynium (Fig. 124 B, C) without brim-like posterior edge.

Remarks: a male from Crescent City, two males and one female from Forest Hill, Placer Co., California, have a largely bare mesonotum with pollinosity only behind the postpronotum but the male genitalia (Figs. 102 and 103) and other characteristics do not show essential differences from doanei. These specimens are kept in Dr. C.H. Martin's collection.

Distribution: Southern Coast Range and Southern Sierra Nevada, California. The four aberrant specimens mentioned above are from the Northern Californian Coast Range and the Northern Sierra Nevada, California (Map 12).

Specimens examined : 26♂♂, 19♀♀.

The media group

Only one species can be placed in this group. It is characterized by the absence of the lateral process of the gonocoxite and the lateral flap-like structure on the aedaegus (Fig. 93).

Eudioctria media Ranks

Dioctria media Ranks 1917: 118.

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

Male: length 8-11 mm.; pollinosity orange yellow; bristles on head black; pile on lower occiput and mouth-parts yellowish; supraalar and dorsocentral bristles black; remaining bristles and pile orange yellow; dorsal surface of anteprenotum pollinose; dorsal half of post-prenotum pollinose; mesonotum entirely pollinose; on mesothoracic pleuron pollinosity present on anterior and posterodorsal corner of sternopleuron, on dorsal half of mesopleuron and on posterior half of hypopleuron; scutellum pollinose; legs black; male genitalia with latero-posterior part of epandrium broad (Fig. 93 B), aedeagus with a pair of lateral flap-like projection (Fig. 93 G, H); hypandrium longer than gonocoxite, slightly constricted at middle (Fig. 93 hpa).

Female: length 9-11 mm.; otherwise same as male.

Distribution: along the Cascade Range, the Coast Range and on the northern parts of the Sierra Nevada,

California. It has also been found in Idaho (Map 6).

Specimens examined: 33♂♂, 31♀♀.

The monrovia group

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

Eudoctria dissimilis new species

Male: length 7-9 mm.; pollinosity and pile orange yellow; mystax with a few brownish bristles; frontovertex pollinose only on sides, bare on area anterior to ocellar tubercle; dorsal half of occiput bare; prothoracic sclerites without pollinosity; mesonotal pollinosity only as triangular spot posterior to postpronotum; pollinosity on mesothoracic pleuron present on anterior and posterodorsal corner of sternopleuron, on dorsal third of mesopleuron and on posteroventral corner of hypopleuron; scutellum bare; legs black; male genitalia with lateroposterior part of epandrium broad (Fig. 95 B, C); hypandrium elongate, extended posteriorly into a brim-like structure (Fig. 95 D); aedeagus with dorsal process compressed laterally, projected dorsally (Fig. 95 G, H).

Female: length 8-9 mm.; ovipositor with genital fork as inverted U-shaped structure (Fig. 118 A); otherwise same as male.

Holotype: ♂, Idyllwild, San Jacinto Mts., Calif., 18.VI.1940 (C.D. Michener), length: 10 mm.; - CAS. Allotype: ♀, Harkey Creek, San Jacinto Mts., Calif., 4.VI.1940 (C.D. Michener) - CAS. - Paratypes: Calif.: 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; Ribbonwood, San Jacinto Mts., 18.V.1940 (all by C.D. Michener) -CAS.(Map 9).

Eudioctria monrovia Wilcox and Martin

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

Male: length 8-9 mm.; pollinosity and pile orange yellow; mystax with a few black bristles; frontovertex entirely pollinose; mesonotum largely pollinose with a pair of lateral bare spots; remaining pattern of pollinosity as in dissimilis; male genitalia almost similar to that of dissimilis but hypandrium without brim-like structure on posterior edge (Fig. 94 D) and dorsal process of aedeagus without dorsal projection (Fig. 94 G).

Female: length 8-10 mm.; ovipositor with genital fork widened at middle (Fig. 117 A); otherwise same as male.

Distribution: on the Coast Range in the southwestern corner of California, from Los Angeles to Laguna Mts. (Map 9).

Specimens examined: 2♂♂, 8♀♀.

The nitida group

The structure of the male genitalia and the ovipositor show the relationship of this group to 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.

Male genitalis with lateroposterior part of epandrium flat and somewhat parallel side, lateral arm of gonocoxite short and dorsal process of aedeagus broad, somewhat appressed dorsoventrally (Figs. 98-100).

The three species assigned to this group are distinguished from each other by their patterns of pollinosity.

Eudioctria denuda Wilcox and Martin

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

This species is certainly distinct from nitida (s.s.) as shown by the characteristics of the male genitalia (Fig. 99). The other morphological distinction is the difference in the pattern of pollinosity and the pattern of pile on the mesonotum.

Male: length 10½-12 mm.; pollinosity orange; frontovertex and occiput (except vertical extension) completely pollinose; prothoracic sclerites with

pollinosity on posterior corner of antep pronotum and dorsal surface of postpronotum; mesonotum largely pollinose with a pair of lateral bare spots; pollinosity on mesothoracic pleuron present on anterior and posterodorsal corner of sternopleuron, on dorsal half of mesopleuron, and on posterior half of hypopleuron; scutellum bare; mystax, bristles on frontovertex, on ocellar tubercle and on dorsal part of occiput black; remaining 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. 99 B, C); dorsal process of aedeagus narrowed at middle (Fig. 99 H).

Female: length $8\frac{1}{2}$ -12 mm.; front femur entirely black; otherwise same as male.

Distribution: the Western slopes of Sierra Nevada, California (Map 8).

Specimens examined: 9♂♂, 31♀♀.

Eudioctria nitida Williston

Dioctria nitida Williston 1884: 8.

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

Male: length 11-13 mm.; pollinosity orange yellow; prothoracic sclerites pollinose on dorsal surface and posterior corner of antep pronotum; mesonotum entirely

pollinose; mesonotal pile suberect; front femur entirely black; male genitalia with dorsal process of aedeagus broadened at middle (Fig. 98 H); otherwise same as denuda.

Female: length 11-15 mm.; posterior margin of mesopleuron pollinose; otherwise same as male.

Distribution: from Southern British Columbia to approximately north of San Francisco along the Coast Range and on the Western slopes of the Northern Sierra Nevada, California (Map 7).

Specimens examined: 24♂♂, 40♀♀.

Eudioctria unica new species

Male: length 14-15 mm.; pollinosity orange yellow; gibbosity on lower face without pollinosity; prothoracic sclerites pollinose only on dorsal surface of postpronotum; posterior margin of mesopleuron pollinose; male genitalia with dorsal process of aedeagus slender but broadened at middle (Fig. 100 H); latero-posterior part of epandrium short (Fig. 100 B); lateral arm of gonocoxite short (Fig. 100 A); otherwise same as nitida.

Female: length 12½-13 mm.; hind femur distinctly stouter than that of male (compare Figs. 67 and 68); otherwise same as male.

Holotype: ♂, 4 road mi. E. Shasta City, Siskiyou Co., Calif., 23.VII.1962, McBride camp ground (D.C. Rentz,

C.D. MacNeill) - CAS. Allotype: ♀, Meadow Valley, Plumas Co., Calif., 5-6000 ft., 20.VI.1924 (E.C. VanDyke) - CAS. Paratypes: 1♂, Segehen Creek, near Hobart Mills, Nevada Co., 17.VI.1964 (M.E. Irwin) - UCR; 1♀, Fallen Leaf Lake, Lake Tahoe, 24.VII.1915 (E.C. VanDyke) - CAS. (Map 7).

The sackeni group

Four species are assigned to this group: brevis, disjuncta, sackeni, and tibialis. Of these four species, sackeni is found in the Western parts of the Nearctic region.

The male genitalia and the ovipositor are good distinguishing characters for this group. 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 (Figs. 105 and 106). In the female the genital fork is fused to the portions of the ninth tergite (Figs. 126 and 127).

Eudioctria brevis Banks

Dioctria brevis Banks 1917: 117.

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

Male: length $8\frac{1}{2}$ -11 mm.; face reddish brown pollinose; frontovertex yellowish pollinose; occiput pollinose on lower two thirds, bare on remaining; mystax, bristles on antenna, on frontovertex, on ocellar

tubercle and on upper part of occiput black, pile on lower part of occiput and on mouthparts yellowish; bristles on prothoracic sclerites black, on lateral cervical sclerite yellowish; prothorax without pollinosity; mesonotum largely reddish brown pollinose, large bare spot present on each side; mesonotal bristles black; pollinosity on mesothoracic pleuron orange yellow, present on anterior and posterodorsal corner of sternopleuron, on dorsal third and posterior margin of mesopleuron and on posterior half of hypopleuron; scutellum bare; legs black; pile on legs and on abdomen yellowish; male genitalia with lateroposterior part of epandrium elongate, club-shaped (Fig. 106 B, C); membranous structure present on dorsal process of aedeagus (Fig. 106 G, H).

Color dimorphism present in the male. Some specimens have orange yellow face, orange yellow mesonotal pollinosity, uniformly orange yellow pile and orange yellow tibiae with black apices. All other characters are similar to those of brevis, therefore, they do not warrant a separate name.

Female: length 8-12 mm.; face and remaining pollinosity orange yellow; ovipositor with genital fork fused to portion of ninth tergite (Fig. 127 A); otherwise same as male.

Distribution: along the Appalachian Ridge from Vermont to Tennessee and North Carolina (Map 14).

Specimens examined: 184 reddish brown-faced ♂♂, 9 orange-faced ♂♂ and 20 ♀♀.

Eudioctria disjuncta new species

Female: length 9 mm.; pollinosity orange yellow; pile orange yellow; face orange yellow; frontovertex entirely pollinose; upper third of occiput bare; prothoracic sclerites pollinose on posterior corner of antepnotum; mesonotum largely pollinose with a pair of bare streaks present on anterior dorsocentral region and bare spot on each side; pollinosity on mesothoracic pleuron present on anterior and posterodorsal corner of sternopleuron, on dorsal half of mesopleuron, on posterior margin of mesopleuron and on posterior half of hypopleuron; basal two thirds of each tibia orange yellow.

Male unknown.

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 14).

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 in the Western parts of the Nearctic region. Polymorphism occurs in both sexes. Melander (1923) described rivalis as a form of sackeni on the base of the color of pollinosity on the frontovertex and on the mesonotum.

Male: length $6\frac{1}{2}$ - $8\frac{1}{2}$ mm.; frontovertex and occiput (except vertical extension) completely pollinose; prothoracic sclerites pollinose on dorsal surface; mesonotum entirely pollinose; pollinosity on mesothoracic pleuron present on anterior and posterodorsal corner of sternopleuron, on dorsal two thirds and posterior margin of mesopleuron and on posterior half of hypopleuron; basal third of scutellum pollinose (Fig. 50); latero-posterior part of epandrium club-shaped (Fig. 105 B); membranous structure present on dorsal process of aedeagus (Fig. 105 G, H).

Form sackeni: pollinosity uniformly orange; pile uniformly orange; front and mid femora each with black dorsal and orange yellow ventral surface; hind femur black with orange apex; each tibia orange with black apex; wing infuscated on apical half, orange on base.

Form rivalis: face silvery white; pollinosity on frontovertex, on occiput, on mesonotum and scutellum

reddish brown; mystax, bristles on antenna, on fronto-vertex, on ocellar tubercle, on occiput and on mesonotum black; legs largely black, base of each tibia orange yellow; wing uniformly infuscated.

Female: length 7-9 mm.; patterns of pollinosity as in male; genital fork of two separate sclerites, each fused to portion of ninth tergite (Fig. 126 A).

Form sackeni: legs largely black, base of each tibia orange yellow; wing uniformly infuscated; otherwise same as male.

Form rivalis: face orange yellow; otherwise same as male.

Remarks: male and female genitalia (Figs. 105 and 126) do not show differences between these two forms.

Distribution: from Southern British Columbia to Los Angeles, along the Cascade Range and the Northern Sierra Nevada, California, east to Northern Idaho and Northwestern Montana (Map 13).

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; change of name.

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.

Male: length $8\frac{1}{2}$ -10 mm.; face reddish brown, remaining pollinosity orange yellow; frontovertex completely pollinose; upper third of occiput bare; mystax whitish mixed with few reddish brown bristles; bristles on antenna, on frontovertex, on ocellar tubercle and on occiput brownish; remaining pile orange yellow; prothoracic sclerites without pollinosity; on mesonotum pollinosity present as small spot posterior to postpronotum; on mesothoracic pleuron pollinosity present on anterior and posterodorsal corner of sternopleuron and ventroposterior corner of hypopleuron; mesopleuron without pollinosity; legs black; wing infuscated.

Female: length $9\frac{1}{2}$ -11 mm.; face orange yellow, bristles orange yellow; otherwise same as male.

Some males have basal halves of the tibiae yellowish; these males were described as var. tibialis (Banks 1917). The variations of the wing and of the tibiae are not interdependent.

Distribution: along the Appalachians from New Jersey to North Carolina, west to Northwestern Arkansas (Mt. Magazine, 2800') (Map 15).

Specimens examined: 37♂♂, 46♀♀.

Genus Metadioctria Wilcox and Martin

Dioctria, subgenus Metadioctria Wilcox and Martin 1941:

19. Type of subgenus: Dioctria rubida

Coquillett; by original designation.

Wilcox and Martin (19141) included two species, rubida and resplendens, but the latter is now assigned to a different genus.

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 a cluster of bristle on each side (Fig. 26); ocellar bristles arranged in two curved rows, each with 4-5 bristles; face flat with distinct gibbosity on lower part; mystax as cluster of bristles; pile on prementum dense; labellum with subapical notch; pollinosity on head only along occipital margin; thorax black, pollinose on anterior corner of postpronotum, on upper margin of mesopleuron, on anterior and posterodorsal corner of sternopleuron and on posterior third of hypopleuron; pile long and dense on prothoracic sclerites, on mesonotum, on dorsal and posterior margins of mesopleuron and on anterior and posterodorsal corner of sternopleuron; scutellum with marginal bristles (Fig. 47); front and midfemora thickest subbasally, gradually tapering on both ends (Fig. 63); tibiae gradually thickening

apically; tarsi without conspicuous swollen hind metatarsus, empodium pollinose only basally (Fig. 74); wing two and one half times as long as wide, infuscated; alula well-developed; abdomen parallel sides, no constriction on intersegment between second and third segment (Fig. 80); epandrium trapezoidal, with blunt epandrial arms (Fig. 89 B); surstylus flat (Fig. 89 C); hypandrium somewhat rounded on base, extended apically as panhandle (Fig. 89 hpa); lateral process of gonocoxite thick and broadened on dorsal part, at apex pointed ventrally (Fig. 89 D, E, F); medioventral process not well developed; gonostylus flattened, tapering apically, curved mesally; aedeagus with lamellate lateral processes (Fig. 89 G, H); ovipositor (Fig. 113) with genital fork semicircular.

Metadioctria rubida Coquillet

Dioctria rubidus Coquillet 1893: 80

Dioctria (Metadioctria)rubida Coquillet: Wilcox and Martin 1941: 19.

Dioctria (Metadioctria)rubida nigripilosa Wilcox and Martin 1941: 19.

Dioctria (Metadioctria)rubida atrides Wilcox and Martin 1941: 20

The male of this species varies in the coloration of the abdomen, the legs and the pile. Wilcox and Martin (1941) described two new forms, nigripilosa and atrides

on the base of this color variation. The female is uniform.

The characteristics shared by both sexes and all forms are as follows: thorax black, coxae and trochanters black, first abdominal segment black, pile on lower occiput, mesothoracic pleura and legs orange yellow, wing infuscated.

Form atripes is distinguished from the other two forms by entirely black legs, black abdominal segments and black pile, except on lower occiput and mesothoracic pleura; nigripilosa is intermediate between the type form and atripes, having femora and basal halves of anterior tibiae orange and the last two abdominal segments orange.

Distribution: Southern California from Ventura to San Bernardino and Riverside Counties (Map 18).

Specimens examined: 7♂♂ atripes, 3♂♂ nigripilosa, 11♂♂ rubida, and 13♀♀.

Genus Myelaphus Bigot

Myelaphus Bigot 1882: xci. Type of genus: Myelaphus melas Bigot (loc. cit.); by monotypy.

Myielaphus Kertész 1909: 96; emendation.

Antennal style two-segmented (Fig. 19), somewhat compressed laterally, half as long as third segment; first antennal segment twice as long as second, four times longer than wide, with bristles mostly on dorsal surface; face with furrows running from pit below antennal bases (Fig. 30); mystax restricted to lower

margin of face; labellum with subapical notch; pile on prementum dense; thorax without pollinosity; prothorax evenly pilose; mesonotum evenly pilose; pile on mesothoracic pleuron present on anterior corner of sternopleuron, mesopleuron continued to posterodorsal corner of sternopleuron, on posterior half of hypopleuron; scutellum evenly pilose; femur thickest subbasally, gradually tapered apically, tibia gradually thickened apically; wing with R_4 ending before wing tip, alula well developed; abdomen parallel sided, subbasal transverse groove present on second segment, turning forward on sides; male genitalia uniform (Fig. 109); epandrial arms directed mesally (Fig. 109 B); lateral process of gonocoxite T-shaped with lateral arm curved (Fig. 109 A, F); aedeagus with lateral processes (Fig. 109 G, H); ovipositor with genital fork of two small sclerites (Fig. 130 A).

Two North American species are assigned to this genus, lobicornis and melas.

Key to the species of Myelaphus

Face with transverse depression between antennal bases and gibbosity, in profile appears as two protuberances; appressed pile on mesopleuron and sternopleuron not reaching midcoxa
 melas Bigot

Face smoothly curved, in profile appears rounded;
 appressed pile on mesopleuron and sternopleuron reaching midcoxa
 lobicornis Osten Sacken

Myelaphus lobicornis Osten Sacken

Ceraturgus lobicornis Osten Sacken 1877: 187.

Myelaphus lobicornis (Osten Sacken) Williston 1884:
 7-8.

This species is recognized by its smoothly curved face and dense mesonotal pile that obscures the ground color. The pile on the mesopleuron is continuous to that on the sternopleuron, reaching the midcoxa.

Distribution: Western Washington, Southern California and Northern Utah (Map 24).

Specimens examined: 6♂♂, 8♀♀.

Myelaphus melas Bigot

Myelaphus melas Bigot 1882: 112.

Myelaphus rufus Williston 1884: 7

This species is very similar to lobicornis, but can be distinguished by a transverse depression on the face between the antennal bases and the gibbosity, so that in profile the face has two protuberances; the pile is sparser than that in lobicornis exposing the ground color of the integument.

Distribution: Southern Sierra Nevada, California,
(Map 24).

Specimens examined: 7♂♂, 3♀♀.

SYSTEMATIC RELATIONSHIPS

The Asiliformia which consists of the Therevidae, Scenopinidae, Apioceridae, Mydidae and Asilidae (and probably also the Bombyliidae and Nemestrinidae) is considered as a monophyletic group (Hennig 1954). One of the synapomorphic characters of the Asiliformia is the presence of spines on the female tenth tergum (acanthophorites). However, these spines are absent in some groups of the Asilidae. In the Tabaniformia, i.e., the lower orthorrhaphous Brachycera, these spines are never present. Therefore some dipterists (e.g. Hull 1962) believe that the absence of spines on the female tenth tergum of these asilid groups is a primitive character. If this were the case, one have to accept the idea that the spines on the female tenth tergum of the Dasypogoninae (Asilidae), Therevidae, Scenopinidae, Mydidae and Apioceridae (and also some Bombyliidae) had developed independently in each of these groups. This idea is not accepted; the arrangement of spines on this structure is uniform in all species possessing it and it is assumed here that the acanthophorites in each family are homologous. In those asilid groups which have lost the spines on the acanthophorites the structure of the

ovipositor differs from that of the Tabaniformia. In these asilid groups, the ninth and tenth tergites are greatly modified showing homology to those of the other groups of the Asiliformia. Therefore, the absence of spines in some groups of the Asilidae on the one hand and in the Tabaniformia on the other is not symplesiomorphic but rather due to convergent development and one must consider the absence of spines on the female tenth tergum of some asilid groups as a derived condition. The validity of this assumption is basic to subsequent arguments.

The Asilidae is a monophyletic group, having synapomorphic characters of its own: the distinctly excavated frontovertex, a distinctly protruding ocellar tubercle, a well developed face, a mystax on the lower part of the face and a rigid labium with heavily sclerotized labella which together form a tubular proboscis. In addition to these characters, the ancestor of the Asilidae is here assumed to have had a well developed alula, open marginal and posterior cells in the wing, a simple aedeagus and a terete (cylindrical or nearly so) seventh abdominal segment in the female with spines on the tenth tergite because mydids and therevids also possess these characters. Based on these assumptions, it can be postulated that the asilid line has split into two branches. In one of these branches, the spines on the female tenth tergite have been retained and the seventh abdominal segment of the female has remained

terete. This branch has given rise to the Dasypogoninae (s.s.). The other branch has lost the spines on the tenth tergite, accompanied by the flattening of the seventh sternite, and has given rise to the Asilinae and Laphriinae. Leptogaster and several related genera, as well as five tribes that were formerly placed by Hull (1962) in the Dasypogoninae, lack spines on the tenth tergite and have a flattened seventh sternite of the female and thus apparently belong to this second line leading to Asilinae and Laphriinae.

The Asilinae and the Laphriinae are closer to each other than either is to any other group. Their interrelationship is indicated by the closed marginal, fourth posterior and anal cell of the wing, the trifold aedeagus, each arm of which has a seminal duct and the elongate and narrow female tenth tergite, giving an impression that the ovipositor is pointed posteriorly. These two groups have never before been considered as two sister groups. However, these characters are here interpreted as synapomorphic; thus the Asilinae and the Laphriinae are considered monophyletic.

Leptogaster and its related genera have been conventionally considered as a sister group of the Asilinae (Hardy 1927, Hull 1962). Martin (1968) even proposed to make Leptogaster and its related genera a

separate family, Leptogastridae. He presented a list of 46 characters of the adult and immature stages that purported to separate the Leptogastridae from the rest of the Asilidae. However, these were minimized into four by Oldroyd (1969). Both of these authors were concerned only with the magnitude of characters that differentiate Leptogaster and its related genera and did not attempt to determine its relationships by means of the principles of phylogenetic systematics (Hennig 1966). Establishing the position of this group is important because of its relationship to Dioctria.

Leptogaster and related genera are monophyletic. This monophyly is indicated by most of the characters listed by Martin (1968). The following characters: the bristleless ocellar tubercle, the absence of a notch on the labellum, the absence of a sternopleural suture, the club-shaped hind femur and hind tibia, the absence of alula, the shape of the abdomen and the well-developed surstyli on the epandrium are shared and peculiar to Leptogaster and related genera and Dioctria, and here believed to be synamorphic within these two groups. Therefore, these groups are here considered monophyletic (Dendr. 2, 4.2).

TABLE 1

0.1 Non-asilid Asiliformia	0.2 Asilidae
Face not developed, or very short.	*Face elongate into a well defined area between antennal bases and clypeus with gibbosity on lower part of face.
Mystax not developed or vaguely defined.	*Mystax well defined as clustered bristles.
Proboscis dilated apic- ally.	*Proboscis rigid, tubular
Frontovertex not ex- cavated.	*Frontovertex excavated in both sexes.
Cells of wings greatly modified.	Marginal, posterior, and anal cells open
1.1 Dasypogoninae	1.2 Asilinae, Laphriinae, Leptogastrinae
Spines on female tenth tergum present.	*Spines on female tenth tergum lost.
In female: posterior edges of seventh tergum and seventh	*In female: posterior edges of seventh sternum open

* asteric sign indicates apomorphic character.

sternum terete (seventh sternum convex ventrally as semicircular band).	elliptically (seventh sternum flat or only slightly convex).
---	--

2.1 Leptogastrinae

Marginal, posterior
 and anal cells of
 wing open.

Transverse groove on
 second tergum
 turned forward on
 sides toward cor-
 ners of segment.

In female; tenth ter-
 gum wider than long,
 as transverse band.

Aedeagus with single
 tube and a pair of
 lateral processes.

Abdomen slender, nar-
 rowest at inter-
 segment between se-
 cond and third seg-
 ments, than gradual-
 ly widened posterior-
 ly to intersegment
 between fifth and
 sixth segments.

2.2 Asilinae and Laphriinae

*Marginal, fourth posterior
 and anal cells of wing
 closed.

Groove on second tergum
 lost.

*In female: tenth tergum
 elongate.

*Aedeagus trifid, each arm
 with a separate seminal
 duct.

Abdomen gradually tapered
 posteriorly.

3.1 Laphriinae

*Antennal style lost.

*Abdomen parallel
sided or broadened
in the middle.

Female eighth tergum
semi-elliptical.

Epandrium not split.

Gonostylus subapical.

3.2 Asilinae

*Antennal style whip-like.

Abdomen gradually taper-
ing apically.

*Female eighth tergum form-
ed as semi-conical
structure.

*Epandrium split.

*Gonostylus subbasal or
basal.

TABLE 2

4.1 Echthodopini	4.2 Dioctriini and Leptogastrini
Ocellar triangle with bristles.	*Ocellar triangle without bristles.
Labellum with subapical notch	*Labellar notch lost.
Sternopleural suture present.	*Sternopleural suture lost.
Hind femur thickened subbasally or in the middle; hind tibia gradually thickened apically.	*Hind femur and hind tibia, each club-shaped.
Alula well developed	*Alula lost
Surstylus on epanthrium flat or lost.	*Surstylus well developed.

TABLE 3

5.1	Dioctriini	5.2	Leptogastrini
	Antennal style		*Antennal style whip-like.
	spoon-shaped.		
	Face broad, paral-		*Face narrow, broader on
	lel sided.		lower part.
	Mystax clustered.		*Mystax linear.
	Mesothoracic pleura		Mesothoracic pleura uni-
	with orange mark-		form in coloration.
	ings on postprono-		
	tum, posterior		
	half of mesopleuron,		
	posterior half of		
	pteropleuron, post-		
	erodorsal corner		
	of sternopleuron,		
	and upper half of		
	hypopleuron.		
	Prothoracic sclerites		Prothoracic sclerites
	bare.		pollinose.
	Hind femora orange with		Hind femora uniform in
	dorsal black streak.		coloration.
	*Hind metatarsi enlarged.		Hind metatarsi not en-
			largened.

Pollinosity on mesothoracic pleura arranged as pattern; on anterior edges of meso- and sternopleuron, upper margin of mesopleuron, upper hind corner of sternopleuron, and posterior half of hypopleuron.

Mesonotal pollinosity on margins.

Pulvilli present

Posterior edge of epandrium slightly concave.

Surstylus thick, attached on posterior corner of ventral surface of epandrium.

Lateral processes of aedeagus present.

Mesothoracic pleura evenly pollinose.

Mesonotum evenly pollinose.

*Pulvilli lost.

*Epandrium deeply cleft posteriorly.

*Surstylus elongate, attached on tip of posterior corner of epandrium.

*Aedeagus without lateral processes.

6.1 Nannodioctria

*Prothoracic sclerites,
esp. postpronotum,
elongate.

Mesopleuron without
ridge.

Occiput pollinose on
lower half.

Antennal bases flat.

*Mystax linear.

Frontovertex pollinose.

First antennal segment
subequal in length to
second segment.

Lateral process of gono-
coxite not bulbous
apically.

6.2 Dioctria (s. s.)

Prothoracic sclerites
short.

*Mesopleuron with ridge
near posterior mar-
gin.

*Occipital pollinose in
a pair of patches
above foramen.

*Antennal bases protrud-
ed.

Mystax clustered.

*Frontovertex bare.

*First antennal segment
elongate, longer than
second segment.

*Lateral process of gono-
coxite bulbous sub-
apically.

Six other genera, Bohartia, Dicolonus, Echthodopa, Eudictoria, Metadictoria, and Myelaphus, share some characters with Dictoria and Leptogaster (Table 1, 2.1). These are the presence of an anteriorly concave transverse subbasal groove on the second abdominal segment, and the band-like female tenth tergite. Another set of characters distinguish these six above mentioned genera (Bohartia, Dicolonus, Echthodopa, Eudictoria, Metadictoria, Myelaphus) from the Dictoria-Leptogaster lineages (see Dendr. 2, 4.1). It is interpreted here that these six genera are monophyletic and a sister group of the Dictoria-Leptogaster lineage.

Based on this analysis the following classification is proposed in this paper:

SUBFAMILY	TRIBE	GENUS	SUBGENUS
Leptogastrinae	Leptogastrini	not treated herein	
	Dictorini	<u>Dictoria</u>	<u>Dictoria</u> <u>Nannodictoria</u>
	Echthodopini	<u>Bohartia</u> <u>Dicolonus</u> <u>Echthodopa</u> <u>Eudictoria</u> <u>Metadictoria</u> <u>Myelaphus</u>	

Systematic Relationships within genus Dioctria Meigen

The uniformity of genus Dioctria is shown by the characters of the mouthparts (Fig. 33), the legs (Figs. 60-62), the wings (Figs. 54-56), the abdomen (Figs. 77-79), the male genitalia (Figs. 83-88), and the ovipositor (Figs. 110-112). However, based on the details of these characters and on some other characters, the species assigned to this genus can be grouped into two major groups: subgenus Nannodioctria, with flat antennal bases (Figs. 16 and 17, B), the occiput pollinose on lower half, elongated prothoracic sclerites (Figs. 35 and 36), the mesopleuron without posterior ridge (Figs. 35 and 36, A) and the lateral process of gonocoxite not enlarged subapically, and subgenus Dioctria, with protruded antennal bases (Figs. 23-25, B), the occiput pollinose in a pair of patches above foramen, shorter prothoracic sclerites (Figs. 37-39), the mesopleuron with posterior ridge (Figs. 37-39, A), and the lateral process of gonocoxite enlarged subapically (Figs. 84-88).

Subgenus Nannodioctria.

There are three species assigned to this group: albicornis, australis, and seminole. Nannodioctria albicornis and seminole show closer relationship to each other than either to australis, having a comparatively more elongate anteprenotum, a common color pattern

of the hind legs and of the abdomen and the mesonotal pollinosity only marginal. Nannodioctria australis has deviated from the other two by the blackening of the abdomen and the hind legs, and the development of pollinosity on the mesonotum arranged as a distinct pattern.

Subgenus Dioctria.

This group is represented in the Palaearctic as well as in the Nearctic region. The North American species (and an undescribed species from Korea) are shown here to be a monophyletic group (Dendr. 3, 6C.1), sharing a linear mystax and mesally curved gonostylus. The Eurasian species (except one species from Korea) (6C.2), shared a clustered mystax and laterally curved gonostylus. These two species groups are considered here as two sister groups because they share the following characters: protruded antennal bases; occipital pollinosity as a pair of patches above the foramen flanking the vertical extension, a mesopleural ridge on each mesopleuron, a bulbous lateral process of gonocoxite and short prothoracic sclerites.

For the purpose of this work, the discussion of the phylogeny of this subgenus is confined to the North American species.

The Korean species and pusio show close relationship by sharing bare antennal bases, bare face below the antennal bases, bare mesopleuron and shortened abdominal segments. This lineage (6G.2) in turn show close relationship with henshawi because they share certain characteristics not found in any other species: the sides of the antennal bases are bare, the pollinosity on the anterior edges of the sternopleuron and mesopleuron is not continuous but interrupted on the border between these two sclerites and the antennal style is scaphiform. Therefore, it is concluded here that henshawi and pusio (and a Korean species) come from a common ancestor (6F.2), which in turn shares an ancestor with vera (6F). This is based on the presence of characteristics confined only to these four species: the shorter abdominal segments, the reduced number and size of the intersegmental orange bands on the abdomen and the absence of pollinosity on the pronotum and mesonotum.

The common ancestry of these four species and pleuralis (6D.2) is shown by the entirely black thorax, the narrow marginal pollinosity on the mesonotum, the bare anteppronotum and the presence of a lateral projection on the surstylus of the epandrium. D. pleuralis (6E.1) has also acquired two apomorphic characters of its own; pollinosity on the postpronotum and the presence of pile on the mesonotum above the wing bases.

Dendrogram 3

Characters	albicornis	seminole	australis	wilcoxi	pleuralis	vera	henshawi	pusio
First two antennal segments orange								
Anterior 1/2 of frontovertex pollinose								
Abdominal segments uniformly colored								
Hind legs uniformly colored								
Mesopleuron without pollinosity								
Upper face below antennal bases with bare markings								
Mesonotal pile reaching mesonotal suture								
Postpronotum pollinose								
Sides of antepronotum pollinose								
Pollinosity on mesonotum behind postpronotum present								
Antennal style scaphiform								
Sternopleural and mesopleural pollinosity interrupted by gap								
Antennal bases not pollinose								
Abdominal segments shortened								
Posterior segments of abdomen without intersegmental bands								
Surstylus with lateral projection								
Orange markings on thorax absent								
Mesonotal pollinosity on lateral margins narrowed								
Antepronotum elongate								
Postpronotum elongate								
First antennal segment elongate								
Lateral process of gonocoxite bulbous subapically								
Occipital pollinosity as two patches								
Mesopleural ridge present								
Antennal bases protruding								

CHART 2 - DIOCTRIA

Characters	<i>albicornis</i>	<i>seminole</i>	<i>australis</i>	<i>wilcoxi</i>	<i>pleuralis</i>	<i>vera</i>	<i>henshawi</i>	<i>pusio</i>
First two antennal segments orange								
Anterior 1/2 of frontovertex pollinose								
Abdominal segments uniformly colored								
Hind legs uniformly colored								
Mesopleuron without pollinosity								
Upper face below antennal bases with bare markings								
Mesonotal pile reaching mesonotal suture								
Postpronotum pollinose								
Sides of antepronotum pollinose								
Pollinosity on mesonotum behind postpronotum present								
Antennal style scaphiform								
Sternopleural and mesopleural pollinosity interrupted by gap								
Antennal bases not pollinose								
Abdominal segments shortened								
Posterior segments of abdomen without intersegmental bands								
Surstylus with lateral projection								
Orange markings on thorax absent								
Mesonotal pollinosity on lateral margins narrowed								
Antepronotum elongate								
Postpronotum elongate								
First antennal segment elongate								
Lateral process of gonocoxite bulbous subapically								
Occipital pollinosity as two patches								
Mesopleural ridge present								
Antennal bases protruding								

CHART 2 - DIOCTRIA

TABLE 5

6A.1 <u>albicornis</u> and <u>seminole</u>	6A.2 <u>australis</u>
Intersegmental orange bands present on abdomen.	*Abdominal segments black.
*Anteprenotum longer	Anteprenotum shorter.
Mesonotum pollinose only on lateral margins.	Mesonotal pollinosity arranged as pattern.
Hind femur orange with black streak in both sexes.	Hind femur entirely black in male, black on dorsal half in female.
6B.1 <u>albicornis</u>	6B.2 <u>seminole</u>
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.
6C.1 Palearctic line	6C.2 Nearctic line (inc. one Korean species)
Mystax clustered	*Mystax linear
*Lateral process of gonocoxite curved laterad.	*Lateral process of gonocoxite curved mesad.

6D.1 wilcoxi

Postpronotum orange brown.

Mesothoracic pleuron with brownish orange markings.

Mesonotal pollinosity on lateral margins wide.

*Side of antepronotum pollinose.

*Mesonotum behind postpronotum pollinose.

Surstylus without lateral projection.

6E.1 pleuralis

*Postpronotum pollinose on anterodorsal corner.

*Mesonotal pile extended to mesonotal suture.

6D.2 four other Nearctic

spp (and the Korean species)

*Postpronotum black.

*Mesothoracic pleuron pleuron entirely black.

*Mesonotal pollinosity on lateral margins narrow.

Antepronotum bare.

Mesonotum behind postpronotum bare.

*Surstylus with lateral projection.

6E.2 vera, henshawi, pusio, and Korean sp.

Postpronotum bare.

Mesonotal pile present only slightly behind postpronotum.

Intersegmental orange
yellow bands from
second to sixth
segment.
Abdominal segments long.

*Intersegmental orange
yellow bands only
to fourth segment
or less.
*Abdominal segments
shorter.

6F.1 vera

Sides of antennal bases
pollinose.
Pollinosity on anterior
edge of meso and ster-
nopleuron continuous.
Antennal style spoon-shap-
ed.

6F.2 henshawi, pusio, and
Korean species

*Sides of antennal bases
bare.
*Pollinosity on anterior
edge of meso and
sternopleuron inter-
rupted.
*Antennal style scaphi-
form.

6G.1 henshawi

Face entirely pollinose
Intersegmental bands on
abdomen present.
Hind femur with dorsal
black streak.

6G.2 pusio and Korean species

*Upper face below anten-
nal bases bare.
*Abdomen without inter-
segmental bands.
*Hind femur without
black streak.

Intersegmental orange
yellow bands from
second to sixth
segment.

Abdominal segments long.

*Intersegmental orange
yellow bands only
to fourth segment
or less.

*Abdominal segments
shorter.

6F.1 vera

Sides of antennal bases
pollinose.

Pollinosity on anterior
edge of meso and ster-
nopleuron continuous.

Antennal style spoon-shap-
ed.

6F.2 henshawii, pusio, and
Korean species

*Sides of antennal bases
bare.

*Pollinosity on anterior
edge of meso and
sternopleuron inter-
rupted.

*Antennal style scaphi-
form.

6G.1 henshawii

Face entirely pollinose

Intersegmental bands on
abdomen present.

Hind femur with dorsal
black streak.

6G.2 pusio and Korean species

*Upper face below anten-
nal bases bare.

*Abdomen without inter-
segmental bands.

*Hind femur without
black streak.

6H.1 pusio

Bare marking on
upper face only
slightly below
antennal bases.

*Abdomen orange.

*Hind leg orange.

6H.2 Korean species

*Bare marking on upper
face occupies one
third of face.

*Abdomen black.

*Hind leg black.

D. wilcoxi (6D.1) has deviated from the other five species by acquiring pollinosity on the sides of the antepnotum and on the mesonotum behind the humeri.

Systematic Relationships in genus Bohartia.

The seven species assigned to this genus, bromleyi, isabella, martini, munda, nitor, senecta and tenuis, are closely related to one another and can be distinguished only by the combination of the pattern of pollinosity, the size, color, and abundance of pile, and the integumental coloration. The genitalia and other structural characters are uniform. However, nitor (Dendr. 4, 10A.2) can be readily distinguished from the other six species (10A.1) by the distinctly long appressed pile on the mesonotum and abdomen, the entirely bright reddish brown legs and the reddish brown wing veins.

Bohartia tenuis and B. martini, having reddish brown abdominal segments from the middle of the second to the seventh segment and comparatively more extensive pollinosity on the pronotum (Fig. 42), are here believed to have been derived from a common ancestor (10B.2).

Bohartia munda and B. senecta share the following characteristics: reddish brown trochanters, reddish brown markings on the tips of the front and midfemora, reddish brown hind femora, and reddish brown tibiae. These characteristics are interpreted here as having

Bohartia

Dendrogram 4

Characters	<i>bromleyi</i>	<i>isabella</i>	<i>munda</i>	<i>senecta</i>	<i>tenuis</i>	<i>martini</i>	<i>nitor</i>
Pile on antenna and ocellar tubercle white and reddish							
Hypandrium bulging							
Fringe of hair on male front tibia							
Second antennal segment with two strong bristles							
Size large (8-9 mm.)							
Ocellar bristles entirely black							
Tibiae and tarsi reddish brown							
Mid and hind femora reddish brown							
Pollinosity on antepronotum at least on upper half							
Abdomen reddish brown							
Legs entirely reddish brown							
Wing veins entirely reddish brown							
Pile on mesonotum and abdomen long and appressed							

CHART 3 - BOHARTIA

Characters	<i>bromleyi</i>	<i>isabella</i>	<i>munda</i>	<i>senecta</i>	<i>tenuis</i>	<i>martini</i>	<i>nitor</i>
Pile on antenna and ocellar tubercle white and reddish							
Hypandrium bulging							
Fringe of hair on male front tibia							
Second antennal segment with two strong bristles							
Size large (8-9 mm.)							
Ocellar bristles entirely black							
Tibiae and tarsi reddish brown							
Mid and hind femora reddish brown							
Pollinosity on antepronotum at least on upper half							
Abdomen reddish brown							
Legs entirely reddish brown							
Wing veins entirely reddish brown							
Pile on mesonotum and abdomen long and appressed							

CHART 3 - BOHARTIA

TABLE 8

10A.1	<u>bromleyi</u> , <u>isabella</u> , <u>munda</u> , <u>martini</u> , <u>senecta</u> and <u>tenuis</u>	10A.2	<u>nitor</u>
	Pile on mesonotum and abdomen short.		*Pile on mesonotum and abdomen dis- tinctly long and appressed.
	Wing veins dark brown		*Wing veins reddish- brown.
	Fore and mid femora black.		*Legs (except coxae and trochanters) entirely reddish brown.
10B.1	<u>bromleyi</u> , <u>isabella</u> , <u>munda</u> , <u>senecta</u>	10B.2	<u>tenuis</u> and <u>munda</u>
	Abdomen entirely black.		*Abdomen from middle of second to se- venth segment reddish brown.
	Pollinosity on ante- pronotum only on upper third		*Pollinosity on ante- pronotum at least on upper half.

10C.1 tenuis

A row of weak
bristles on post-
erior surface of
male front tibia
distinct.

Hypandrium of equal
thickness throughout
pile entirely white.

10C.2 martini

*Bristles on post-
erior surface of
male front tibia
mixed with long
hairs forming a
fringe of hairs.

*Hypandrium bulging
subbasally an-
tennal pile red-
dish brown and
black, ocellar
bristles black.

10D.1 bromleyi

*Two bristles on ven-
tral surface of
second antennal
segment strong,
distinct.

*Larger, 8-9 mm.

10D.2 isabella, munda and
senecta

One bristle on ven-
tral surface of
second antennal
segment weak.

Smaller, 6-7mm.

10E.1 isabella

Legs entirely black

10E.2 munda and senecta

*Tips of front and
mid femora, large
part of hind

femur, and basal half
of each tibia brownish.

10F.1 munda

Apical half of
each tibia
black; tarsi
black.

Ocellar bristles
mixed black
and white.

10F.2 senecta

*Tibiae entirely reddish
brown; tarsi reddish
brown basally gradual-
ly darkened to black
toward apices.

Ocellar bristles entirely
black.

been derived from a common origin. This lineage (10E.2) shares a pattern of pollinosity and a pattern of pile with isabella (10E.1); these two lineages are interpreted here as having a common ancestor (10D.2), which in turn has common characteristics, i.e., the entirely black abdomen and the comparatively less extensive pronotal pollinosity with bromleyi (10D.1).

The ancestor of tenuis and martini on one side (10B.2) and that of bromleyi, isabella, munda and senecta (10B.1) on the other, share the following characteristics: the pile on the mesonotum and dorsum of abdomen short, the wing veins dark brown and the front and mid femora black. These are here believed to have been developed from a common origin (10A.1), separating these six species from nitor (10.2).

Systematic Relationships in genus Dicolonus.

This is a uniform group in which the five species can be distinguished only by the combination of the length, texture, color and abundance of the pile.

Among these five, sparsipilosum and pulchrum are almost identical in regard to lack of bristles on the mesonotum and length and texture of the pile which is short and appressed, on the posterior edge of scutellum only as long as the thickness of the scutellum. In pulchrum the mesonotal pile is comparatively denser

Dendrogram 5

Characters	<i>sparsipilosum</i>	<i>pulchrum</i>	<i>medium</i>	<i>nigricentrum</i>	<i>simplex</i>
Ocellar bristles shortened
Mesonotal pile bicolored
Mesonotal bristles black
Hair of pile curled at tip
Mesonotal pile as long as mesonotal bristles
Mesonotal bristles present
Scutellar bristles long
Pile erect, long

CHART 4 - DICOLONUS

TABLE 9

11A.1	<u>sparsipilosum</u> and <u>pul-</u> <u>chrum</u>	11A.2	<u>medium</u> , <u>nigricentrum</u> , and <u>simplex</u>
	Pile on mesonotum, dorsum of abdomen, and femora appres- sed.		*Pile in general long and somewhat erect.
	Pile on posterior edge of scutellum as long as thick- ness of scutellum.		*Pile on posterior edge of scutellum exceeding thickness of scutellum.
	Mesonotal bristles absent.		*Mesonotal bristles present.
11B.1	<u>medium</u> and <u>nigricentrum</u>	11B.2	<u>simplex</u>
	Pile on mesonotum short- er making mesonotal bristles easily dis- tinguished.		*Mesonotal bristles obscured by long pile.
	Pile of straight hairs		*Each tip of hair curled.
11C.1	<u>medium</u>	11C.2	<u>nigricentrum</u>
	Dorsocentral bristles orange yellow.		*Dorsocentral bristles black.
	Mesonotal pile uni- formly orange yellow.		*Pile on posterior two third of mesonotum brownish.

11D.1 sparsipilosum

*Pile on mesonotum

sparse, orange
yellow on anterior
one fourth
of mesonotum,
brownish on the
rest.

Ocellar bristles about
equal in length to
the first antennal
segment.

11D.2 pulchrum

*Pile on mesonotum

dense, uniformly
orange yellow,
obscuring the
ground color of
integument.

*Ocellar bristles

short, only one
third the length
of first antennal
segment.

obscuring the ground color of the mesonotum, and the ocellar bristles are shorter, only one third as long as the length of the first antennal segment. In sparsipilosum the pile on the mesonotum is sparse, orange yellow on anterior fourth of the mesonotum, brownish on the rest and the ocellar bristles almost equal in length to that of the first antennal segment.

Dicolonus medium and D. nigricestrum, having erect mesonotal pile and distinct mesonotal bristles, are here considered as monophyletic (Dendr. 5, 11B.1). Dicolonus nigricestrum is distinguished from medium by having black mesonotal bristles and brownish pile on the posterior two third of the mesonotum. This lineage in turn shares a common ancestor with simplex (11B.2) for all three have erect pile, mesonotal bristles, and pile on the edge of scutellum exceeding the thickness of the scutellum. In simplex, each hair tip is curled and the mesonotal bristles are obscured by long pile.

Systematic Relationships in Echthodopa.

The three species assigned to this genus are closely related to each other. However, the shape of the hypandrium can be used for inferring the phylogeny of these flies.

Dendrogram 6

Characters	<i>pubera</i>	<i>formosa</i>	<i>carolinensis</i>
Bristles on genitalia black
Mystax black
Hypandrium constricted
Distributed in Eastern North America

CHART 5 - ECHTHODOPA

TABLE 7

8A.1 <u>pubera</u>	8A.2 <u>formosa</u> and <u>carolinensis</u>
Hypandrium parallel sided.	*Hypandrium constricted subapically.
Western.	*Eastern.
8B.1 <u>formosa</u>	8B.2 <u>carolinensis</u>
Mystax orange yellow.	*Mystax black.
*Bristles on male and female genitalia black.	Bristles on male and female genitalia orange yellow.

Echthodopa carolinensis and E. formosa share a characteristic shown by the constricted hypandrium. These species are distinguished from each other by the black bristles on the male and female genitalia in formosa, and the black mystax in carolinensis. These characteristics distinguish this lineage (Dendr.6, 8A.2) from pubera (8A.1) which has orange bristles on the mystax and on the genitalia in both sexes and has an unstricted hypandrium (Fig. 109).

Systematic Relationships in Eudioctria.

The male genitalia of this genus are of value in specific recognition as well as indicating the relationships between the species. The ovipositors and the patterns of pollinosity are to some extent also helpful for the phylogenetic deductions.

The 14 species assigned to this genus are grouped into six species groups: the albius, doanei, media, monrovia, nitida, and sackeni groups.

The albius group (Dendr.7, 8L.2) with albius and propinqua is characterized by the scoop-like lateral process of gonocoxite, the shape of the aedeagus (Figs. 96 and 97) and the presence of polymorphism in the males. The species are distinguished from each other by the patterns of pollinosity and the shape of the tip of the dorsal process of the aedeagus. In

Dendrogram 7

Characters	<i>nitida</i>	<i>unica</i>	<i>denuda</i>	<i>monrovia</i>	<i>dissimilis</i>	<i>propinqua</i>	<i>albus</i>	<i>media</i>	<i>doanei</i>	<i>beameri</i>	<i>sackeni</i>	<i>disjuncta</i>	<i>brevis</i>	<i>tibialis</i>
Posterior part of epandrium shifted dorsally	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Bare marking on gibbosity present	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Dorsal process of aedeagus narrowest at middle	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Mesonotal and mesopleural hairs shorter	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Genital fork broadened at middle	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Dorsal process of aedeagus with dorsal projection	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Posterior edge of hypandrium formed into brim-like structure	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Medioventral process of gonocoxite absent	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Hypandrium elongate	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Tip of dorsal process of aedeagus hook-like	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Lateral process of gonocoxite scoop-like	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Polymorphism in male present	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Dorsal process of aedeagus compressed laterally	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Posterior edge of lateral valve of hypogynium brim-like	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Tibiae black	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Pollinosity on upper hind corner of sternopleuron extended forward	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Pollinosity on anterior edge of mesopleuron not reaching lower margin	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Dorsocentral region with bare streak	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Anteprenotum pollinose	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Mesopleuron bare	■	■	■	■	■	■	■	■	■	■	■	■	■	■
A pair of sclerites present behind ninth tergite	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Dorsal process of aedeagus bulbous and membranous	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Aedeagus with lateral flaps	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Lateral process of gonocoxite absent	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Scutellum pollinose	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Distributed in Eastern North America	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Genital fork not divided	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Mesonotum with bare markings	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Upper half of occiput bare	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Genital fork fused to ninth tergite	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Posterior part of epandrium club-shaped	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Posterior part of epandrium with projection	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Lateral process of gonocoxite with anterior extension	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Gonostylus with subapical bulge	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Dorsal process of aedeagus membranous	■	■	■	■	■	■	■	■	■	■	■	■	■	■

CHART 6 - EUDIOCTRIA

Characters	<i>nitida</i>	<i>unica</i>	<i>denuda</i>	<i>monrovia</i>	<i>dissimilis</i>	<i>propinqua</i>	<i>albius</i>	<i>media</i>	<i>doanei</i>	<i>beameri</i>	<i>sackeni</i>	<i>disjuncta</i>	<i>brevis</i>	<i>tibialis</i>
Posterior part of epandrium shifted dorsally	■													
Bare marking on gibbosity present		■												
Dorsal process of aedeagus narrowest at middle			■											
Mesonotal and mesopleural hairs shorter			■											
Genital fork broadened at middle				■										
Dorsal process of aedeagus with dorsal projection					■									
Posterior edge of hypandrium formed into brim-like structure					■									
Medioventral process of gonocoxite absent			■	■										
Hypandrium elongate			■	■										
Tip of dorsal process of aedeagus hook-like						■	■							
Lateral process of gonocoxite scoop-like					■	■								
Polymorphism in male present					■	■								
Dorsal process of aedeagus compressed laterally			■	■	■	■					■			
Posterior edge of lateral valve of hypogynium brim-like										■				
Tibiae black			■	■			■		■					
Pollinosity on upper hind corner of sternopleuron extended forward												■		
Pollinosity on anterior edge of mesopleuron not reaching lower margin												■		
Dorsocentral region with bare streak												■		
Anteprenotum pollinose					■	■					■			
Mesopleuron bare														■
A pair of sclerites present behind ninth tergite									■	■				
Dorsal process of aedeagus bulbous and membranous									■	■				
Aedeagus with lateral flaps								■						
Lateral process of gonocoxite absent								■						
Scutellum pollinose								■			■			
Distributed in Eastern North America					■	■						■	■	■
Genital fork not divided			■	■								■	■	■
Mesonotum with bare markings			■	■	■		■					■	■	■
Upper half of occiput bare												■	■	■
Genital fork fused to ninth tergite											■	■	■	■
Posterior part of epandrium club-shaped											■	■	■	■
Posterior part of epandrium with projection									■	■	■	■	■	■
Lateral process of gonocoxite with anterior extension									■	■	■	■	■	■
Gonostylus with subapical bulge									■	■	■	■	■	■
Dorsal process of aedeagus membranous									■	■	■	■	■	■

CHART 6 - EUDIOCTRIA

TABLE 6

8C.1 <u>albius-</u> , <u>media-</u> , <u>mon-</u> <u>rovia</u> , and <u>nitida</u> groups	8C.2 <u>doanei-</u> and <u>sackeni</u> groups
Lateroposterior part of epandrium broad and flat.	*Lateroposterior corner of epandrium extend- ed into outgrowth.
Dorsal process of ae- deagus as a curved sclerotized struct- ure.	Dorsal process of ae- deagus extended into membranous structure.
Gonostylus tapered apically.	*Gonostylus with sub- apical bulge.
Lateral process of ae- deagus not extended along inner edge of gonocoxite.	*Lateral process of ae- deagus extended as a flap along inner edge of gonocoxite.
8D.1 <u>doanei</u> group Posterior part of epandrium, lateral to the cleft broad and short, half as long as epandrial length.	8D.2 <u>sackeni</u> group *Posterior part of epan- drium elongated as club-shaped structure, two thirds as long as epandrial length.

<p>*Dorsal process of aedeagus extended long membranous bulbous structure.</p>	<p>Dorsal process of aedeagus extended as short bubble-like membranous structure.</p>
<p>*A pair of sclerites present posterior to portions of ninth tergite.</p>	<p>No sclerites behind portions of ninth tergite.</p>
<p>Genital fork not fused to ninth tergite.</p>	<p>*Genital fork fused to ninth tergite.</p>
<p>8E.1 <u>sackeni</u></p>	<p>8E.2 <u>disjuncta</u>, <u>brevis</u>, <u>tibialis</u></p>
<p>Occiput, except vertical extension, entirely pollinose.</p>	<p>*Upper 1/3 of occiput bare</p>
<p>Mesonotum entirely pollinose.</p>	<p>*Mesonotum with bare markings.</p>
<p>*Scutellum pollinose.</p>	<p>Scutellum bare.</p>
<p>Genital fork not fused to each other</p>	<p>*Genital fork fused on anterior ends.</p>
<p>8F.1 <u>disjuncta</u> and <u>brevis</u></p>	<p>8F.2 <u>tibialis</u></p>
<p>Mesonotum pollinose with a pair of</p>	<p>*Mesonotum largely bare, pollinosity</p>

<p>bare markings above wing bases. Mesopleuron pollinose.</p>	<p>present only post- erior to postpronotum. *Mesopleuron bare.</p>
<p>8G.1 <u>disjuncta</u> Posterior corner of antepronotum polli- nose. *Anterior dorsocentral region with bare streak. Mesopleural pollinosi- ty on anterior edge reaching lower mar- gin of mesopleuron. *Pollinosity on postero- dorsal corner of sternopleuron extend- ed forward on lower part almost reaching sternopleural suture.</p>	<p>8G.2 <u>brevis</u> Anteppronotum bare Anterior dorsocentral regions entirely pollinose. Mesopleural pollinosity not reaching lower margin of mesopleuron. Pollinosity on postero- dorsal corner of sternopleuron not ex- tended forward.</p>
<p>8H.1 <u>doanei</u> Tibiae orange basally. Outgrowth on epandrium short, stumpy.</p>	<p>8H.2 <u>beameri</u> Tibiae black. *Outgrowth on epandrium elongate.</p>

<p>Lateral arm of hypogynium
gradually thinning posteriorly.</p>	<p>*Lateral arm of
hypogynium
abruptly thinning posteriorly to form posterior brim.</p>
<p>8J.1 <u>nitida</u>-, <u>monrovia</u>-, and
<u>albius</u> groups   Scutellum bare   Lateral process of
gonocoxite present.   Aedeagus without lateral
flap-like structure.</p>	<p>8J.2 <u>media</u></p> <p>*Basal half of
scutellum pollinose.   *Lateral process of
gonocoxite absent   *Aedeagus with a pair
of lateral flap-like structure.</p>
8K.1 <u>nitida</u> group Dorsal process of aedeagus flattened dorsoventrally.	8K.2 <u>albius</u>- and <u>monrovia</u> groups Dorsal process of aedeagus compressed laterally.
8L.1 <u>monrovia</u> group Side of pronotum not pollinose. *Hypandrium elongate, longer than gonocoxite.	8L.2 <u>albius</u> group Side of pronotum pollinose. Hypandrium short, at the 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, form- ing an inverted U- shaped structure.	Genital fork as two separate sclerites.

8M.1 propinqua

Mesonotum entirely
pollinose.

Posterior margin of
mesopleuron pollinose.

Tip of dorsal process
of aedeagus pointed.

8M.2 albius

*Mesonotum with a pair
of sublateral bare
markings.

*Posterior margin of
mesopleuron polli-
nose only on upper
half.

*Tip of dorsal process
of aedeagus blunt,
formed as a hook.

8N.1 monrovia

Mesonotum largely
pollinose with a
pair of bare mark-
ings.

Posterior edge of
hypandrium not
formed as brim-
like extension.

Dorsal process of
aedeagus without
dorsal projection.

*Genital fork broad-
ened at middle.

8P.1 nitida and unica

Mesonotum entirely
pollinose.

*Mesonotal and meso-
pleural hairs long-
er.

*Dorsal process of ae-
deagus broadened
in the middle.

8N.2 dissimilis

*Mesonotum largely
bare, pollinose
only posterior to
postpronotum.

*Posterior edge of
hypandrium extend-
ed at brim.

*Dorsal process of
aedeagus with
dorsal projection.

Genital fork horse-
shoe-shaped.

8P.2 denuda

*Mesonotum with bare
spots.

Mesonotal and meso-
pleural hairs
shorter.

*Dorsal process of
aedeagus narrowed
in the middle.

8Q.1 nitida

Face entirely
pollinose.

*Posterior part of
epandrium more
horizontal than
than vertical

8Q.2 unica

*Face with triangular
bare marking on
gibbosity.

Posterior part of
epandrium more
vertical.

albius a pair of bare markings are present on the mesonotum above the wing bases, the bare lower half of the posterior margin of the mesopleuron and the blunt tip of the dorsal process of the aedeagus formed as a hook (Fig. 96), while in propinqua the mesonotum is entirely pollinose, the hind margin of the mesopleuron is pollinose and the tip of the dorsal process of the aedeagus is pointed (Fig. 97).

In the doanei group (8D.1), beameri and doanei share the presence of a projection on the posterolateral corner of the epandrium, of a membranous bulbous structure on the dorsal process of the aedeagus (Figs. 101-104), and of a pair of sclerites posterior to the female ninth tergite (Figs. 124 and 125). These two species are separated from each other by the color pattern of the tibiae, which are black in beameri and orange basally but black apically in doanei. In beameri the postlateral projection of the epandrium is longer and the hypogynial lateral arms (Figs. 124, 125) have a posterior brim-like structure.

Eudioctria media is the only representative of its group (8J.2). It is distinguished from the other species of Eudioctria by the absence of the lateral process of the gonocoxite and by the presence of a pair of flaps on the sides of the aedeagus.

The monrovia group (8L.1) is characterized by the shape of the epandrium which is elongate, longer than the gonocoxites and by the absence of strong reduction of the medioventral process of the gonocoxite (Figs. 94 and 95), and by the anteriorly fused genital fork which forms an inverted U-shaped structure (Figs. 117 and 118). There are two species assigned to this group: dissimilis with the mesonotum largely bare, pollinose only behind the humeri, the hypandrium ending in a brim-like edge posteriorly, the dorsal process of the aedeagus protruded dorsally and the genital fork in the female horseshoe-shaped; monrovia with the mesonotum largely pollinose, bare above the wing bases, the hypandrium without a brim-like edge, the dorsal process of the aedeagus without dorsal protrusion and the genital fork broadened medially on each side.

The nitida group (8K.1) with three species assigned to it, denuda, nitida and unica, is characterized by the shape of the dorsal process of the aedeagus, dorsoventrally flattened and curved downward at the tip forming a hook. Eudiotria nitida and E. unica (8P.1) share the following characters: entirely pollinose mesonotum, comparatively longer mesonotal and mesopleural hairs, and medially broadened dorsal process of the aedeagus (Figs. 98 and 100), while denuda (8P.2) stands

apart from these two by having bare markings on the mesonotum, shorter mesonotal and mesopleural pile, and the slender process of the aedeagus (Fig. 106). The differentiation into nitida in one line (8Q.1) and unica in the other (8Q.2) can be traced by certain apomorphic characters in each species. Eudioctria unica has acquired a triangular bare marking on the gibbosity, and in nitida the lateroposterior part of the epandrium has shifted to a more dorsal position (Fig. 98).

The four species in the sackeni group (8D.2), brevis, disjuncta, tibialis and sackeni, have nearly identical male genitalia (Figs. 105 and 106) with an elongated, club-shaped lateroposterior part of the epandrium and a broad dorsal process of the aedeagus extended into a short membranous bubble-like structure. In the female the genital fork is fused posteriorly to the ninth tergite (Figs. 126 and 127).

Eudioctria brevis and E. disjuncta (8F.1) are closer to each other than either to other species with a character in common and confined to these two (as far as the sackeni group is concerned), i.e., a pair of bare markings on the mesonotum. Eudioctria disjuncta is distinguished from brevis by the presence of polli-nosity on the sides of the anteprenotum and by the bare streaks on the mesonotum.

Among these six species groups, the doanei and sackeni groups show relationship by having a projection on the posterolateral corner of the epandrium, the gonostylus with subapical dorsal expansion (Figs. 101-106) and the dorsal process of the aedeagus short and extended into a membranous bulb. Therefore these two species groups are interpreted here as monophyletic (8C.2).

The other four species groups (8C.1) share the following characteristics: flat and broad epandrium without any outgrowth, gradually tapered gonostylus and a completely sclerotized, downwardly curved dorsal process of the aedeagus (Figs. 93-100). These characteristics are interpreted here to have been acquired as a result of common ancestry. Within this lineage, the monrovia- and albius groups are close to each other by having the dorsal process of the aedeagus laterally compressed and pointed apically. They are here believed to have been derived from a common ancestor (8K.2). This lineage shows a close relationship to the nitida group. The common ancestor of these two lineages (8J.1) is characterized by the well defined dorsal process of the aedeagus curved downward at the tip and distinguished from media (8J.2) which has deviated from the albius, monrovia, and nitida groups by losing the lateral process of the gonocoxite and by having a pair of flaps on the sides of the aedeagus obscuring the shape of the dorsal process of the aedeagus (Fig. 93).

Systematic Relationships in the Echthodopini.

Six genera are assigned to this tribe: Bohartia, Dicolonus, Echthodopa, Eudioctria, Metadioctria, and Myelaphus. Two of these, Echthodopa and Eudioctria (Dendr. 2, 7.2), show close relationship to each other and may be developed from a common stock. This relationship is shown by the lateral arm of the gonocoxite, the deep cleft on the hind margin of the epandrium, the flattened and broad lateral process of gonocoxite and the epandrial arm and the depression on the mesopleuron lost. The splitting into two genera has been followed by independent development in each lineage. In the Eudioctria lineage (8.1), the pollinosity on the frontovertex, the bare pteropleuron and the cleft epandrium have been retained. However, this lineage has also developed apomorphic characters: bare scutellum, presence of tubercles on hind femur and tibia, well developed lateral arm of the gonocoxite and dorsal process of the aedeagus. In the Echthodopa lineage (8.2) the pollinosity on the frontovertex has been lost, the anterior half of the pteropleuron has become pollinose and pilose and the epandrium has been split into two lateral halves. However, the scutellum is pilose, the hind leg smooth, the lateral arm of gonocoxite stumpy and the aedeagus is without a dorsal process.

Characters	Dicolonus	Myelaphus	Bohartia	Metadictia	Eudictia	Echthodopa	Dioctria
Anterior 1/2 of pteropleuron pollinose							
Lateral arms of gonocoxite well developed							
Scutellum bare							
Pollinosity of face only on lower part							
Antennal style two-segmented							
Antenna compressed laterally							
Gibbosity with a triangular bare spot							
Hypopleuron without pile							
Mesopleuron completely pilose							
Pile on first antennal segment uniform							
Front corner of sternopleuron without pollinosity							
Pile on second abdominal segment undifferentiated							
Frontovertex parallel-sided							
Anterior 1/2 of pteropleuron pilose							
Occiput without pollinosity							
Lateral processes of aedeagus lamellate							
Upper part of face with hairs							
Male abdomen without constriction between segments two and three							
Mesopleuron without depression							
Lateral process of gonocoxite flattened							
Epandrial arms reduced							
Hind margin of epandrium deeply cleft							
Gonocoxite with lateral arm							
Sternopleural suture absent							
Pile on prementum on tip only							
Labellum without notch							
Hind metatarsus swollen							
Ocellar tubercle without bristles on dorsal surface							
Surstyli on epandrium well developed							
Alula absent							
Hind femur and hind tibia each club-shaped							

CHART 1 - ECHTHODOPINI

TABLE 4

7.1 <u>Dicolonus</u> , <u>Myelaphus</u> , <u>Bohartia</u> and <u>Meta-</u> <u>dioctria</u>	7.2 <u>Eudioctria</u> and <u>Echtho-</u> <u>dopa</u>
Depression on postero- dorsal of mesopleu- ron present.	*No depression on postero- dorsal of mesopleuron.
*Abdominal segments paral- lel sided.	Abdominal segments nar- rowest at intersegment between second and third segment.
*Upper half of face with hairs.	No hairs on upper half of face.
Hind margin of epandrium moderately concave; epandrial arms present.	*Hind margin of epandrium deeply cleft, epan- drial arms lost.
Gonocoxite simple.	*Gonocoxite with lateral outgrowth on subapex.
Lateral process of gono- coxite elongate.	Lateral process of gono- coxite flattened and broad.
Lateral process of aede- agus present.	*Lateral process of ae- deagus lost.

8.1 Eudioctria

Frontoververtex polli-
nose.

Pteropleuron bare

*Scutellum bare.

*Hind femur and hind
tibia tuberculate.

Epandrium deeply cleft

*Lateral outgrowth (arm)
of gonocoxite long
and curved.

*Aedeagus with distinct
dorsal process.

8.2 Echthodopa

Frontoververtex bare.

*Pteropleuron pollinose
and pilose on ant-
erior half.

Scutellum pilose.

Hind leg sooth.

*Epandrium split into
two lateral halves.

Lateral arm of gono-
coxite stumpy.

Aedeagus without dorsal
process.

9.1 Bohartia and Metadioctria 9.2 Dicolonus and Myelaphus

Pile on ventral surface
of first antennal segment
longer than that on
dorsal surface.

Frontoververtex narrowed
toward antennal bases.

Sternopleuron pollinose.

*Pile on first antennal
segment uniform in
length.

*Frontoververtex parallel
sided.

*Sternopleuron bare.

Pile on upper face
linear on each
side.

Pile on mesonotum and
abdomen erect.

Pile on mesopleuron
marginal.

Pile on abdomen, esp-
ecially on sides of
second segment,
differentiated in
length.

Lateral aedeagus lamel-
late.

Pile on upper face not
linear.

Pile on mesonotum and
abdomen flat.

Pile on mesopleuron ex-
tending from upper
margin to sternopleuron.

Abdominal pile uniform in
length.

Lateral process of aede-
gus not lamellate.

10.1 Bohartia

Frontovertex and occi-
put pollinose.

Mesonotum pollinose.

Depression on upper
corner of meso-

Mesonotal pile short
and sparse.

Abdomen wider in the
middle.

10.2 Metadioctria

Frontovertex and occiput
not pollinose.

Mesonotum bare.

*Mesopleuron without de-
pression.

Mesonotal pile long and
dense.

Abdomen parallel sided.

11.1 Dicolonus

Antennal style

spoon shaped,
one segmented.

Upper face around
antennal bases
pilose and pol-
linose.

*Gibbosity with
triangular
marking.

First antennal seg-
ment densely pil-
ose.

*Sternopleural suture
lost.

Lateral processes of
aedeagus greatly
reduced.

11.2 Myelaphus

*Antennal style

compressed
laterally,
two segmented.

*Upper face bare.

Lower face polli-
nose.

*First antennal
segment bare.

Sternopleural
suture present

Lateral proces-
ses of aedeagus
present.

The close relationship of Metadioctria and Bohartia (9.2) is shown by a row of hairs on each side of the upper face below the antennal bases and the lamellate lateral process of the aedeagus. The differentiation into Metadioctria is accompanied by the loss of pollinosity on the occiput and the mesonotum, loss of the depression on the posterodorsal of the mesopleuron and the long dense mesonotal pile. Bohartia (10.1) on the other hand, has retained these characters in plesiomorphic condition, but developed comparatively wider and shorter abdomen.

Dicolonus and Myelaphus (9.1) are here believed to have been derived from a common ancestor, based on the uniform pile on the first antennal segment, parallel sided frontovertex, somewhat rounded antennal bases, uniform abdominal pile, especially on the sides of the second segment, clustered hairs around the antennal bases, short and recumbent pile on the mesonotum and abdomen, and lack of pollinosity on the sternopleuron. This branch (9.1) split into Myelaphus (11.2) and Dicolonus (11.1), each of these developed its respective apomorphic characters.

Myelaphus is characterized by laterally compressed two-segmented antennal style, completely bare antennal bases, loss of pollinosity on upper face, and reduction of pile on first antennal segment. These

characters are retained in plesiomorphic condition in Dicolonus, but this genus has developed apomorphic characters of its own: triangular bare spot on gibbosity, absence of sternopleural suture, and greatly reduced lateral processes of the aedeagus.

These two lineages, Metadioctria and Bohartia (9.2) in one side and Dicolonus and Myelaphus (9.1) in the other, in turn are related to each other (7.2) by sharing a depression on the upper corner of the mesopleuron, a trapezoidal epandrium. (with posterior arms), a simple gonocoxite with elongate lateral process, hairs on the upper face below the antennal bases, and parallel sided abdomen.

ZOOGEOGRAPHY

The existence of Dioctria in both the Palaearctic and Nearctic regions indicates the occurrence of migration and this raises questions as to the origin of the genus and the direction and time as well as the route of migration.

The Palaearctic species of the subgenus Dioctria, except for an undescribed Korean species, are considered a monophyletic group (Dendr. 3, 6C.2). The Nearctic species of Dioctria, together with the Korean species, are also monophyletic (6C.1). The sister group of these two monophyletic groups, i.e. Dioctria, subgenus Nannodioctria, is confined to North America.

Of several possibilities for the origin of the genus Dioctria, only two, i.e., Asia or North America, seem probable. If the Palaearctic region was the site of origin of the entire group migration must have taken place after the two subgenera had become differentiated. One of them, the ancestor of Nannodioctria, migrated to North America without leaving any 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. 3, 6C.1), without

leaving representatives in Asia, the other remaining in Asia to develop into the Palaearctic species group (Dendr. 3, 6C.2). The presence of an unnamed species in Korea (6H.2), which shares a common ancestor with the most derived Nearctic species (pusio), indicates a more recent migration from North America to Asia.

A parallel case is found in the Catostomidae which originated in Asia and radiated secondarily in North America, with one species, Catostomus catostomus subsequently returning to Asia (Darlington 1957). This example shows that the primitive ancestors of a group (in this case of the Catostomidae) can remain, and continue to evolve, at the site of their origin.

If, on the other hand, Dioctria originated in North America, the occurrence of the Palaearctic species group would be a consequence of migration of its ancestor from the New World to the Old. At a later date the ancestor of the Korean species split off from its sister species, which became pusio, and moved to the Palaearctic region. The Palaearctic species group of Dioctria and the Korean species have both been shown in this paper to have more apomorphic characters than their respective sister group counterparts in North America, suggesting that all the Nearctic forms are relatively more primitive. Since it is possible for the more primitive group

to remain and evolve at the site of origin, as exemplified above by the ancestors of the Catostomidae, it is equally possible for the genus Dioctria to have originated and radiated in North America. A Nearctic origin for Dioctria is also consistent with the exclusive occurrence of Nannodioctria and nearly all of the Echthodopini in the Nearctic Region.

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 consider 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 Beringia (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 Palaeractic group of Dioctria took place during the Miocene.

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

All the genera of the Echthodopini, i.e., Bohartia, Dicolonus, Echthodopa, Eudioctria, Metadioctria and Myelaphus, are present in Western North America and four of them are not found elsewhere (Map 6-24). This

part of North America was isolated during the Oligocene by climatic barriers, i.e., reduced rainfall (MacGinitie 1958) and is thus a plausible site of origin of this tribe.

Echthodopa and Eudioctria are both represented in Eastern as well as Western North America. From this fact one can infer that each of these genera must have become transcontinental. This pattern of distribution probably developed after the breakdown of these climatic barriers in the Miocene (MacGinitie, loc. cit.). Gradually, however, the formation of the Rocky Mountains and of the central plain east of them interrupted these transcontinental distributions. When the ice age began in the Pleistocene the surviving peripheral populations were pushed southward. With repeated glatiations these populations have speciated and respeciated forming the present-day species of Echthodopa and Eudioctria.

Map 1

Map 2

Map 3

Map 4

Map 5

Map 6

Map 7

Map 8

Map 9

Map 10

Map 11

Map 12

Map 14

Map 13

Map 15

Map 18

Map 19

Map 20

Map 21

Map 22

Map 23

Map 24

Figure 1. Head; A. frontal aspect; B. lateral aspect; ant.b-antennal bases; fc-face; fv-frontovertex; mx-mystax.

Figure 2. Thorax, lateral aspect; apn-antepronotum; hpp-hypopleuron; lcs-lateral cervical sclerite; mpr-mesopleural ridge; msp-mesopleuron; msn-mesonotum; ppn-postpronotum; ptp-pteropleuron; stp-sternopleuron.

Figure 3. Hind leg, lateral aspect; cx-coxa; fm-femur; mts-metatarsus; tb-tibia; tr-trochanter.

Figure 4. Wing; R_4 -anterior branch of third vein; Ac-anal cell; Mc-marginal cell; P-posterior cell; Sm-submarginal cell; al-alula.

1mm

Figure 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.

Figure 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.

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

1 mm

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

21 A

B

22 A

B

A

23

B

24

A

25

B

A

26

B

1mm

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

30 A

1mm

Figures 31 and 32. Head; Eudioctria albius; 32. Echthodopa pubera.

Figures 33 and 34. Mouthparts; 33. Dioctria pusio;
34. Eudioctria albius; a. proboscis,
lateral aspect; b. epipharynx;
c. labium, ventral aspect; d. maxilla,
ventral aspect; e. hypopharynx,
dorsal aspect; f. right lateral blade
of hypopharynx, lateral aspect.

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

1mm

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

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

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

1mm

2mm

Figures 60-68. Hind leg; 60. Dioctria albicornis;
61. D. Seminole; 62. D. pleuralis;
63. Metadioctria rubida; 64. Bohartia
isabella; 65. B. martini; 66. Eudioc-
tria albius; 67. E. unica, male;
68. E. unica, female.

Figures 69-70. Hind leg; 69. Dicolonus medium;
70. D. nigracentrum.

Figures 71-76. Empodium; 71. Dioctria albicornis;
72. D. seminole; 73. D. pleuralis;
74. Metadioctria rubida; 75. Bohar-
tia isabella; 76. Eudioctria albius.

Figures 77.78. First three segments of abdomen.
A. lateral aspect; B. dorsal aspect;
77. Dioctria albicornis; 78. D.
seminole.

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

2mm

Figures 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; 83. Dioctria albicornis; 84. D. wilcoxi; 85. D. pleuralis; 86. D. henshawi; 87. D. vera; 88. D. pusio.

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

1mm

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

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

Figures 105-109. Male genitalia; 105. Eudioctria
sackeni; 106. E. brevis; 107.
Dicolonus simplex; 108. Echthodo-
pa pubera; 109. Myelaphus lobicornis.

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

1mm

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

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

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