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# A Monograph of the Genus *Polyphylla* Harris in America North of Mexico (Coleoptera: Scarabaeidae: Melolonthinae)

Ronald M. Young

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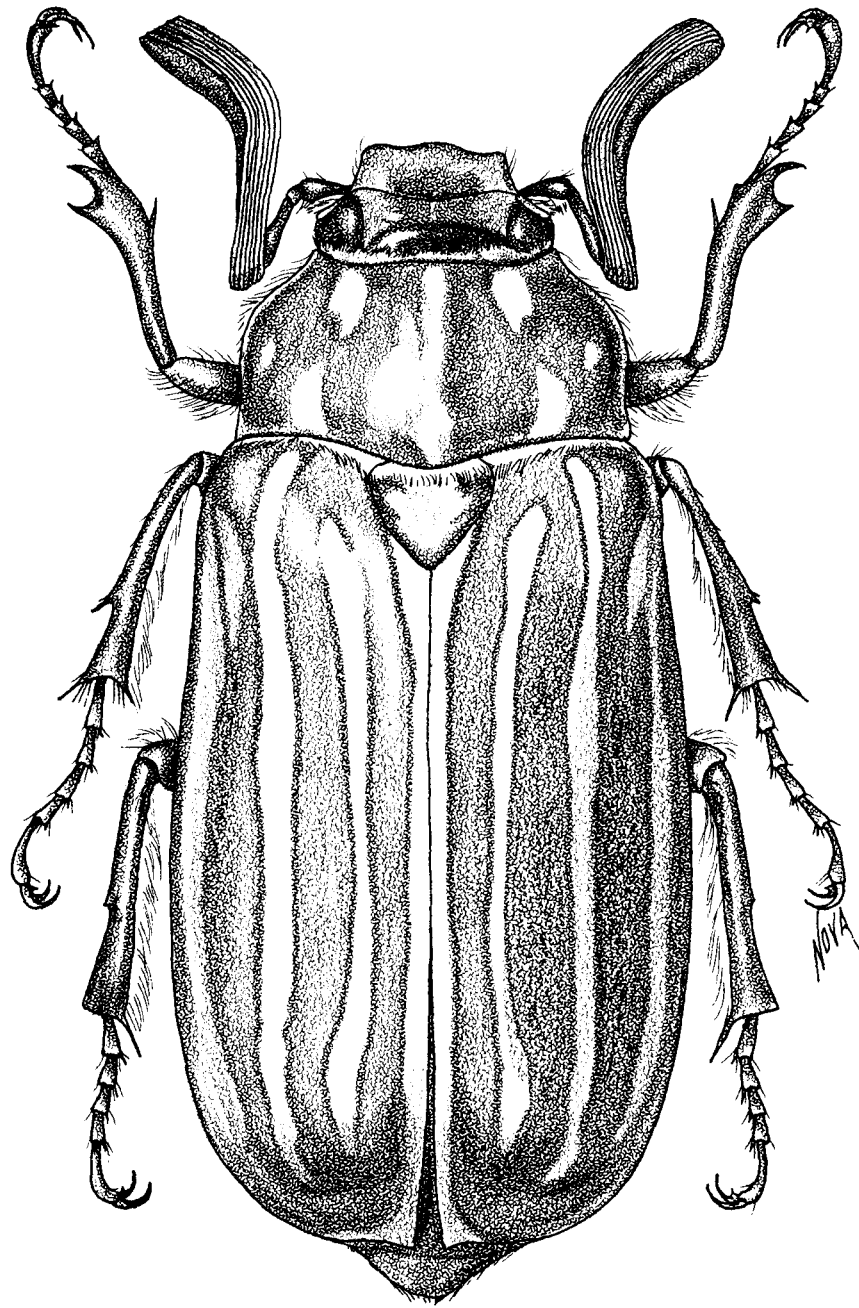
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Frontispiece.—*Polyphylla decemlineata* (Say). Male.

## ABSTRACT

### A Monograph of the Genus *Polyphylla* Harris in America North of Mexico (Coleoptera: Scarabaeidae: Melolonthinae)

Ronald M. Young

The North American species of the genus *Polyphylla* Harris, 1841, are defined and revised for the first time since Fall (1928). All name bearing types were examined except those of *P. oklahomensis* Hatch and *P. subvittata* LeConte (synonyms of *P. hammondi*), which are lost. A lectotype is designated for *P. gracilis* Horn, and neotypes for *P. decemlineata* (Say), *P. occidentalis* (L.), and *P. variolosa* (Hentz). New synonyms of *P. decemlineata* are *P. comstockiana* von Bloeker, *P. matrona* Casey, and *P. potsiana* Casey. New synonyms of *P. crinita* LeConte are *P. pacifica* Casey and *P. ruficollis perversa* Casey. *P. alleni* Cazier is a new synonym of *P. diffracta* Casey. *P. crinita nigra* Casey is raised to specific rank and *P. incolumis relicta* Casey, *P. incolumis robustula* Casey, *P. martini* von Bloeker, and *P. santacruzae* von Bloeker are its new synonyms. New synonyms of *P. hammondi* LeConte are *P. latifrons* Casey, *P. rufescenta* Tanner, *P. speciosa* Casey, and *P. speciosa acomana* Casey. *P. marginata* is a *nomen nudum*. Descriptions of first known females are given for *P. barbata* Cazier, *P. devestiva* Young, and *P. erratica* Hardy and Andrews. *P. mescalerensis* is a new species from southeastern New Mexico. Of the 71 names established since 1767 which represent *Polyphylla*, 28 are recognized as valid. Females are unknown for 12 species. These species cluster morphologically and geographically into four species complexes. A key to larvae is provided for the four species having described larvae. A key to adults is provided, and all taxa are described or redescribed and illustrated by photographs. Available biological information is included. Distributional data and maps based on 14,094 specimens are provided. A cladistic interpretation and hypothetical phylogeny of the genus are constructed.

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## INTRODUCTION

The melolonthine genus *Polyphylla* Harris is found worldwide between ca. 15 and 53 degrees North latitude. In the New World the southernmost record is Honduras and the northernmost is Quesnel, British Columbia (Fig. 1).

Distribution is typically discontinuous with many species restricted to specific, isolated, sandy environmental refugia. Of the 28 species in America north of Mexico, 8 (ca. 30%) are broadly distributed across three to many states. Five species (18%) are narrowly distributed, typically found in only two or three states. The remaining 15 species (ca. 54% of the North American fauna), are endemic to one or two localities which tend to be unique sandy or sand dune areas.

All science is a step process with current scientists correcting, refining, and adding to the work of their forerunners. Data such as "flying at dusk over sand dunes" or "in dry grasslands" probably seemed insignificant to the writer of the pin labels, yet they pro-

vide clues to understanding the species. The work of Downes and Andison (1941), Johnson (1954), Young (1966, 1972), and Hardy and Andrews (1978), among others, now enables us to predict which general habitat types will support *Polyphylla*. I have an impression that accumulation of dissimilarity in these animals is a fairly rapid process in isolated interbreeding populations; therefore it may be predicted that additional species will be discovered with intensified investigations of sand/grass associations. It may also be predicted that our knowledge of immature stages, adult feeding habits and periodicity, and the females which remain unknown in 12 species, will increase.

Endemism of a taxon to a relatively small area is common in insects; perhaps so common that entomologists began to take it for granted. Yet when one stops to consider, it seems quite remarkable that of all the spectrum of biotic diversity on Earth, this taxon is found only in this place. It seems a tenuous hold on existence. This work establishes that 54% of the North American species of *Polyphylla* are so restrict-



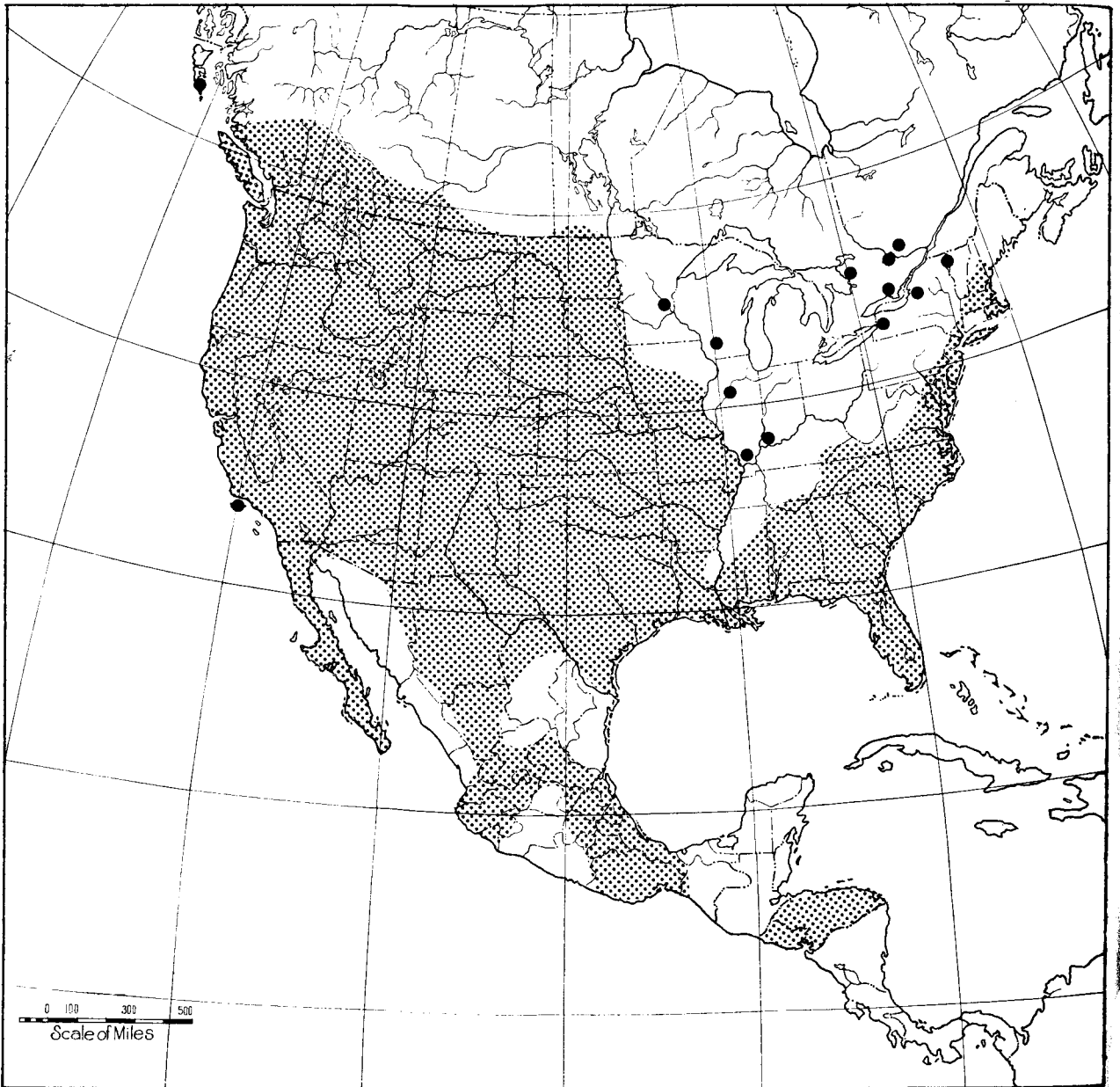


Fig. 1.—Distribution of *Polyphylla* in North and Central America. Mexican and Central American records are incomplete. Dots indicate disjunct demes.

ed—to one sand dune complex or one mountain top. I believe it is encumbant on those of us within the scientific community to ensure their continued existence.

The 28 valid species recognized in this revision cluster geographically and morphologically into four

species groups or complexes which are interpreted as distinct evolutionary lineages within the genus. The genus is recorded from all conterminous states except Connecticut, Michigan, Ohio, and West Virginia. Geographically disjunct populations existing in sandy environmental refugia are recorded from Alabama

Illinois, Indiana, Minnesota, and Wisconsin. In Canada, the genus is represented in the southern portions of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, and Quebec (Fig. 1 and Young, 1972).

The eastern coastal and southeastern *occidentalis* complex (Fig. 2) includes four species: *P. comes* Casey, 1914; *P. gracilis* Horn, 1881; *P. occidentalis* (L.), 1767; and *P. variolosa* (Hentz), 1830. These species are distinguished from all others by their distribution, the aedeagus which is cleft for much less than half its length (except for *P. gracilis*), and a unique lateral groove on the distal one-third to one-half of the length of the aedeagus. Viewed laterally, this groove causes a dorsal ridge to be formed. *P. gracilis* is placed within this complex by its floridian distribution and the unusually broad tip of the aedeagus

(Fig. 3). In Part I of this revision (Young, 1967) I included the aberrant floridian species *P. pubescens* Cartwright, 1939 in this complex. The comparative work of Hardy (1974) argues well for placing this taxon in the monotypic genus *Polylamina*.

Young (1967) treated the western *diffracta* complex of species, which is herein reconsidered. Extensive nomenclatural adjustments are made and one new species is named. Two of Hardy and Andrews' five species from 1978 fall within this complex. As finally defined, this complex includes the following 15 species: *P. avittata* Hardy and Andrews, 1978; *P. barbata* Cazier, 1938; *P. crinita* LeConte, 1856; *P. devastiva* Young, 1966; *P. diffracta* Casey, 1891; *P. hirsuta* Van Dyke, 1933; *P. mescalerensis* new species; *P. modulata* Casey, 1914; *P. nigra* Casey, 1914; *P. nubila* Van Dyke, 1947; *P. pottsorum* Hardy and An-

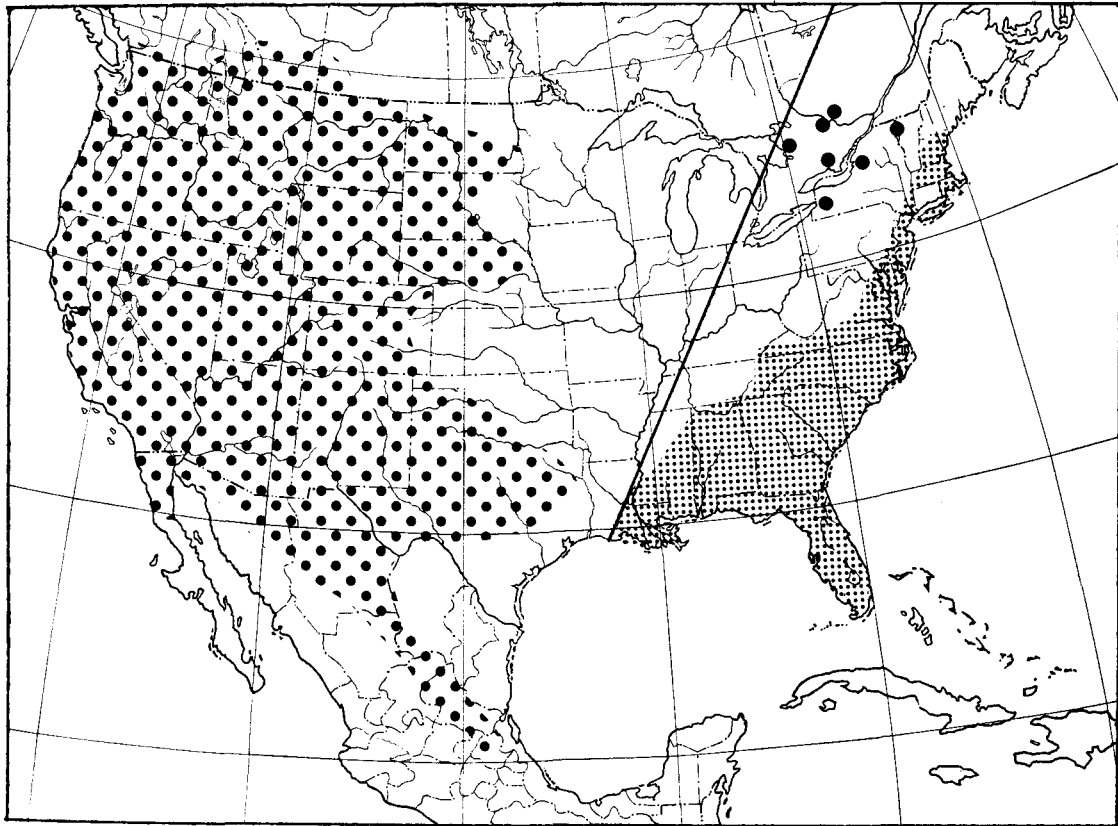


Fig. 2.—Distributions of the *decemlineata* (western) and *occidentalis* (eastern) complexes. Line marks the western-most occurrence of the *occidentalis* complex (See Key No. 2 to Adults, couplet 1).

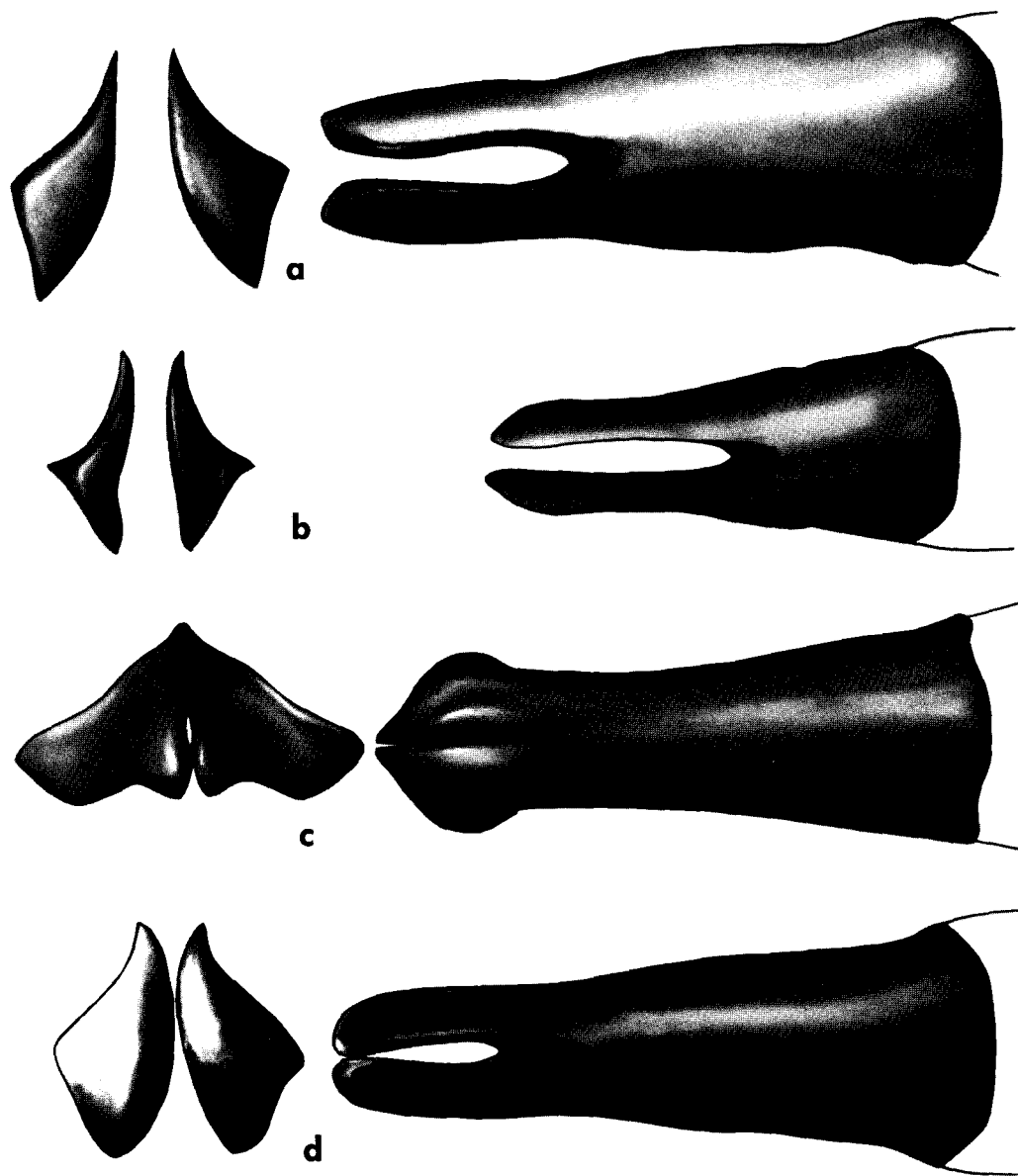


Fig. 3.—Dorsal (right) and caudal (left) views of the aedeagi of the *occidentalis* complex. (a).—*P. comes*. (b).—*P. gracilis*. (c).—*P. occidentalis*. (d).—*P. variolosa*.

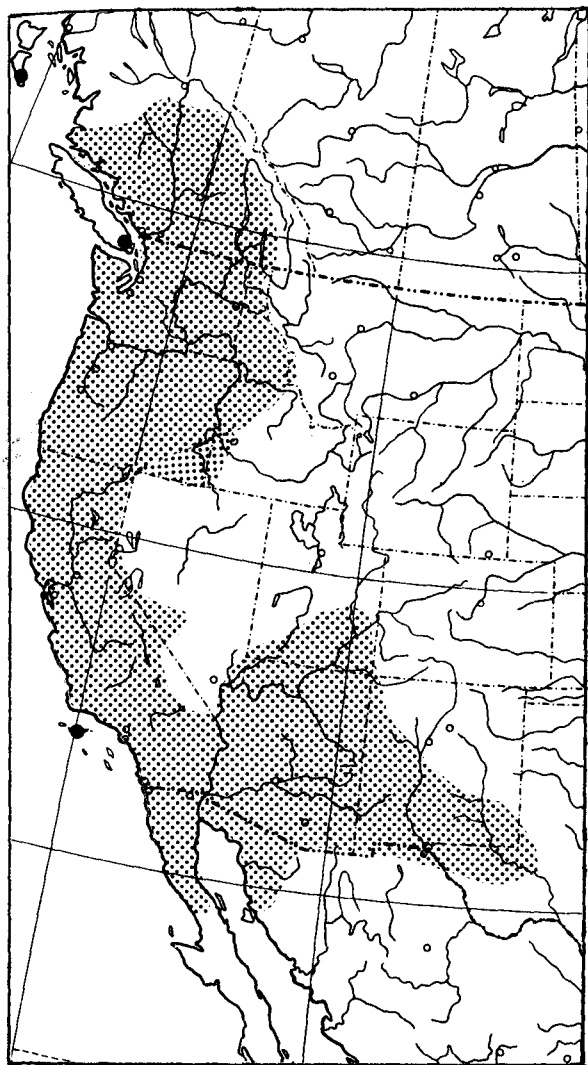


Fig. 4.— Distribution of the *diffracta* complex.

draws, 1978; *P. ratcliffei* Young, 1986; *P. rugosipennis* Casey, 1914; *P. sobrina* Casey, 1914; and *P. stellata* Young, 1986. Species of this complex are distributed primarily in the southwestern states and California (Fig. 4) and constitute more than half the known North American species. They are separated from all other species by the presence of hairs over most or all of the pronotum, and the aedeagus in dorsal aspect is gradually, smoothly narrowed from phallobase to apex, lacking the lateral groove seen in the *occidentalis* complex (Figs. 3 and 5).

The *decemlineata* complex has the broadest distribution of the four North American complexes. Ranging discontinuously over the large area shown in Fig. 2, its species are often sympatric with those of the *diffracta* and *hammondi* complexes. For many years the name *P. decemlineata* (Say), 1824, has served as a catchall for "ten-lined June beetles." The existence of undescribed populations suspected earlier (Young, 1967) has, however, been disproved. The species *P. decemlineata* is a surprisingly homogeneous one. Slight color variations show up along portions of the Pacific Coast but nothing of a subspecific nature. This complex also includes *P. arguta* Casey, 1914 and *P. monahansensis* Hardy and Andrews, 1978. The latter species, which is sympatric with *P. pottorum* of the *diffracta* species cluster, is quite remarkable morphologically. At a glance it appears to be *P. sobrina* which is most commonly taken in the area of Yosemite National Park. *P. monahansensis* is known from only west-central Texas and Chihuahua, Mexico; aedeagal configuration immediately places it within the *decemlineata* complex. It seems to represent another example of convergence, which is common in species of this genus. These three species may be separated from all others by the aedeagus which does not smoothly narrow from phallobase to apex but becomes markedly broader at the beginning of the cleft between the parameres and narrows to a pointed distal tip (Fig. 6).

The *hammondi* complex is the most heterogeneous and difficult of the genus. It reaches its greatest concentration in the southwest but ranges farther to the east than previously realized. Disjunct populations surviving in sandy environmental refugia are found in Illinois, Indiana, Minnesota, and Wisconsin (Young, 1972); a new species has been described from southern Alabama (Young, 1986 and Fig. 7). The six species in this complex are: *P. anteronivea* Hardy and Andrews, 1978; *P. brownae* Young, 1986; *P. cavifrons* LeConte, 1854; *P. erratica* Hardy and Andrews, 1978; the polymorphic *P. hammondi* LeConte, 1856 with a northern and eastern avittate phase, a southern avittate phase, and a southern vittate phase; and *P. squamiventris* Cazier, 1939. This complex is separated from all others by the lack of hairs over the entire pronotal surface (except in *P. brownae*), lack of clumped squamae in some species, the unique reddish-brown elytral color, and the aedeagus which does not broaden at the cleft, with the apex parallel-

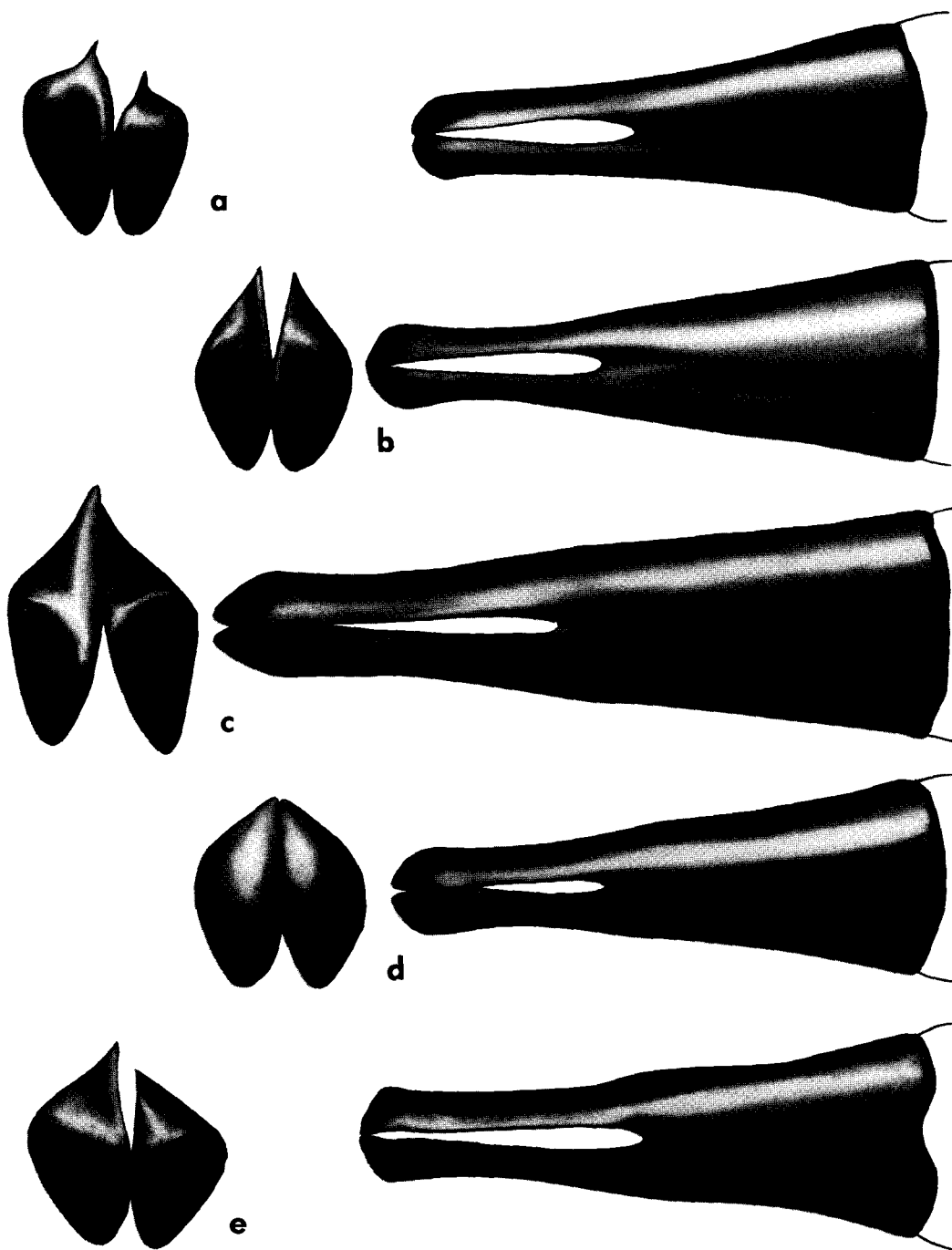
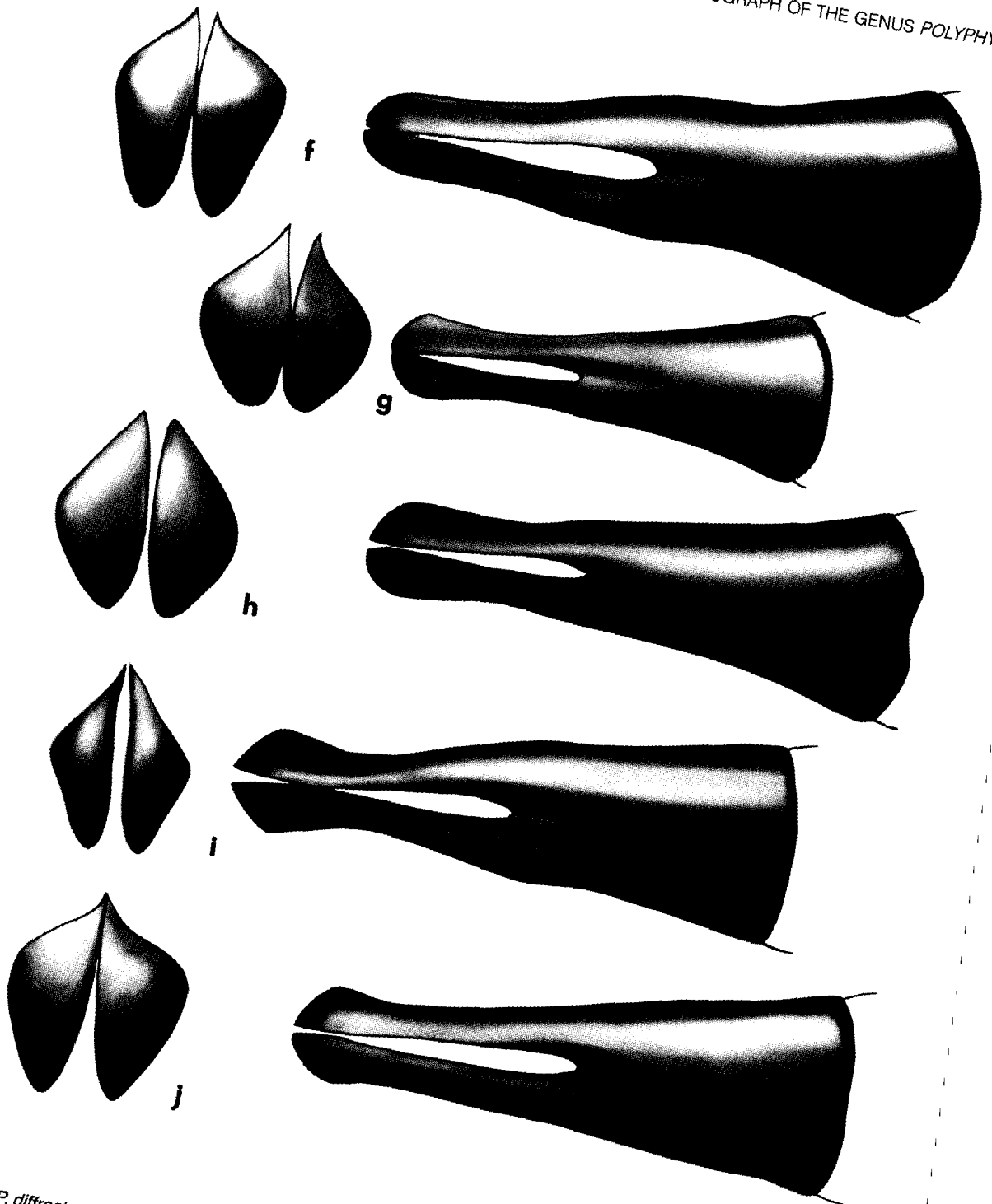


Fig. 5.—Dorsal (right) and caudal (left) views of the aedeagi of the *diffracta* complex. (a).—*P. avittata*, holotype. (b).—*P. barbata*, metatype. (c).—*P. crinita*. (d).—*P. devestiva*, metatype. (e).—*P. diffracta*, avittate phase.



(cont.).— (f).—*P. diffracta*, vittate phase. (g).—*P. hirsuta*, holotype. (h).—*P. mescalerensis*, holotype. (i).—*P. modulata*. (j).—*P. nigra*.

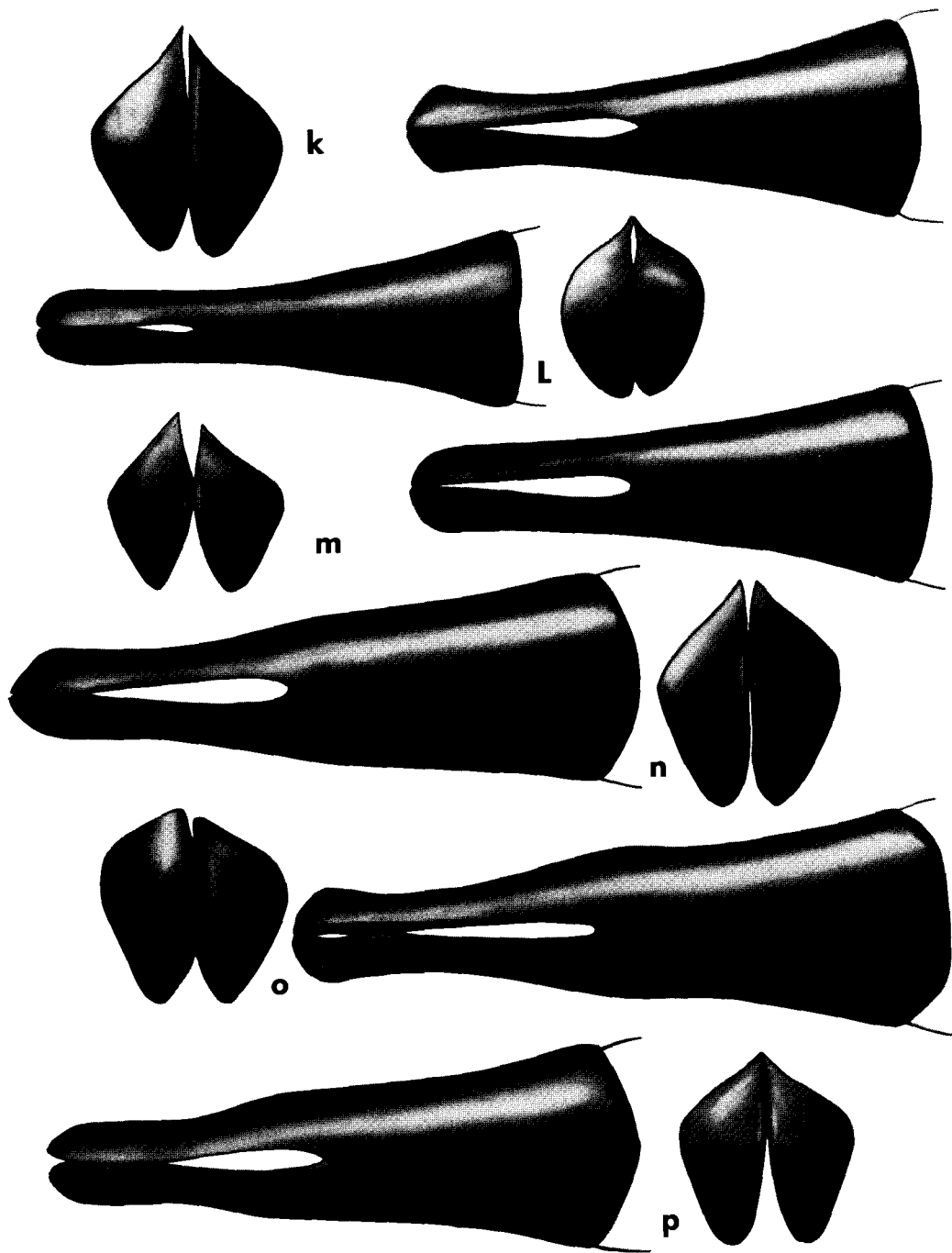


Fig. 5 (cont.).— (k).—*P. nubila*, holotype. (l).—*P. pottorum*, holotype. (m).—*P. ratcliffei*, holotype. (n).—*P. rugosipennis*. (o).—*P. sobrina*. (p).—*P. stellata*, paratype.

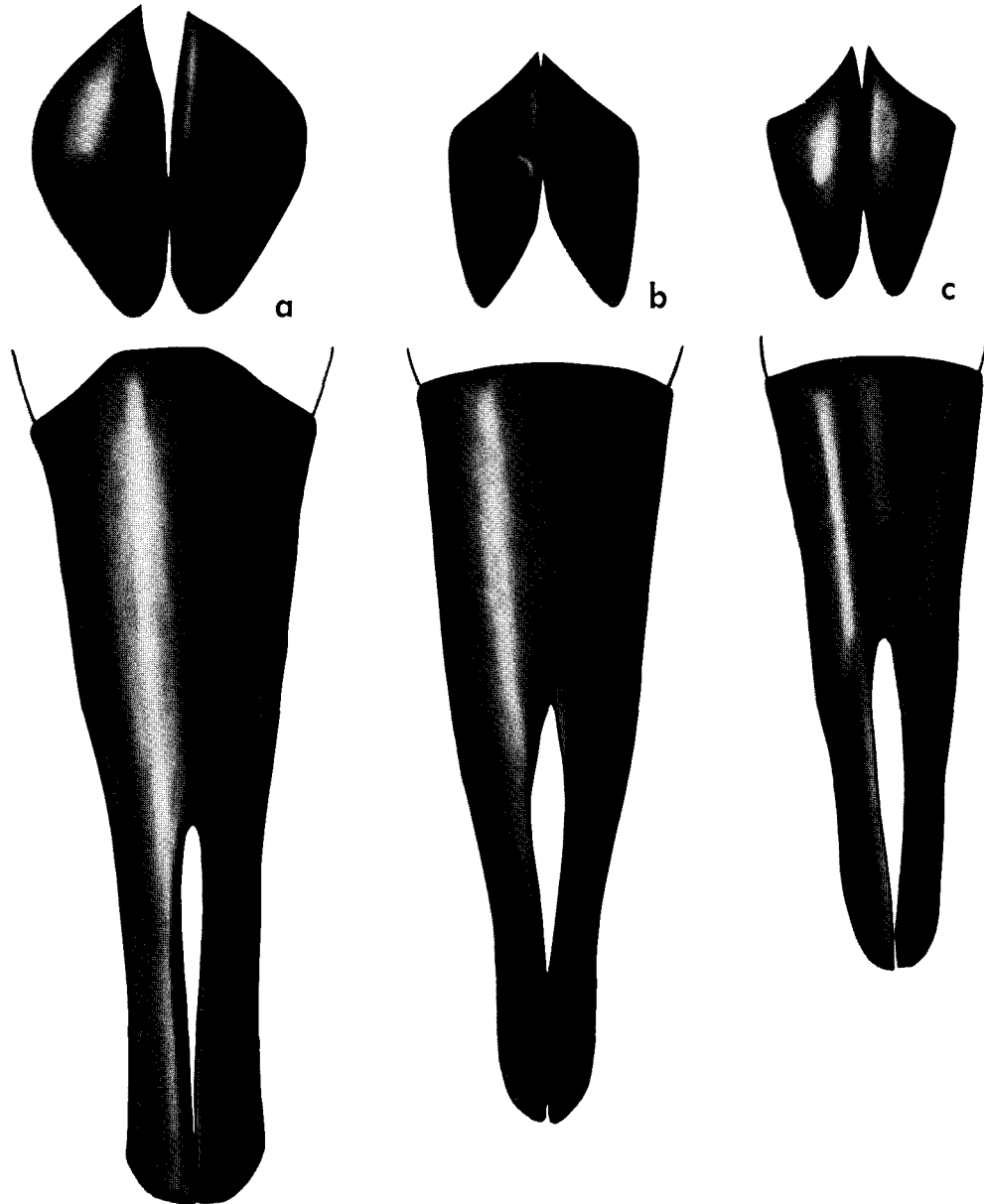


Fig. 6.— Dorsal (lower) and caudal (upper) views of aedeagi of the *decemlineata* complex. (a).—*P. arguta*. (b).—*P. decemlineata*. (c).—*P. monahansensis*, paratype.



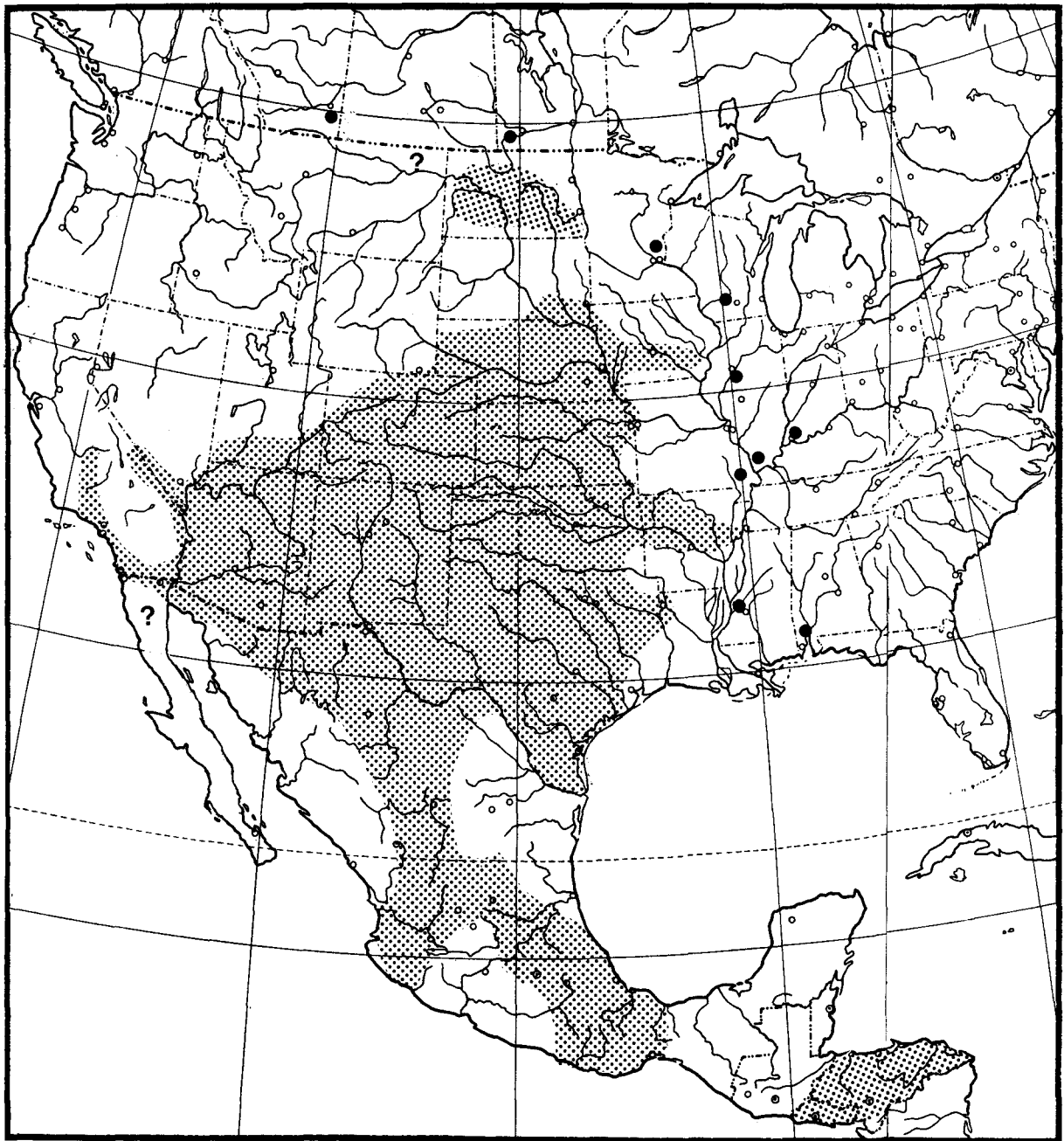


Fig. 7.—Distribution of the *hammondi* complex.

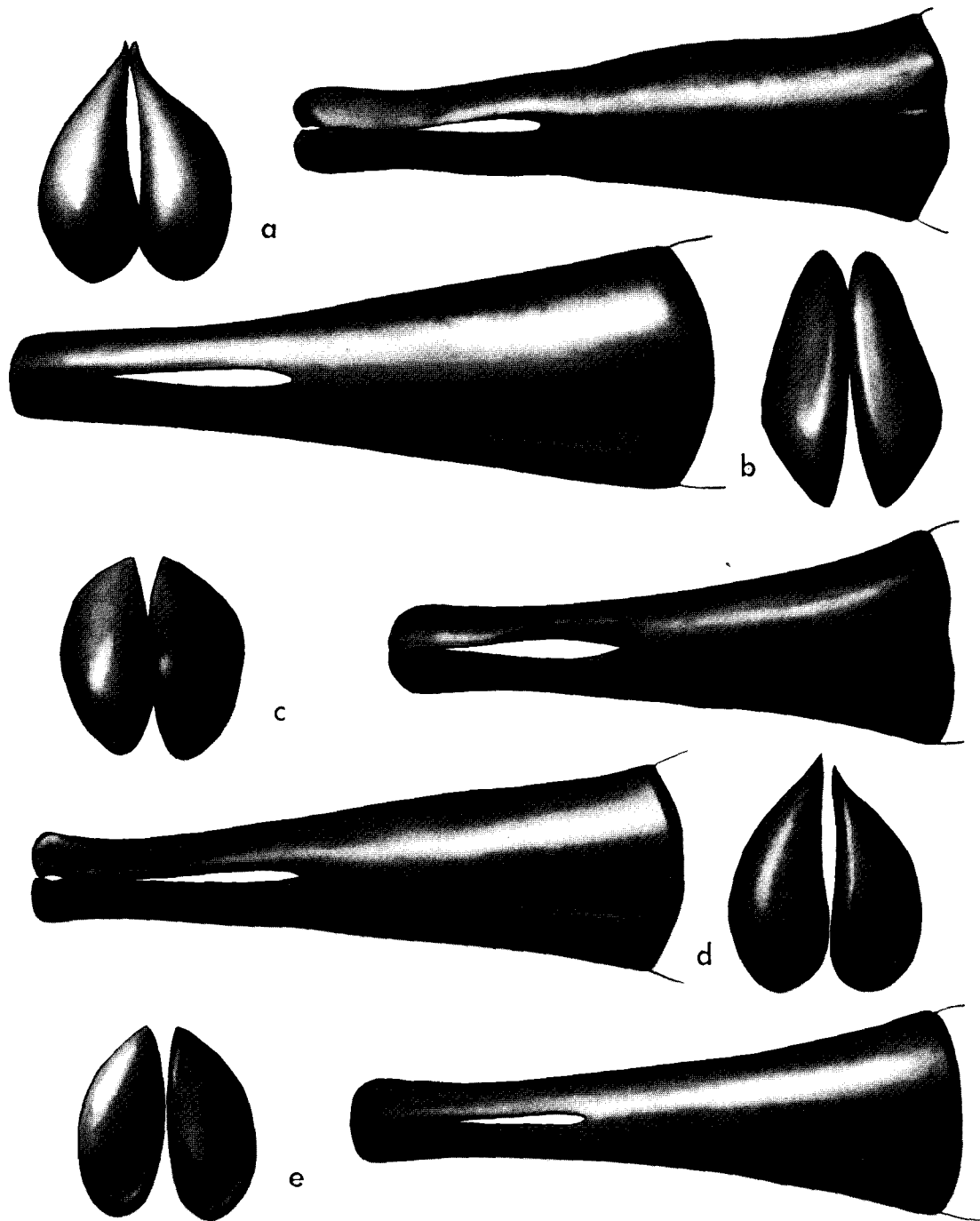


Fig. 8.— Dorsal and caudal views of the aedeagi of the *hammondi* complex. (a).—*P. anteronivea*. (b).—*P. brownae*, paratype. (c).—*P. cavifrons*. (d).—*P. erratica*, paratype. (e).—*P. hammondi*, northern avittate phase.

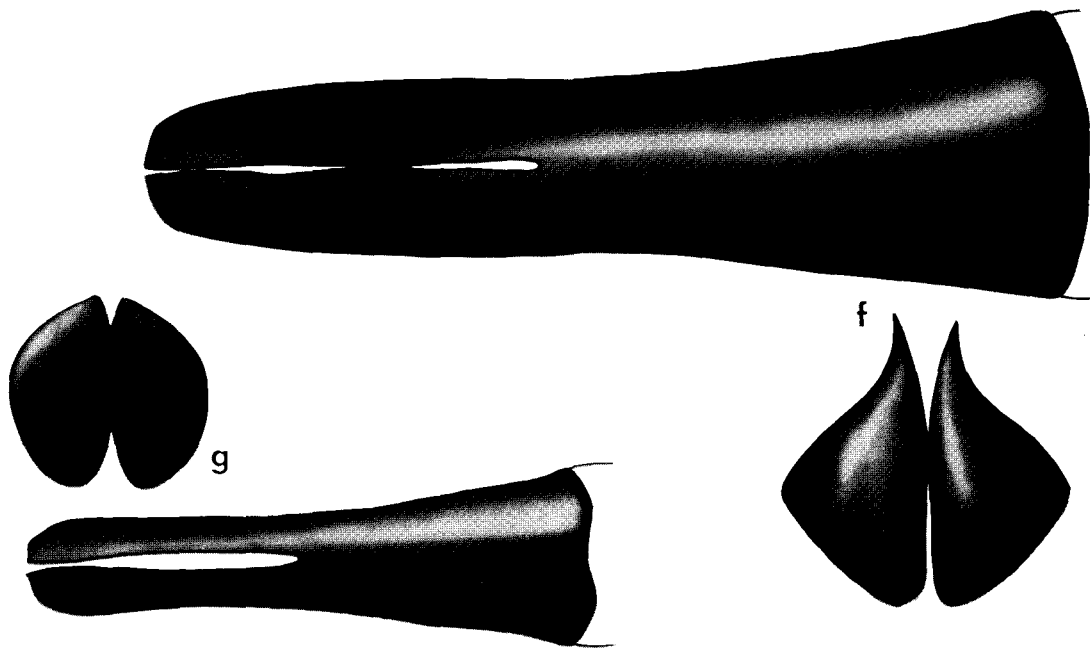


Fig. 8 (cont.).— (f).—*P. hammondi*, southern vittate phase. (g).—*P. squamiventris*.

sided to broadly spatulate and appearing truncated when viewed dorsally (Fig. 8).

Table 1 summarizes the nomenclature discussed above.

#### ACKNOWLEDGEMENTS

This revision could not have been accomplished without the generous cooperation of many institutions and individuals. They are listed here alphabetically by state or province, with my sincere thanks for their cooperation. Standard abbreviations (Arnett and Samuelson, 1969) used later in the text are given after the full name of the institution.

UNITED STATES: Auburn Univ.; Arizona St. Univ.; Univ. Arkansas; California Academy of Sciences (CASC); Los Angeles County Museum (LACM); Univ. California, Berkeley (UCBC); Univ. California, Davis (UCDC); Peabody Museum of Natural History, Yale Univ.; Univ. Connecticut; Univ. Delaware; Univ. Georgia; Univ. Idaho; Field Museum of Natural History

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B.C. Ratcliffe, Curator of Insects at the Univ. of Nebraska State Museum, has been important in bringing this work to completion. Finally, a special thanks to my wife, Nova Brown Young, whose unyielding support over the years made publication possible.

## REVIEW OF LITERATURE

Before *Polyphylla* was established by Harris in 1841, three species names that would be transferred to *Polyphylla* were in the literature, all under *Melolontha* F., 1775. These were *M. decemlineata* Say, 1824; *M. occidentalis* (L.), 1767; and *M. variolosa* Hentz, 1830. *M. variolosa* Hentz was transferred to *Polyphylla* by Harris (1841) when he designated the genus. *P. decemlineata* (Say) is first mentioned by LeConte (1854) and *P. occidentalis* (L.) by LeConte (1856). LeConte (1854) also proposed one new species and added two more in his 1856 paper. LeConte (1863) is the first catalog of *Polyphylla*, listing seven species. In 1873, Crotch proposed the genus *Macranoxia* for the European species of *Polyphylla*. *Polyphylla* sensu Lacordaire, 1856, was placed as its synonym but it was further marked as "cited in error." Under this name Crotch catalogued the same seven species of LeConte's catalog. Austin (1880) cited *Polyphylla* Harris, 1841, as the valid name in his supplement to the Crotch catalog, with *Macranoxia* Crotch, 1873 as its synonym.

Horn (1881) first revised the genus when it included seven species names; one he proposed as new and one he synonymized. These same names were catalogued by Henshaw (1885). Casey (1889, 1891, 1895) and Fall (1908) added five more specific names.

In 1914 Casey treated *Polyphylla* in detail. As a classical typologist he established 34 new names. This is the primary nomenclatural fragmentation of the genus from which it has never recovered. Leng (1920) catalogued these names, listing 32 species and 14 subspecies. Hatch (1926) added one more name and in 1928 Fall's revision appeared. Fifteen valid names were listed with 29 of Casey's names being synonymized. Tanner (1928) and Van Dyke (1933) added three more new names. Kuntzen (1933) tried to apply the *rassenkreis* concept to the genus, which resulted in Blackwelder (1939) cataloguing two *rassenkreis* "species" and 27 "races."

Cazier (1938) added one new name and discussed variability of morphological characters used by past workers. It was a major step in straightening out the nomenclatural confusion in the genus. Cartwright (1939), Cazier (1939), and von Bloeker (1940) established eight more new species.

Cazier's major discussion of the genus appeared in 1940, primarily as a well founded critique of Kuntz-

en (1933). Twenty-three valid names were listed. Brown (1940) treated the four Canadian species and Van Dyke (1943, 1947) added two new specific names and one new subspecific name. Blackwelder and Blackwelder (1948) catalogued 26 specific names and one subspecific name.

Young (1966) named one new species and in 1967 Part I of this revision was published, in which nine valid specific names were retained in the *diffRACTA* complex. A tenth name was placed as a *nomen dubium*; it is herein synonymized. Seven new synonyms were established in my 1967 paper. Hatch (1971) added one new species (see below) and in 1972 I first recorded the genus from Wisconsin and discussed the zoogeographical implications of that record. Arnett and Blackwelder (1974) catalogued 33 species and one subspecies in North and Central America, Mexico and the West Indies.

In 1971 Hatch named *P. dubia* as a new species. The holotype female (USNM) is labelled (1) Seattle, Wash., (2) Type female, *Polyphylla bidentata*, 1928-M. Hatch, (3) *Polyphylla concurens* Csy., Wm. Hazeltine-1953, mid-Mex. to Colombia, (4) Type female, *Polyphylla dubia*, 1962-M. Hatch, and (5) protib. 2-dentate in *concurrrens* Csy. type, M. Hatch-1968. Considering Hazeltine's determination of *P. concurrrens* Casey (incorrectly spelled *concurens* on his label), Hatch suggested that this specimen was adventitious to Seattle. My conclusions are:

1. This specimen does not represent wild populations that occur in America north of Mexico. It is either falsely labelled or represents an introduced individual.

2. *P. bidentata* is an unpublished name and nothing written here is intended to change that. It is a name without status.

3. *P. dubia* Hatch 1971 represents a specimen of the common Central American species *P. petiti* Gaer. 1830, and it is here synonymized.

4. *P. concurrrens* Casey, 1889 is probably also a synonym of *P. petiti* but no final decision is reached here as the Central American material on hand is insufficient.

Hardy (1974) revised *Thyce* LeConte and related genera. In this work he removed the floridian species *P. pubescens* Cartwright, 1939, from *Polyphylla* and established the monotypic new genus *Polylamina*. I concur with this action, as *P. pubescens* is very aberrant from the range of characters expressed within *Polyphylla*. It seems to form a "bridge" between *Po-*

*lyphylla*, *Hypothyce* Howden and allied genera; placing it as a distinct genus is, I believe, a clear way to express that position. In 1978 Hardy and Andrews discovered five new species from western sand dune refugia (see also Young, 1966, 1972) and Hardy's 1981 paper considers the five species of Baja California, one of which is new. Young (1986) named three new species from Alabama, California and Utah.

This monograph recognizes 28 species as valid in America North of Mexico and no subspecies. One new species is recognized and one subspecies is raised from synonymy and given specific rank. Fourteen new junior synonyms are designated (Table 1).

## SURVEY OF MORPHOLOGICAL CHARACTERS

For over 160 years coleopterists have struggled to identify stable species level characters in this genus. The earliest, used by Say (1824), Hentz (1830), and LeConte (1854, 1856) included the degree of clypeal emargination, clypeal concavity, and basal narrowing of the clypeus. Presence or absence of humeral vittae, protibial dentition (an especially persistent invalid character), and size of pronotal and elytral squamae were also considered significant.

The first key to the North American species (Horn, 1881) was based primarily on protibial dentition and elytral vestiture. Protibial dentition was introduced by LeConte (1854) in his original description of *P. cavifrons*.

In his 1889 and 1891 papers Casey continued to use the pattern of elytral vestiture as introduced by Horn (1881). Casey also considered configuration of the terminal joint of the maxillary palpi, ratio of male antennal club length to stem length, and pygidial vestiture as significant characters. The couplet based on protibiae tridentate in both sexes versus protibiae bidentate in males and tridentate in females was the first one in Casey's 1914 key, as originated (in key form) by Horn (1881). This character persists (see Hardy, 1981) primarily because it may sometimes work if the geographic sample is small enough or if only a few species are being considered. On a broader basis, however, this character is rejected due to its extreme intraspecific and geographic variability. Much of the rest of Casey's 1914 key is a description of individual variants (all named) and is essentially unusable.

After the appearance of Casey's 1914 paper a con-

**Table 1.** Nomenclature of *Polyphylla* in America North of Mexico. Listed are (1) the full name of each species, (2) deposition of the name-bearing type and (3) when applicable, author and year first synonymized.

*Polyphylla* Harris 1841 (not 1842 of various authors)

*Macranoxia* Crotch 1873

SPECIES EXCLUSIVELY EAST OF THE MISSISSIPPI RIVER

- A. The *occidentalis* complex
1. *comes* Casey 1914. USNM.
  2. *gracilis* Horn 1881. ANSP.
  3. *occidentalis* (L.) 1767. USNM.
  4. *variolosa* (Hentz) 1830. USNM. Type species of the genus.

SPECIES PRIMARILY WEST OF THE MISSISSIPPI RIVER

- B. The *decemlineata* complex
- 5(1) *arguta* Casey 1914. USNM.
  - 6(2) *decemlineata* (Say) 1824. U. Nebraska State Museum.  
*comstockiana* von Bloeker 1939. LACM. New synonymy.  
*decemlineata laticauda* Casey 1914. USNM. Fall 1928.  
*decemlineata parilis* Casey 1914. USNM. Fall 1928.  
*decemlineata reducta* Casey 1914. USNM. Fall 1928.  
*matrona* Casey 1914. USNM. New synonymy.  
*potsiana* Casey 1914. USNM. New synonymy.  
*ruficollis* Casey 1914. USNM. Fall 1928.  
*ruficollis castanea* Casey 1914. USNM. Fall 1928.  
*ruficollis oregona* Casey 1914. USNM. Fall 1928.  
*squamotecta* Casey 1914. USNM. Fall 1928.
  - 7(3) *monahansensis* Hardy and Andrews 1978. CASC.
- C. The *diffracta* complex
- 8(1) *avittata* Hardy and Andrews 1978. CASC.
  - 9(2) *barbata* Cazier 1938. AMNH.
  - 10(3) *crinita* LeConte 1856. MCZC.  
*crinita mystica* Casey 1914. USNM. Fall 1928.  
*incolumis* Casey 1914. USNM. Fall 1928.  
*ona* von Bloeker 1939. LACM. Cazier 1940.  
*pacifica* Casey 1895. USNM. New synonymy.  
*ruficollis perversa* Casey 1914. USNM. New synonymy.  
*santarosae* von Bloeker 1939. LACM. Cazier 1940.
  - 11(4) *devestiva* Young 1966. USNM.
  - 12(5) *diffracta* Casey 1891. USNM.  
*adusta* Casey 1914. USNM. Fall 1928.  
*alleni* Cazier 1939. AMNH. New synonymy.  
*diffracta arida* Van Dyke 1947. CASC. Young 1967.  
*fuscula* Fall 1908. MCZC. Fall 1928.  
*laevicauda* Casey 1914. USNM. Young 1967.  
*opposita* Casey 1914. USNM. Young 1967.  
*uteana* Tanner 1928. BYUC. Young 1967.
  - 13(6) *hirsuta* Van Dyke 1933. CASC.
  - 14(7) *mescalarensis* new species. CASC.
  - 15(8) *modulata* Casey 1914. USNM.  
*decemlineata modulata* sensu Cazier 1939.
  - 16(9) *nigra* Casey 1914. USNM. Resurrected name, raised to species status.  
*incolumis relicta* Casey 1914. USNM. New synonymy.

**Table 1.** Nomenclature of *Polyphylla* in America North of Mexico. Listed are (1) the full name of each species, (2) deposition of the name-bearing type and (3) when applicable, author and year first synonymized (*cont'd.*).

- incolumis robustula* Casey 1914. USNM. New synonymy.  
*martini* von Bloeker 1939. LACM. New synonymy.  
*santacruzae* von Bloeker 1939. LACM. New synonymy.
- 17(10) *nubila* Van Dyke 1947. CASC.  
 18(11) *pottorum* Hardy and Andrews 1978. CASC.  
 19(12) *ratcliffei* Young 1986. CASC.  
 20(13) *rugosipennis* Casey 1914. USNM.  
       *peninsularis* Van Dyke. CASC. Young 1967.  
 21(14) *sobrina* Casey 1914. USNM.  
 22(15) *stellata* Young 1986. UCDC.
- D. The *hammondi* complex
- 23(1) *anteronivea* Hardy and Andrews 1978. CASC.  
 24(2) *brownae* Young 1986. ANSP.  
 25(3) *cavifrons* LeConte 1854. MCZC.  
 26(4) *erratica* Hardy and Andrews 1978. CASC.  
 27(5) *hammondi* LeConte 1856. MCZC.  
       *diffusa* Casey 1914. USNM. Fall 1928.  
       *latifrons* Casey 1914. USNM. New synonymy.  
       *oblita* Casey 1914. USNM. Fall 1928.  
       *oblita impigra* Casey 1914. USNM. Fall 1928.  
       *oklahomensis* Hatch 1926. Type lost. Fall 1928.  
       *pimalis* Casey 1914. USNM. Fall 1928.  
       *proba* Casey 1914. USNM. Fall 1928.  
       *rufescenta* Tanner 1928. BYUC. New synonymy.  
       *sejuncta* Casey 1914. USNM. Fall 1928.  
       *speciosa* Casey 1889. USNM. New synonymy.  
       *speciosa acomana* Casey 1914. USNM. New synonymy.  
       *squamicauda* Casey 1914. USNM. Fall 1928.  
       *squamicauda molesta* 1914. USNM. Fall 1928.  
       *subvittata* LeConte 1856. Type lost. Fall 1928.  
       *subvittata bisinuata* Casey 1914. USNM. Fall 1928.  
       *verecunda* Casey 1914. USNM. Fall 1928.
- 28(6) *squamiventris* Cazier 1939. AMNH.

NOMEN NUDUM - *marginata* Casey 1885.

trovsky arose over the seemingly superficial nature of the characters being used to separate species and species groups. At the May 6, 1919 meeting of the New York Entomological Society, Mutchler presented his study of male genitalic characters from about 50 specimens. His hope was that "differences in genitalia would support the rather feeble characters by which the species described since LeConte's time are differentiated. Thus far the result was not favorable to the retention of many names."

Fall (1928) brought together the literature on *Polyphylla*, with an especially critical eye on Casey's

work and his choice of key characters. Considering Mutchler's genitalic dissections as well as his own, Fall stated that the male copulatory sheath in the *P. decemlineata* and *P. crinita* groups was so similar as to be scarcely distinguishable except for very minor differences.

Species included in this work were *P. cavifrons*, *P. crinita*, *P. hammondi*, *P. variolosa*, and *P. occidentalis*. Besides the genitalic characters, Fall rejected use of the male antennal club length:stem length ratio and the size of squamae characters because they were "known to be unstable within specific limits." He

continued to use the characters of protibial dentition, nature of elytral vittae, and humeral vittae. Primary new characters introduced in Fall's key were ratio of male antennal club length to head length, presence or absence of pronotal hairs, basal elytral color, depth of cleft in the aedeagus and its configuration, and head with or without erect hairs.

Tanner (1928) emphasized the character of protibial dentition. In 1933 Van Dyke named *P. hirsuta* based primarily on its lack of vittae and unicolorous appearance.

Cazier (1938) included a critical look at the characters used by Casey and Fall. In his original description of *P. barbata*, Cazier used the unusually long, erect elytral hairs as a specific character. He rejected use of protibial dentition, presence or absence of erect hairs on the pronotal disc, size of squamae, and nature of humeral vittae; all because they were subject to broad variation within a given sample of a single-species population. He also warned that the nature of the elytral vittae should be used with caution.

During 1939 and 1940, Cartwright and Von Bloeker named new species. New characters used by the latter author included the humeral vittae joining with the next inner vittae to form a Y-shaped pattern (*P. martini*), and an unusually dense, snow white mat of pronotal and elytral scales in *P. comstockiana*. Brown (1940), in his treatment of the Canadian species, introduced use of interstitial scale color and the difference between pronotal and elytral basal color.

Hardy and Andrews (1978), and Hardy (1981) used protibial dentition and various combinations of prothoracic and elytral vestiture to separate species. As stated earlier, protibial dentition works only if the sample is small enough. Characters relating to vestiture of various body parts do, on the other hand, stand up quite well in large samples.

Table 2 summarizes the array of characters considered for use as key characters. Most were rejected. A character or character state was rejected for use on the species level for any of the following four reasons.

1. Subject to broad individual variations within a deme. Protibial dentition falls into this category. States for this character vary from edentate to weakly tridentate in a given geographic sample of a single species. This same intraspecific variability caused most clypeal and mouthpart characters to be rejected, as well as several characters relating to bodily vestiture and coloration.

2. Showing a lack of variation between samples; that is, characters which are so broadly shared as to be unusable. Since Mutchler's genitalic dissections in 1919, we have known that most (not all) aedeagal characters may be rejected on this basis. Mutchler (1919), Fall (1928) and Cazier (1938) all demonstrated this point. During this work I have extracted ca. 700 aedeagi, plus examined the hundreds dissected by Hazeltine (unpublished). Rarely I find the length of aedeagal cleft holding true on a specific level, and *P. ratcliffei* was established on unique aedeagal characters; other than those few cases the aedeagi are not productive on the specific level.

Concerning the character of overall aedeagal configuration, what was suspected by Fall (1928) has proven true. The four species complexes originally proposed by Casey and profitably used by many workers since then, are best separated by this character. Whenever the placement of a species within this framework is in doubt, an examination of the aedeagus will suffice to indicate its proper position. This is especially reinforced by the discovery of five new species by Hardy and Andrews (1978) and four by Young (1986 and this monograph); they all are easily placed within one of the four species complexes by aedeagal configuration while certain external characters are misleading.

3. Subject to sexual dimorphism. Clypeal concavity, shape of the epistomal suture, excavation of the terminal segment of the maxillary palpi, and most antennal characters, were all rejected on this basis.

4. Impracticality. This is a difficult area as one does not wish to use practical unstable characters or impractical stable ones. In *Polyphylla* most ventral external characters are so covered with dense hairs that one must partially or wholly destroy the specimen to see them. The subapical ridge on the procoxae is a case in point, as the configuration of this ridge seems to show significant differences between the *P. hammondi* and *P. decemlineata* samples checked. A more striking example is the shape of the median longitudinal depression on the bulbous, grossly over-developed metatergum; a character which readily separates several of the common western species. Nonetheless, these characters have been rejected because they are so impractical.

This monograph presents two keys for adult *Polyphylla*, one excluding and one including aedeagal characters. Carefully used, the exclusive key should produce a correct identification. For the occasional



**Table 2.** Survey of Morphological Structures Considered for use as Key Characters.

Character	Author or New	Accepted on species level as stable	Rejected on species level, unstable	Accepted on species group level
1. Emargination of clypeus	Hentz, 1830		X	
2. Concavity of clypeus	LeConte, 1854		X	
3. Lateral margins of clypeus parallel or narrowing basally	LeConte, 1854	X		
4. W. or w/o erect hairs on clypeal disc	New		X	
5. Epistomal suture straight or curved	New		X	
6. Shape and degree of central cleft in labrum	New		X	
7. Mandibular dentition	New		X	
8. Vestiture on exterior surface of mandibles	New		X	
9. Configuration of terminal segment of maxillary palpi	Casey, 1889	X		
10. W. or w/o excavation on terminal segment of maxillary palpi	New		X	
11. Configuration and/or length of eye canthus	New		X	
12. W. or w/o erect hairs on head	Fall, 1928		X	
13. Length of male antennal club:length of head ratio	Fall, 1928		X	
14. Overall length of male antennal club	New	with caution		
15. Degree of recurve in male antennal club	New	with caution		
16. W. or w/o erect hairs on male antennal club	New	X		
17. Length of male antennal club:length of stem ratio	Casey, 1891		X	
18. Size of pronotal squamae	LeConte, 1856		X	
19. W. or w/o erect hairs on pronotal disc	Fall, 1928	X		X
20. Nature of depression on pronotum	New		X	
21. Nature of clefts on lateral margins of pronotum	New		X	
22. W. or w/o pronotal squamae	New	X		
23. Nature of pronotal punctures	Many authors		X	
24. Depth and shape of procoxal intrusion into pronotal margin	New		X	
25. Shape of subapical ridge on procoxae	New		X	
26. Protibial dentition	Many authors	Used once as accessory charac.		
27. Dentition of pretarsal claws (as used in <i>Phyllophaga</i> )	New		X	
28. Number of meso- and metatibial spines	New		X	
29. Configuration of metatrochanter	New		X	
30. Length of metatrochanter: length of metafemur ratio	New		X	

**Table 2.** Survey of Morphological Structures Considered for use as Key Characters (*cont'd.*)

Character	Author or New	Accepted on species level as stable	Rejected on species level, unstable	Accepted on species group level
31. Size and depth of pit between metacoxae	New		X	
32. Shape and length of phlanges between metacoxae	New		X	
33. Configuration of metathoracic epimera	New		Sutures hidden	
34. Configuration of median depression of metatergum	New		Not visible	
35. Veination of metathoracic wings	Hazeltine, unpubl.		X	
36. Size of elytral squamae	LeConte, 1856		X	
37. W. or w/o erect hairs on elytra	Horn, 1881	X		
38. W. or w/o elytral squamae	Horn, 1881	X		
39. W. or w/o formed elytral vittae	Horn, 1881	X		
40. W. or w/o disjunct clump of squamae posterior to elytral vittae	von Bloeker, 1940		X	
41. W. or w/o Y-shaped pattern formed by elytral vittae	von Bloeker, 1940		X	
42. W. or w/o humeral vittae	LeConte, 1854		X	
43. W. or w/o humeral vittae disconnectedly continued posteriorly	Fall, 1928		X	
44. W. or w/o naked area on each side of elytral vittae	New	In one case		
45. Basal elytral color:vittae color:interstitial scale color	New	With caution		
46. Basal elytral color:basal pronotal color	Brown, 1940		X	
47. Vestiture of abdominal segments ventrally	New		X	
48. W. or w/o pygidial hairs	Casey, 1891	X		
49. Configuration of aedeagus	Fall, 1928			X
50. Length of aedeagal split	Fall, 1928	Rarely		X
51. Overall length	Brown, 1940	Rarely		
52. Overall width	Brown, 1940	Rarely		

problem specimen and for the highest degree of confidence in the results, the user is referred to the key which includes aedeagal characters to define species complexes. Figures 3, 5, 6 and 8 illustrate the aedeagi of all species.

### **POLYPHYLLA Harris**

*Polyphylla* Harris 1841: 30; Burmeister 1844: 403; Erichson 1847: 658; Lacordaire 1856: 294; LeConte 1854: 222; LeConte 1856: 228; LeConte 1863: 39; Marseul 1866: 56; Scudder 1869: 362; Crotch 1873: 61; LeBaron 1874: 86; Austin 1880: 26; Horn 1881: 73; D'Herculeis 1882: 204; Casey 1885: 283; Henshaw 1885: 92; Bates 1888: 214; Casey 1889: 168; Casey 1891: 17; Casey 1895: 607; Henshaw 1895: 23; Fall 1908: 161; Dalla Torre 1912: 256; Casey 1914: 306; Leng 1920: 257; Dawson 1922: 118; Essig 1926: 443; Hatch 1926: 145; Fall 1928: 30; Hayes and McCulloch 1928: 249; Tanner 1928: 276; Kuntzen 1933: 458; Leng and Mutchler 1933: 39; Van Dyke 1933: 116; Brimley 1938: 204; Cazier 1938: 161; Blackwelder 1939: 53; Cartwright 1939: 362; Cazier 1939: 199; Von Bloeker 1939: 148; Brown 1940: 185; Cazier 1940: 134; Heit and Henry 1940: 944; Downes and Anderson 1941: 5; Boving 1942: 175; Essig 1942: 579; Pratt 1943: 69; Van Dyke 1943: 103; Blackwelder 1944: 227; Van Dyke 1947: 160; Blackwelder and Blackwelder 1948: 33; Ritcher 1949: 19; Keen 1952: 28; Johnson 1954: 717; Landin 1956: 12; Ritcher 1958: 311; Arnett 1962: 404; Onsager 1966: 480; Ritcher 1966: 84; Young 1966: 233; Young 1967: 279; Howden 1968: 545; Kirk 1969: 40; Ritcher 1969: 872; Erwin 1970: 52; Hatch 1971: 475; Lilly and Shorthouse 1971: 1757; Baker 1972: 148; Stein and Kennedy 1972: 18; Young 1972: 31; Blackwelder and Arnett 1974: R30.68; Hardy 1974: 5; Hardy and Andrews 1978: 1; Lago 1979: 63; Fowler and Whitford 1981: 215; Hardy 1981: 299; Young 1986: 47.

*Macranoxia* Crotch 1873: 61.

**GENERIC NOMENCLATURE**—The generic names *Scarabaeus* Linn., 1758; *Melolontha* F., 1775; and *Polyphylla* Harris, 1841, must be considered in establishing a type species for *Polyphylla*. These generic names are connected because the name *melolontha* Linn., 1758, was originally described under the genus *Scarabaeus* Linn., 1758, but was also in-

cluded in the original descriptions of the other two genera. Conclusions are as follows.

Crotch (1870) recorded that MacLeay (1819) retained *S. sacer* Linn., 1758, as the type species of *Scarabaeus* Linn., 1758. The original citation of this has not been located in the literature; nonetheless, *S. sacer* Linn., 1758, is valid by means of subsequent designation (Art. 69a of the Code). *S. melolontha* Linn., 1758, is therefore released for any subsequent type species designations.

Latreille (1810) listed only *M. vulgaris* Fab., 1775, under *Melolontha* Fab. 1775. By subsequent ruling (Opinion nos. 11 and 136) this may become a valid type species designation. Westwood (1838) also cited this species as the type of *Melolontha* Fab., 1775. Furthermore *M. vulgaris* Fab., 1775, is figured as the type species by Blanchard (1844). Duponchel (1840) cites *Scarabaeus melolontha* Linn., 1758, as the type species of *Melolontha* Fab., 1775, but Latreille's designation remains the first citing of an available name. All of this, however, is superseded by Article 68e of the Code. When *S. melolontha* Linn., 1758, was moved to *Melolontha* Fab., 1775, becoming thereby *Melolontha melolontha* (Linn.), 1758, it became *ipso facto* the type species of the genus by absolute tautonymy. That it was first placed as a synonym is irrelevant.

There has been considerable confusion with regard to the name *Polyphylla* Harris, 1841, primarily because of the unclear writing of Harris when he proposed the name. He seemed to be creating it as a replacement for *Melolontha* Fab., 1775. If that were true, some individuals consulted feel *Polyphylla* Harris, 1841, becomes a synonym of *Melolontha* Fab., 1775. In addition, *Macranoxia* Crotch, 1873, becomes the valid name of the genus. In the final analysis, however, it does not matter what Harris said or intended as long as the new generic name had an originally included species and a type species different from that of *Melolontha* Fab., 1775.

There have been two type species designations in the history of *Polyphylla* Harris, 1841, both incorrect. Lacordaire (1856) cited *S. fullo* Linn., 1758, (at the time placed under *Melolontha* Fab., 1775) as the type species of the genus, but this name was not available as it was not included at time of original description of *Polyphylla* Harris, 1841. Hardy's 1974 citation of this species is likewise incorrect. I made the same mistake in 1967 in citing *P. cavifrons* LeConte, 1854, as the type species. Obviously, both of these des-

ignations are invalid. The only originally included names are *M. variolosa* Hentz, 1839, and *S. melolontha* Linn., 1758. Harris must have been unaware of the status of the latter species, as its positioning under *Melolontha* Fab., 1775, was finally clear as outlined above.

In summary the type species of *Scarabaeus* Linn., 1758, is *S. sacer* Linn., 1758 by subsequent designation. The type species of *Melolontha* Fab. 1775, is *S. melolontha* L., 1758, by absolute tautonomy. *M. variolosa* Hentz, 1830, is the type species of *Polyphylla* Harris, 1841, here designated.

**DIAGNOSIS**—Scarabaeidae: Melolonthinae: Melolonthini. *Polyphylla* clusters with the genera *Polylamina*, *Hypothyce*, *Plectrodes*, *Parathyce*, *Thyce*, *Dinacoma* and *Hypotrichia*. It is distinguished from all of them except *Polylamina* by the antennal club which is five segmented in the female and seven segmented in the male. Most similar to *Polylamina* from which it may be distinguished by the unpigmented flight wings, presence of scales on the body (in some species) and the lack of enlargement in the male metafemora.

**DESCRIPTION**—Adults of the North American species are robust, elongate beetles 15 to 45 mm in length and 7.7 to 18.3 mm in width. The antennal club is outwardly recurved, 7 segmented and 4–10 mm (1.5–2.5 times the length of the basal segments) long in the male or straight, 5 segmented and short (ca. 2 mm) in the female. General vestiture of the body is composed of scales and/or hairs. The larvae are generalized grass root feeders and have been recorded on a variety of domestic crops (see biology of *P. decemlineata*, *P. diffracta*, *P. comes*, *P. crinita*, and *P. hammondi*). Of the 28 North American species, the immature stages of 23 are unknown. Adult females are unknown for 12 species.

**HEAD:** Basal color black; eyes large and protuberant; surface generally punctate and/or rugose, each puncture bearing a scale or hair centrally, disc sometimes heavily plumose, vestiture becoming more concentrated laterally and along epistomal suture; clypeus shallowly to deeply concave, anterior edge sometimes perpendicular to disc, straight or centrally cleft, lateral edges straight or narrowing posteriorly; disc punctate in varying degrees, punctures usually bearing horizontal or subvertical scales (squamae), fine hairs sometimes randomly interspersed be-

tween scales, smaller squamae concentrated anteriorly and laterally; eye canthus bisecting one-third to two-thirds of eye width, squamose, with erect hairs intermixed; antennae ten-segmented, lamellate club recurved outwardly, composed of seven fully developed segments (males); maxillary palpi four-segmented, bearing minute hairs, terminal segment 1.5–2 times as long as penultimate one, sometimes bearing a dorsal concavity; labial palpi three-segmented, much smaller, terminal segment cone-shaped and pointed distally.

**THORAX:** Pronotum much wider than long, slightly to abruptly convex, widest point usually at mid-length with lateral edges narrowing both posteriorly and anteriorly, bearing irregular random indentations of varying degrees; posterior and anterior margins bearing a solid mat of depressed hairs, midline shallowly to deeply depressed, bearing a broken to well-defined vitta, lateral vittae not so well-formed, most often broken on depressed anterior one-third, surface generally punctate, especially so on disc, interstitial vestiture composed of broad horizontal squamae which become smaller and more concentrated laterally or fine erect hairs which become more concentrated centrally, disc sometimes heavily setaceous; ventral edges barely to solidly squamose, sometimes bearing dense suberect hairs as well; pro- and mesosternum squamose in varying degrees or heavily setaceous, mesosternum bearing a longitudinal median suture sometimes deeply depressed, metasternum always covered with a solid mat of similar hairs, an abrupt pit with two posteriorly directed phalanges between metacoxae.

**LEGS:** Femora broadly flattened, robust, randomly squamose and hairy; protibiae outwardly edentate to strongly tridentate, rarely robust and heavy, bearing a single large spine on proximal edge, surface barely to moderately punctate, lateral edges with irregularly scattered spinose hairs; meso- and metatibiae slender, slightly broadened and bearing two major spines distally, surfaces squamose outwardly, with hairs on inner edge; tarsal formula 5–5–5, claws long and acute, bearing subapical tooth medially, bisetose onychium between claws.

**ELYTRA:** Basal color yellowish-brown to black, often darker on humeral umbones, lighter laterally, surface irregularly punctate and/or rugose under vestiture; most common vestiture composed of four major stripes (vittae) on each elytron plus one short vitta arising on the humeral umbone, varying from

absent to sharply delineated, or erect hairs in normally vittate areas, interstitial areas bearing a scattering of squamae of varying densities and/or randomly scattered erect hairs, vestiture sometimes totally absent.

**ABDOMEN:** Basal color yellowish-brown to black, becoming lighter on penultimate and terminal segments and laterally on all segments; six sterna visible, first one somewhat hidden under metatrochanter and femora, also sharply raised between metacoxae; segments connate and immobile, vestiture composed of minute squamae of varying densities or erect hairs, squamae more concentrated on posterior two-thirds of each segment, last sternum with a terminal tuft of hairs.

**AEDEAGUS:** Showing little or no variation between species; entire structure rigid and heavily sclerotized; basal plate smooth and abruptly U-shaped in cross section; two lateral parameres movably joined to basal plate, parameres themselves centrally fused for one- to three-fourths of their length, with or without dorsal ridge on distal tip when viewed laterally, in dorsal aspect narrow and parallel-sided to broadly based and narrowing distally, distal tip in dorsal aspect pointed, truncate, or abruptly broadened, all of these characters dependent upon species complexes; sternal sclerite of ninth segment reduced to a V-shaped bar, attached ventral apodeme resulting in a Y-shaped structure naturally lying between the parameres.

**FEMALE:** Unknown in 12 of the 28 North American species, rarely collected in many others; genitalia not studied; primary sexual dimorphism in larger body size, reduced clypeus, and 5-segmented antennal club; body generally broader, more robust; clypeus not so well developed, tending towards a more greatly reduced, flatter structure than in the male, edges sometimes gently reflexed; antennae ten-segmented, small lamellate club composed of five fully developed segments, next proximal segment slightly lengthened alongside club; protibiae edentate to tridentate, often broad, robust, and tridentate, meso- and meta-tibiae abruptly broadened distally, usually bearing two lateral teeth somewhere along length; similar to males in other features.

**THIRD-INSTAR LARVA:** Undescribed in 24 species. Larvae of *Polyphylla* may be distinguished by the following characters (from Ritcher 1966).

Head without eye spots. Frons with transverse row

of 3 or 4 posterior frontal setae on each side. Labrum symmetrical. Epipharynx without epizygum; zygum indistinct. Haptomerum with a group of 15 or more heli. Plegmatia present; plegmata short. Proplegmatia present or absent. Dexiophoba extending along much or all of the right side of the pedium. Haptolachus with or without microsensilla. Maxilla with a row of 14 or more fairly long, conical stridulatory teeth. Lacinia with a longitudinal row of 3 stout unci.

Anal slit transverse, more or less angular. Ventral anal lobe not cleft. Raster with 2 short, longitudinal, parallel palidia. Preseptular hamatae setae numerous. Claws of prothoracic and mesothoracic legs long and falcate, those of mesothoracic leg slightly smaller. Claws of methathoracic legs minute.

### KEY TO LARVAE

(Modified from Ritcher 1966)

1. Proplegmatia present, well developed. Raster with tegilla extending in front of palidia for a distance equal to one half the length of the palidia ..... *P. occidentalis* (L.)  
Proplegmatia absent or inconspicuous. Raster with tegilla extending in front of palidia for a distance equal to the length of the palidia... .. 2
2. Haptolachus of epipharynx with crepidal punctures (microsensilla) .... *P. variolosa* (Hentz)  
Haptolachus of epipharynx without crepidal punctures (microsensilla)..... 3
3. Maximum width of head capsule 7.8 mm or greater ..... *P. decemlineata* (Say)  
Maximum width of head capsule less than 6.8 mm ..... *modulata* Casey

**SPECIMENS EXAMINED**—For the species in America north of Mexico, 14,094. In addition to this material, specimens from the Federal District of Mexico and the following Mexican states are on hand (detailed localities given under each species): Baja California Norte, Baja California Sur, Chihuahua, Durango, Guadalajara, Morelos, Oaxaca, Puebla, San Louis Potosi, and Veracruz. Three males and one female have been seen from Rabinal, Guatemala and the southern-most New World record seen is Honduras: Valle de Angeles, 3.2 mi. SW, Francisco Morazan. An additional 170 specimens were exam-

ined at the British Museum (Natural History), all representing Old World species.

All measurements in the keys below were taken in a straight line.

**KEY TO THE SPECIES OF *POLYPHYLLA* IN AMERICA NORTH OF MEXICO, ADULTS, AEDEAGAL CHARACTERS PRIMARILY EXCLUDED**

- Elytral vittae, excluding sutural one, distinct, continuous, whether smooth or rough-edged ..... 2
- Elytral vittae, excluding sutural one, broken, often reduced to discontinuous clumps of scales ..... 12
- Elytral vittae, excluding sutural one, absent ..... 23
- 2(1). Southern Mississippi, Florida, to southern tip of Virginia (Fig. 9) .....  
..... *occidentalis* (L.) (p. 33)
- Not distributed as above ..... 3
- 3(2'). Pronotum setigerous somewhere, excluding edges ..... 4
- Pronotum not setigerous, excluding edges ..... 10
- 4(3). Ward Co. Texas (Monahans Sandhills State Park) and Chihuahua, Mexico (Fig. 20) .....  
..... *monahansensis* Hardy and Andrews (p. 51)
- Not distributed as above ..... 5
- 5(4'). Elytral vittae rough-edged ..... 6
- Elytral vittae more distinct, hard-edged ..... 7
- 6(5). Elytra with long erect hairs, excluding suture; yellow interstitial scales meeting vitta without naked area in between (Fig. 28) .....  
..... *rugosipennis* Casey (p. 72)
- Elytra without long erect hairs, excluding suture; white (or rarely yellow) interstitial scales not meeting vitta, area between naked (Fig. 24) .....  
..... *diffracta* Casey (vittate phase, p. 60)
- 7(5'). Basal color of elytra distinct yellowish-brown, primarily Lake Tahoe south to include Yosemite National Park (Fig. 25) .....  
..... *sobrina* Casey (p. 73)
- Basal color of elytra black, primarily north, south or west of above referenced area ..... 8
- 8(7'). Overall length not exceeding 25 mm., primarily Oregon and Washington, especially Sisters, Oregon (Fig. 25) .....  
..... *modulata* Casey (p. 65)
- Overall length exceeding 25 mm., or if less, then only from southern California ... 9
- 9(8'). Male pronotum not setigerous, female heavily so; length usually greater than 30 mm, body heavy and robust; basal color of pronotum and elytra a deep olivaceous brown to black, vittae white, broadly spaced interstitial squamae yellow, giving a unique tricolorous appearance. British Columbia, California, Pacific Northwest (Fig. 23) .....  
..... *crinita* LeConte (p. 55)
- Male pronotum usually heavily setigerous, female variable; overall length usually less than 30 mm, body generally elongate and slim; basal color of pronotum and elytra not so visible as yellow interstitial squamae are closely packed. Baja California, California, Oregon, Washington (Fig. 26) .....  
..... *nigra* Casey (p. 67)
- 10(3'). Basal color of elytra reddish-brown; overall length up to 45 mm, the largest of North American *Polyphylla*; southwestern (Fig. 30) .....  
..... *hammondi* LeConte (vittate color phase, p. 79)
- Basal color of elytra black; overall length rarely exceeding 35 mm ..... 11
- 11(10'). Elytral vittae smooth-edged, interstitial scales often yellow. Widely distributed (Fig. 20) .... *decemlineata* (Say) (p. 40)
- Elytral vittae very rough-edged, interstitial scales white. Primarily Nevada and Utah, rarely in adjoining portions of Arizona, Colorado, Idaho and Wyoming (Fig. 19) .....  
..... *arguta* Casey (p. 39)
- 12(1'). Overall length not exceeding 22 mm, usually smaller. Primarily Florida (Fig. 17) .....  
..... *gracilis* Horn (p. 30)
- Overall length greater than 22 mm. Not from Florida ..... 13
- 13(12'). Occurring only east of a north-south line from central Louisiana (Iberia Co.) to western New York State; in Canada only east of Georgian Bay, Lake Huron, On-

- tario (Fig. 2) ..... 14  
 Occurring only west of the aforementioned line ..... 15
- 14(13). Distinct broad vittae often formed adjacent to suture; length of male antennal club 5.15–7.05 mm; primarily the Great Smoky Mts., scattered throughout the southeastern states except Florida (Fig. 9) ..... *comes* Casey (p. 28)  
 Sutural vittae variable; male antennal club length 3.20–5.00 mm; coastal Virginia north and west into Quebec and Ontario. The only *Polyphylla* from this area. (Fig. 18) ..... *variolosa* (Hentz) (p. 35)
- 15(13'). Elytral vittae broken but still forming identifiable lines ..... 16  
 Elytral vittae reduced to discontinuous clumps of scales, not forming lines .. 21
- 16(15). Santa Cruz Co., California (Mt. Hermon) or Death Valley, California and Nye Co., Nevada ..... 17  
 Not distributed as above ..... 18
- 17(16). Santa Cruz Co., California (Mt. Hermon) (Fig. 22) .....  *barbata* Cazier (p. 53)  
 Death Valley, California and Nye Co., Nevada (Fig. 29) .....  
 ..... *erratica* Hardy and Andrews (p. 78)
- 18(16'). Chaves Co., New Mexico (Mescalero Dunes) and Chihuahua, Mexico (Fig. 22) .....  
 ..... *mescalarensis* new species (p. 64)  
 Not distributed as above ..... 19
- 19(18'). Pronotum not setigerous, excluding edges. Primarily Nevada and Utah, rarely in adjoining portions of Arizona, Colorado, Idaho and Wyoming (Fig. 19) .....  
 ..... *arguta* Casey (p. 39)  
 Pronotum setigerous somewhere, excluding edges. Primarily Arizona, western New Mexico and southern Utah, rarely in southern California and Baja California Norte ..... 20
- 20(19'). Elytra with long erect hairs, excluding suture; yellow interstitial scales meeting vitta without naked area in between (Fig. 28) ..... *rugosipennis* Casey (p. 72)  
 Elytra without long erect hairs, excluding suture; white (or rarely yellow) interstitial scales not meeting vitta, area between naked (Fig. 24) .....  
 ... *diffracta* Casey (vittate phase, p. 60)
- 21(15'). San Luis Obispo Co., California (Fig. 22) .....  
 ..... *nubila* Van Dyke (p. 69)  
 Utah ..... 22
- 22(21'). Parameres unequal in caudal view, left paramere with translucent dorsal flange, right paramere with smaller flange; male protibiae bidentate; southwestern Utah (Fig. 22) .....  
 ..... *avittata* Hardy and Andrews (p. 52)  
 Parameres equal in caudal view, dorsal flanges absent; male protibiae weakly to deeply tridentate; east central Utah (Fig. 22) ..... *ratcliffei* Young (p. 71)
- 23(1"). Occurring only east of a north-south line from southern coastal Mississippi to western New York State; in Canada only east of Georgian Bay, Lake Huron, Ontario ..... 24  
 Occurring only west of the aforementioned line ..... 26
- 24(23). From Newport News, Virginia north to Trois Rivieres, Quebec, west to Lake Ontario and Georgian Bay, Lake Huron, Ontario. The only *Polyphylla* from this area (Fig. 18) ..... *variolosa* (Hentz) (p. 35)  
 Alabama or Florida ..... 25
- 25(24'). Overall length not exceeding 22 mm, usually smaller; elytra scaled; Florida, rarely southeastern Alabama (Fig. 17) .....  
 ..... *gracilis* Horn (p. 30)  
 Overall length exceeding 22 mm, usually near 30 mm; elytra not scaled; southwestern Alabama (Washington Co.) (Fig. 30) ..... *brownae* Young (p. 75)
- 26(23'). Death Valley, California and Nye Co., Nevada (Fig. 29) .....  
 ..... *erratica* Hardy and Andrews (p. 78)  
 Not distributed as above ..... 27
- 27(26'). Pronotum and scutellum covered with an opaque layer of white scales; Inyo Co., California (Saline Valley Dunes) or Contra Costa and Sacramento Co.'s, California ..... 28  
 Not as above ..... 29
- 28(27). Pronotum and scutellum covered with an opaque layer of white scales; Inyo Co., California (Saline Valley Dunes) (Fig. 29) .....  
 ..... *anteronivea* Hardy and Andrews (p. 75)  
 Pronotum and scutellum not an opaque

- layer of white scales; Contra Costa and Sacramento Co.'s, California (Fig. 25)  
 ..... *stellata* Young (p. 74)
- 29(27'). Idaho: Canyon, Elmore and Owyhee Co.'s (Fig. 22) ..... *devestiva* Young (p. 59)  
 Not distributed as above ..... 30
- 30(29'). Pronotum and elytra without scales; Santa Cruz Co., Arizona (Mt. Washington) (Fig. 22) ..... *hirsuta* Van Dyke (p. 63)  
 Pronotum and/or elytra with scales somewhere; widely distributed ..... 31
- 31(30'). Utah: Grand Co. (Fig. 22) .....  
 ..... *ratcliffei* Young (p. 71)  
 Western Texas: Ward and Winkler Co.'s and Chaves Co., New Mexico (Mescalero Dunes) (Fig. 27) ..... *pottorum* Hardy and Andrews (p. 70)  
 Not distributed as above ..... 32
- 32(31"). Pronotum setigerous somewhere, excluding edges (Fig. 24) ..... *diffracta* Casey (avittate phase, p. 60)  
 Pronotum not setigerous, excluding edges ..... 33
- 33(32'). Minute squamae scattered densely but singly over elytra and pronotum; pruinose. Southern portions of Arizona, California, Nevada (Fig. 29) .....  
 ..... *cavifrons* LeConte (p. 77)  
 Never pruinose; widely distributed ..... 34
- 34(33'). Small species, length less than 23 mm; male antennal club minute, not exceeding 4 mm in length, barely recurved; elytra often unicolorous brown with only a sutural vitta. Presidio, Texas and Chihuahua, Mexico (Fig. 29) .....  
 ..... *squamiventris* Cazier (p. 90)  
 Larger species, length greater than 23 mm; male antennal club exceeding 4 mm in length, deeply recurved; elytra unicolorous yellowish-brown to deep brown with only a sutural vitta. The Great Plains of the U.S. and Canada and discontinuously east to southwestern Indiana (Fig. 30) ..... *hammondi* LeConte (avittate phase, p. 79)

**KEY TO THE SPECIES OF *POLYPHYLLA* IN AMERICA NORTH OF MEXICO, ADULTS, AEDEAGAL CHARACTERS INCLUDED**

1. Occurring only east of a north-south line from central Louisiana (Iberia Co.) to western New York State; in Canada only east of Georgian Bay, Lake Huron, Ontario (Fig. 2) ..... 2  
 Occurring only west of the aforementioned line ..... 6
- 2(1). Entire body without squamae, except for a few scattered isolates; vestiture everywhere composed entirely of hairs; Mobile Co., Alabama (Fig. 30) .....  
 ..... *brownae* Young (p. 75)  
 Squamae present somewhere, or (rarely) if devoid of all squamae, occurring along the eastern seaboard; the *occidentalis* complex ..... 3
- 3(2'). Elytra unicolorous brown or squamose but well defined vittae never formed except along suture which may or may not be vittate; in either case all other squamae scattered in disjunct clusters which may become more concentrated in normally vittate areas ..... 4  
 Elytra vittate, especially the second line laterad to the suture; southern Mississippi, all of Florida, to southern tip of Virginia (Fig. 9) ..... *occidentalis* (L.) (p. 33)
- 4(3). Overall length less than 20.2 mm, width at widest portion of elytra less than 10 mm (except for an occasional female); elytral squamae randomly scattered, never forming well defined vittae; Florida (Fig. 17) ..... *gracilis* Horn (p. 30)  
 Overall length greater than 20.2 mm, width at widest portion of elytra greater than 10 mm; elytral squamae absent or present; southeastern states except Florida, north into the eastern seaboard, Great Smoky Mts., Quebec, and Ontario ..... 5
- 5(4'). Distinct broad vittae often formed adjacent to suture; length of male antennal club 5.15–7.05 mm; primarily the Great Smoky Mts., scattered throughout the southeastern states except Florida (Fig. 9) ..... *comes* Casey (p. 28)  
 Sutural vittae variable; male antennal club



- length 3.20 mm-5.00 mm; coastal Virginia north and west into Quebec and Ontario (Fig. 18) .....  
 ..... *variolosa* (Hentz) (p. 35)
- 6(1'). Aedeagus in dorsal aspect usually gradually, smoothly narrowing from phallobase to apex (rarely broader at beginning of cleft), which is slightly to abruptly broader; tip rounded; pronotum sparsely to densely setigerous; the *diffracta* complex (Figs. 4,5) ..... 7
- Aedeagus in dorsal aspect not smoothly narrowing from phallobase to apex but markedly broader at beginning of cleft; becoming narrower towards apex; tip pointed; pronotum without setae or with setae and elytral color reddish-brown; the *decemlineata* complex (Figs. 2,6) ... 21
- Aedeagus in dorsal aspect gradually to suddenly narrowing from phallobase to apex, never broadening at cleft; apex parallel-sided to broadly spatulate; tip truncate; pronotum without setae; the *hammondi* complex (Figs. 7,8) ..... 23
- 7(6). Elytra with scattered erect hairs, excluding the suture ..... 8
- Elytra without scattered erect hairs, excluding the suture ..... 15
- 8(7). Pronotal and elytral scales absent; unicolorous brown; Arizona (Fig. 22) .....  
 ..... *hirsuta* Van Dyke (p. 63)
- Pronotal scales present, elytral scales variable ..... 9
- 9(8'). Elytral scales present, forming vittae, pattern barely to clearly striped; pronotal hairs long (up to two-thirds length of pronotum), dense ..... 10
- Elytral scales absent, or if present not forming vittae, pattern blotched; pronotal hairs nearly absent to medium length (not exceeding one-half length of pronotum) ..... 12
- 10(9). Lateral margins of clypeus parallel; elytral vittae clear, definite, white; interstitial scales yellow, dense; Arizona, Baja California (Fig. 28) .....  
 ..... *rugosipennis* Casey (p. 72)
- Lateral margins of clypeus narrowing posteriorly; elytral vittae barely suggested to interrupted lines; interstitial scales white, broadly scattered ..... 11
- 11(10'). Elytral hairs long, numerous; California (Fig. 22) ..... *barbata* Cazier (p. 53)
- Elytral hairs short, sparse, barely visible; southeastern New Mexico, Chihuahua (Fig. 22) .....  
 ..... *mescalarensis* new species (p. 64)
- 12(9'). Utah ..... 13
- California, Idaho ..... 14
- 13(12). Parameres unequal in caudal view, left paramere with translucent dorsal flange, right paramere with smaller flange; male protibiae bidentate; southwestern Utah (Fig. 22) .....  
 ..... *avittata* Hardy and Andrews (p. 52)
- Parameres equal in caudal view, dorsal flanges absent; male protibiae weakly to deeply tridentate; east central Utah (Fig. 22) ..... *ratcliffei* Young (p. 71)
- 14(12'). Terminal segment of maxillary palpi truncate at tip; male protibiae bidentate; California (Fig. 22) .....  
 ..... *nubila* Van Dyke (p. 69)
- Terminal segment of maxillary palpi pointed at tip; male protibiae tridentate; Idaho (Fig. 22) ..... *devestiva* Young (p. 59)
- 15(7'). Small species, length not exceeding 22 mm; basal color of elytra tannish-yellow; Western Texas, southeastern New Mexico (Fig. 27) ..... *pottsum* Hardy and Andrews (p. 70)
- Larger species, length greater than 22 mm; basal color of elytra reddish-brown through deep-brown to black; widely distributed ..... 16
- 16(15'). Pygidium with fine horizontal or erect hairs randomly interspersed between squamae, sometimes long and erect in females; pronotal surface covered with long erect hairs or absent (in males) and animal large, robust, tricolorous; elytral vittae broken or solid ..... 17
- Pygidium without hairs interspersed between squamae or if present they are short, stout, and suberect; pronotal surface without long erect hairs or having them concentrated only on the anterior half; never tricolorous; elytral vittae absent to solid ..... 19
- 17(16). Elytral vittae broken and ragged, rarely to-

- tally disintegrated causing a unicolorous brown or black appearance; each vitta when present with a broad naked area on each side. Arizona, southern California, New Mexico, Utah (Fig. 24) .....  
 ..... *diffRACTA* Casey (p. 60)
- Elytral vittae not broken but distinct and well defined; vittae without naked area on each side; British Columbia, California, Pacific Northwest ..... 18
- 18(17'). Male pronotum not setigerous, female heavily so; length usually greater than 30 mm, body heavy and robust; basal color of pronotum and elytra a deep olivaceous brown to black, vittae white, broadly spaced interstitial squamae yellow, giving a unique tricolorous appearance. British Columbia, California, Pacific Northwest (Fig. 23) .....  
 ..... *CRINITA* LeConte (p. 55)
- Male pronotum usually heavily setigerous, female variable; overall length usually less than 30 mm, body generally elongate and slim; basal color of pronotum and elytra not so visible as yellow interstitial squamae are closely packed. Baja California, California, Oregon, Washington (Fig. 26) ..... *nigra* Casey (p. 67)
- 19(16'). Elytral vittae absent, white squamae scattered over entire black surface without clumping, giving a speckled appearance; W. Central California (Fig. 25) ...  
 ..... *stellata* Young (p. 74)
- Elytral vittae broken or well defined but always present; California, Nevada, Oregon ..... 20
- 20(19'). Basal color of elytra a distinctive yellow-brown to reddish-brown; vittae with rough edges, often disintegrated posteriorly. California, Yosemite National Park, Lake Tahoe (Fig. 25) .....  
 ..... *sobrina* Casey (p. 73)
- Basal color of elytra never yellow-brown or reddish-brown but a deep brown to black; vittae with smooth distinct edges, not disintegrated posteriorly. California, Idaho, Oregon, Washington (Fig. 25) .....  
 ..... *modulata* Casey (p. 65)
- 21(6'). Pronotum densely setigerous, excluding edges, especially on central third of width; pronotum and elytra yellowish to reddish-brown. Ward Co., Texas (Fig. 20) .....  
 ..... *monahansensis* Hardy and Andrews (p. 51)
- Pronotum not setigerous, excluding edges; basal color of pronotum and elytra deep brown to black; widely distributed ... 22
- 22(21'). Elytra with distinct smooth edged vittae, squamae of interstitial areas often yellow (Fig. 20) .... *decemlineata* (Say) (p. 40)
- Elytra with vittae formed but edges rough and heavily broken, sometimes degenerating into squamal clumps in the normally vittate areas; squamae of vittae and interstitial areas white. Primarily Nevada and Utah, rarely in parts of Arizona, Colorado, Idaho, and Wyoming (Fig. 19) ..  
 ..... *arguta* Casey (p. 39)
- 23(6'). Small species, length less than 23 mm; male antennal club minute, not exceeding 4 mm in length, barely recurved; elytra often unicolorous brown with only a sutural vitta. Presidio, Texas, Chihuahua, Mexico (Fig. 29) .....  
 ..... *squamiventris* Cazier (p. 90)
- Larger species, length greater than 23 mm; male antennal club far exceeding 4 mm, deeply recurved; elytral vittae absent to present but never sutural one alone; widely distributed ..... 24
- 24(23'). Pronotum and scutellum covered with an opaque layer of white scales, basal color not visible to barely so. Saline Valley Dunes, Inyo Co., California (Fig. 29) .....  
 ..... *anteronivea* Hardy and Andrews (p. 75)
- Not as above ..... 25
- 25(24'). Elytra with at least some concentrations of squamae in normally vittate areas to full, hard-edged vittae ..... 26
- Elytral vittae never formed, instead squamae scattered singly over surface in varying densities ..... 27
- 26(25). Elytral vittae present in varying degrees but at least always some concentration of squamae in normally vittate areas, to strong and hard-edged; anterior angles of clypeus sometimes produced, tooth like, gradually reflexed; male antennal club 1.5–2.0 times the length of basal

- segments; overall length up to 45 mm, the largest of *Polyphylla* (Fig. 30) .....  
 .....*hammondi* LeConte (vittate color phase) (p. 79)
- Elytral squamae clumped in normally vittate areas forming heavily broken lines; anterior angles of clypeus suddenly produced, tooth like, strongly reflexed; male antennal club greater than 2 times length of basal segments; overall length not exceeding 27 mm. Death Valley (Saratoga Springs, Tecopa), California, Nye Co., Nevada (Fig. 29) .....  
 .....*erratica* Hardy and Andrews (p. 78)
- 27(25'). Minute squamae scattered densely but singly over elytra and pronotum; pruinose. Southern portions of Arizona, California, Nevada (Fig. 29) .....  
 .....*cavifrons* LeConte (p. 77)
- Broad white squamae scattered widely over elytra and pronotum, giving a unicolorous brown or black appearance, or, squamae distinctly yellow on a black base (Fig. 30) .....*hammondi* LeConte (avittate color phase) (p. 79)

**SPECIES EXCLUSIVELY EAST OF  
 THE MISSISSIPPI RIVER  
 (THE OCCIDENTALIS COMPLEX)**

**GENERAL DISTRIBUTION**—The southeastern and eastern *occidentalis* complex includes four species: *P. comes*, *P. gracilis*, *P. occidentalis*, and *P. variolosa*. The westernmost record is for *P. comes*, found in Iberia Co., Louisiana. From this point the complex spreads eastward through all of Alabama, Georgia, and Florida. It continues up the Atlantic Coast through the Carolinas, the eastern edge of Tennessee, the Virginias and north into the southern edges of Quebec and Ontario (Fig. 2).

***Polyphylla comes* Casey**  
 (Figs. 3a, 9–16, 40)

*Polyphylla comes* Casey 1914: 351; Leng 1920: 257; Fall 1928: 33; Kuntzen 1933: 462; Leng and Mutchler 1933: 39; Brimley 1938: 204; Blackwelder 1939: 53; Cazier 1940: 138; Blackwelder and

Blackwelder 1948: 33; Kirk 1970: 41; Blackwelder and Arnett 1974: R30.69; Hardy 1974: 5. (Holotype male USNM 35652. Type locality: KENTUCKY: No other data.)

**Holotype Male.**—Body elongate, broad, parallel sided. Length 26 mm, width 9.8 mm. Head black, pronotum deep brown, elytra rich brown, becoming darker anteriorly and laterally. Clypeus with broad, recumbant, yellowish hairs on disc, lateral margins deeply narrowing basally. Head with elongate white squamae and stiff yellow hairs matted over surface. Antennal club extremely large, one and two-thirds longer than combined length of head and clypeus, distal one-third abruptly recurved outwardly. Prothorax one and two-thirds broader than long, depressed midline bearing a heavy vitta composed of exceptionally elongate white and yellow squamae, lateral vittae not truly formed, composed of only two disjunct concentrations of similar squamae, lateral areas bearing yellowish hair-like squamae. Elytra just over one and one-half times longer than broad, sutural vitta clear cut and composed of small, thin, white squamae; all other normally vittate areas degenerate, with clumps of similar squamae scattered randomly over surface, squamae between clumps minute and fine, scattered randomly. Abdominal segments connate, clothed with similar fine white scales; stiff, suberect, yellowish hairs randomly scattered throughout. Pygidium with similar hairs forming a solid mat. Protibiae deeply bidentate.

**Female.**—Larger, more robust. Elytra nearly devoid of grouped squamae except for heavy sutural vittae; with rare clumps of scales, especially along anterior half of lateral margins, generally covered with widely scattered fine scales. Protibiae deeply tridentate.

**Distribution.**—Specimens examined: 196 males, 15 females. Male to female ratio 13:1. *P. comes* is primarily restricted to the inland mountainous areas covering the borders of Georgia, extreme SE Kentucky, North Carolina, South Carolina, extreme eastern Tennessee and SW Virginia (Fig. 9). It is most commonly collected near or within Great Smoky Mountains National Park. Additional collecting may extend this range to the southwest as I have seen one male each from Butler and Winston Counties, Alabama; one male from Iberia Co., Louisiana; and

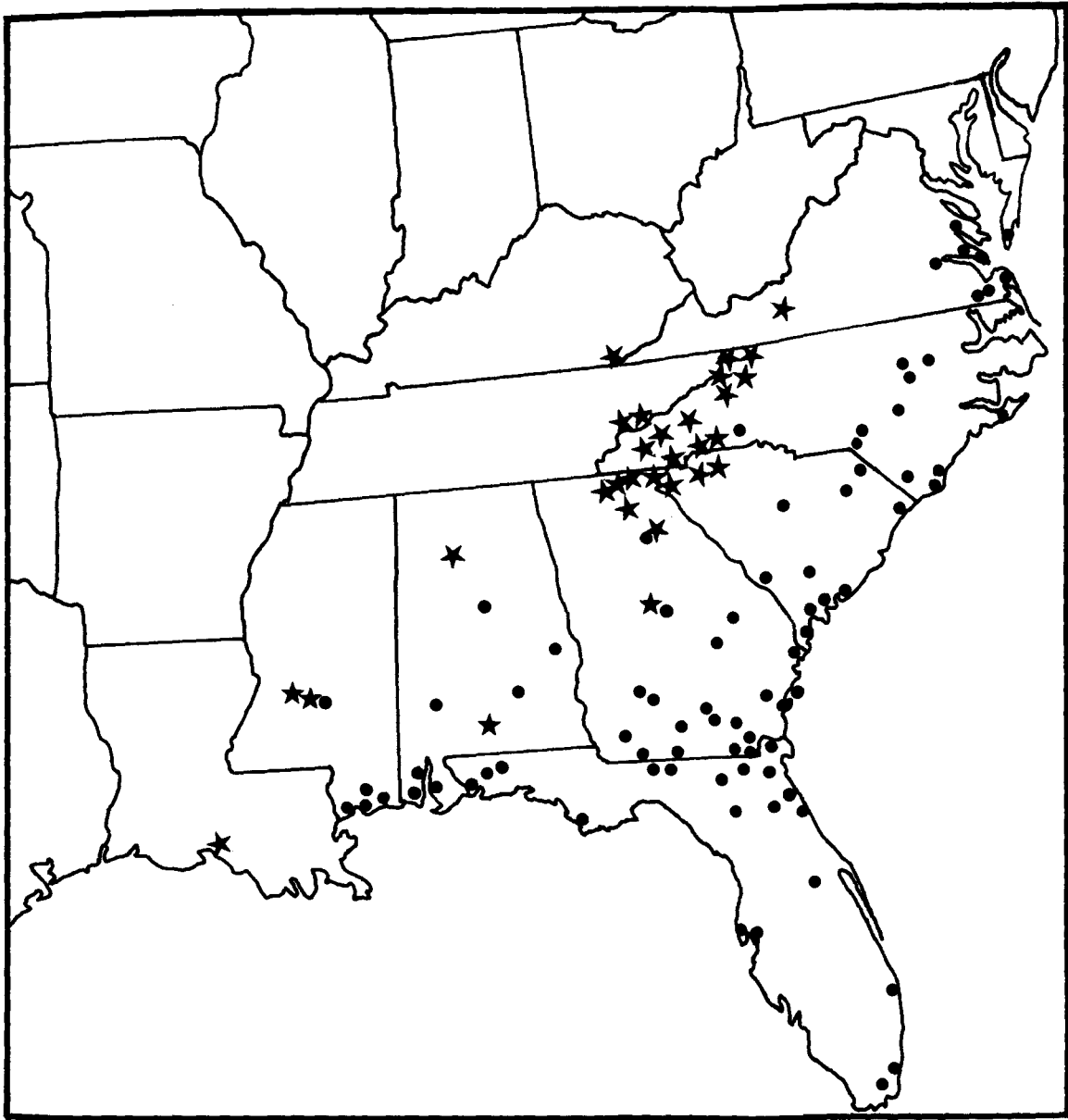


Fig. 9.— Distributions of *P. comes* (★) and *P. occidentalis* (●).

one male each from Hinds and Rankin Counties, Mississippi.

ALABAMA: *Butler Co.*: No data. *Winston Co.*: National Forest.

GEORGIA: *Clarke Co.*: Athens. *Fannin Co.*: Blue Ridge. *Lumpkin Co.*: Dahlonega. *Macon Co.*: Macon. *Rabun Co.*: Lake Rabun, Camp Flanigen, Rabun Bald. *Towns Co.*: Hiawassee. *Towns/Union Co. border*: Mt. Enotah. *Union Co.*: Blairsville. *County Unknown*: Brookton, Neel Gap.

KENTUCKY: *Bell Co.*: Pineville.

LOUISIANA: *Iberia Co.*: New Iberia.

MISSISSIPPI: *Hinds Co.*: Raymond. *Rankin Co.*: 12 mi. S. Jackson.

NORTH CAROLINA: *Alleghany Co.*: Sparta, Laurel Springs, 4 mi. ENE Laurel Springs. *Ashe Co.*:

Grandfather Mt., Todd, West Jefferson. *Buncombe Co.*: Asheville (Bent Creek), Black Mt., Swannanoa. *Caldwell Co.*: Lenoir. *Haywood Co.*: Balsam. *Henderson Co.*: Hendersonville. *Iredell Co.*: Jennings. *Jackson Co.*: Glensville. *Macon Co.*: Coweeta Hydro Lab, Highlands. *Polk Co.*: Tryon. *Transylvania Co.*: Brevard, Cedar Mtn. *Watauga Co.*: Blowing Rock, Boone. *Wilkes Co.*: No data. *County Unknown*: Crossmore, Doughton Park, Lake James, Naimur, Pineola, Smokemount, Tablerock.

SOUTH CAROLINA: *Greenville Co.*: Greenville, Lake Lanier. *Oconee Co.*: Oconee St. Park. *Pickens Co.*: Pickens. *Spartenburg Co.*: Spartanburg. *County Unknown*: Sassafras Mtns.

TENNESSEE: *Blount Co.*: Great Smoky Mtns. *Sevier Co.*: Elkmont, Gatlinburg. *County Unknown*: Crabtree.

VIRGINIA: *Montgomery Co.*: Redford Arsenal. *County Unknown*: Fancy Gap.

JUNE (30), JULY (62), AUGUST (15), SEPT. (2).

**Biology.**—Michael G. Klein, USDA Horticultural Insects Research Lab, Wooster, Ohio, has generously supplied all of the following (unpublished) data:

The USDA was called because white grubs were attacking newly planted Fraser fir Christmas trees at Todd, North Carolina. In the Spring of 1983, many trees had their roots pruned by *P. comes*, *Phyllophaga anxia* and *Phyllophaga fusca*. In the Fall of 1983 there was also heavy damage to nearby pastures, all caused by larval *P. comes*. In some areas large flocks of crows searching for *P. comes* larvae had completely destroyed the turf (Fig. 10). Densities reached 40 larvae/sq. ft. in some of these pasturelands (Fig. 11). Larvae were feeding just under the sod at the soil-thatch interface. During May-June, *P. comes* pupae were found just under the sod (Fig. 12).

On July 24, 1984, 2043 males and 43 females were collected at seven light traps; on July 25, 5129 males and 55 females at nine traps; and on July 26, 2350 males and 20 females at eight traps. Adult flight of both sexes started at dusk, increased to a peak around midnight, with little or no dawn flight.

In laboratory tests some *P. comes* larvae were successfully infected with *Bacillus popilliae* (milky disease). In the Fall of 1984, two *Tiphia* pupae were collected; attached head capsules were identified as larval *P. comes*. While digging for larvae in late August, 1985, Klein and his colleagues collected six *Tiphia* females working through the soil. They also col-

lected ca. 15 *P. comes* larvae with *Tiphia convexa* larvae attached (Fig. 13). The parasite larva eventually devoured the host larva (Fig. 14) and then pupated (Fig. 15). Fifteen *P. comes* larvae were collected with *Tiphia* eggs attached to the ventral metathorax near the legs.

Label data show this species collected at light, at 3800 ft., and at 3850 ft.

**Remarks.**—*P. comes* is distinguished from the other eastern species by its robust, large body which varies between 23 to 26 mm in length and 10 to 12.6 mm in elytral width. Elytral squamae are randomly scattered except along the suture where they most often form a distinct heavy vitta. It is most similar to the more northern *P. variolosa*, from which it may be distinguished by its primary restriction to the Great Smoky Mountains, presence of the sutural vitta in most cases and the male antennal club length which varies from 5.15 mm to 7.30 mm (Figs. 16a, b, c).

In addition to overall size, basal elytral color is highly variable, ranging from a light yellowish-brown to deep mahogany. *P. comes* tends to a greater concentration of broad heavy scales in the normally vittate areas of the elytra than *P. variolosa*. True vittae are never formed however except along the suture. In repose the elytra show a broad white band down their center composed of two adjacent vittae separated only by the suture. This character in combination with the others identified above is diagnostic for the species.

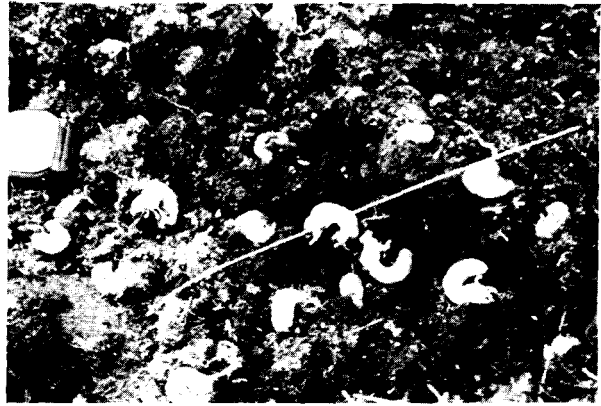
### *Polyphylla gracilis* Horn

(Figs. 3b, 17, 41)

*Polyphylla gracilis* Horn 1881: 75; Henshaw 1885: 92; Dalla Torre 1912: 259; Casey 1914: 353; Leng 1920: 257; Fall 1928: 31; Tanner 1928: 277; Blatchley 1929: 70; Kuntzen 1933: 462; Leng and Mutchler 1933: 39; Blackwelder 1939: 53; Cazier 1940: 135; Blackwelder and Blackwelder 1948: 33; Young 1967: 284; Hatch 1971: 477; Blackwelder and Arnett 1974: R30-69; Hardy 1974: 5. (Lectotype male, ANSP 3642.1, Type locality: nr. Jacksonville, Florida, collected by W.H. Ashmead. Also four males and three females, ANSP numbers 3642.2-3642.9 [3642.4 missing] all labeled Florida and as paratypes. In addition there is one male specimen in the LeConte collection at MCZC which bears holotype label 8054. It was incorrectly so labeled by Banks and is not the name bearing type



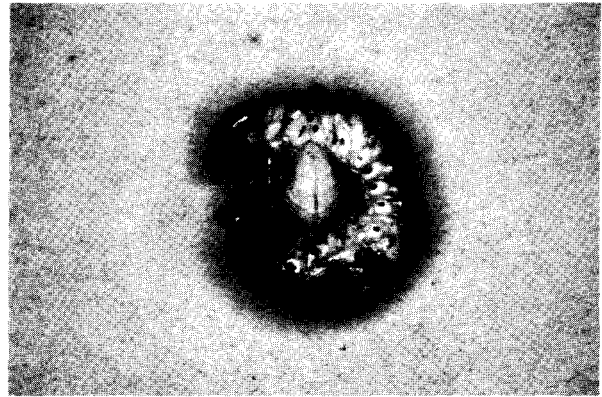
10



11



12



13



14



15

Figs. 10–15.—*P. comes* immatures, photographs courtesy of M. G. Klein, USDA Horticultural Insects Research Laboratory, Wooster, Ohio. 10.—Turf destruction near Todd, North Carolina caused by crows feeding on larvae. 11.—Larvae in soil. 12.—Ventral view of pupa in soil. 13.—Third instar larva parasitized by larva of *Tiphia convexa* (Hymenoptera: Tiphidae). 14.—Remnants of third instar larva parasitized and devoured by larva of *Tiphia convexa*. 15.—*Tiphia convexa* pupating in soil after destroying third instar larva.

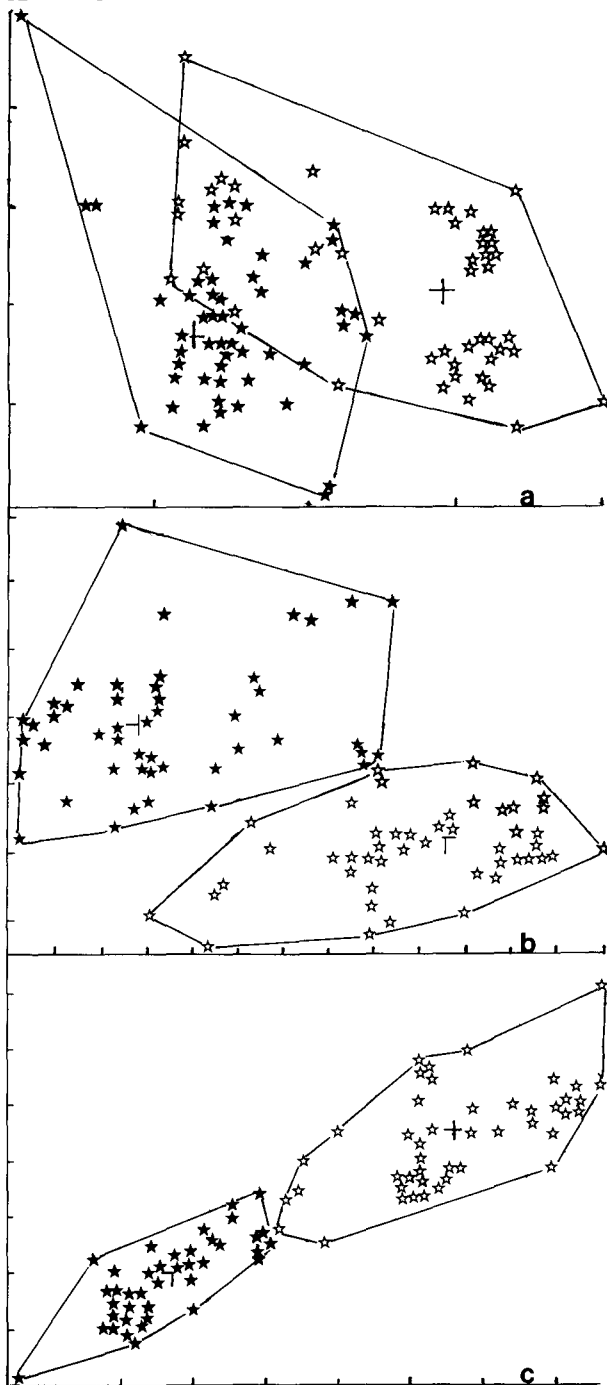


Fig. 16.—Scattergrams and limiting polygons showing character displacement in samples of *P. comes* (☆) and *P. variolosa* (★). Central cross marks mean for 50 measurements of each character, all of which are not plotted because of extreme clustering. All measurements in mm. at widest portion of structure and across curves. (a).—Abcissa, pronotal length; ordinate, ratio of pronotal width to pronotal length. (b).—Abcissa, pronotal width; ordinate, ratio of pronotal width to male antennal club length. (c).—Abcissa, male antennal club length; ordinate, ratio of male antennal club length to pronotal length.

[J.F. Lawrence, personal communication]. Lectotype male and seven paralectotypes here designated).

**Lectotype Male.**—Elongate, narrow, slightly broader posteriorly. Clypeus and head shining black, pronotum and elytra pale brown testaceous. Length 19 mm, width 8.6 mm. Thorax just over twice as wide as long, surface bearing delicate white squamae which concentrate into a median and two lateral vittae, scales becoming heavily concentrated in lateral-posterior corners. Elytra with scattered, fine, white squamae which may become more concentrated in normally vittate areas, clear vittae not formed but squamae in scattered clumps. Pygidium with minute, white scales and fine hairs. Protibiae unidentate.

**Paralectotype Female.**—With normal sexual dimorphism in antennal club, robust, broader body and flat degenerate clypeus. Similar to male in other characters except for a slightly greater tendency toward elytral vittae and strongly bidentate protibiae.

**Distribution.**—Specimens examined: 70 males, 16 females for a male to female ratio of ca. 4.4:1. *P. gracilis* is almost exclusively a floridian species. The northernmost record on hand is Ozark, Dale Co., Alabama. It has not been recorded from southern Georgia though further collecting will probably show its occurrence there (Fig. 17).

ALABAMA: *Dale Co.*: Ozark.

FLORIDA: *Brevard Co.*: Eau Gallie. *Dade Co.*: Miami. *Duval Co.*: Jacksonville. *Highlands Co.*: Jct. Hwy 66 & St. Rd. 635. *Hillsborough Co.*: Tampa. *Lake Co.*: Tavares. *Liberty Co.*: Torreya. *Orange Co.*: Orlando, Winter Park. *Osceola Co.*: Kissimmee. *Palm Beach Co.*: Lake Worth. *Pasco Co.*: Elfers. *Pinellas Co.*: Dunedin. *Polk Co.*: Lakeland. *Putnam Co.*: Crescent City. *Seminole Co.*: Sanford. *Volusia Co.*: Pierson. *County Unknown*: Ashmead, Enterprise, Natal, Sherman.

MARCH (3), APRIL (9), MAY (6), JUNE (1), JULY (1).

**Biology.**—Immatures not described or associated with adults. Blatchley (1929) records *P. gracilis* as "uncommon on pine" and "beaten from young pine." Dozier (1920) recorded that this species feeds on pine foliage but is not very abundant. Label data show it collected at light, and on citrus species.

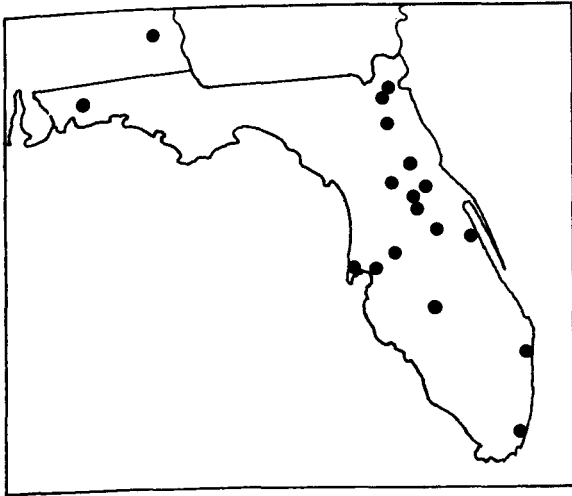


Fig. 17.—Distribution of *P. gracilis*.

**Remarks.**—*P. gracilis* may be separated from other floridian species by its diminutive size and clumped elytral squamae which do not form defined vittae. Overall width varies from 7.75 mm–9.11 mm while length varies from 18.8 mm–21.15 mm in an exceptionally large male on hand. Specimens are always narrow and elongate and most significantly, never show well formed or clear cut elytral vittae.

***Polyphylla occidentalis* (L.)**

(Figs. 3c, 9, 42)

*Scarabaeus occidentalis* Linnaeus 1767: 555; Drury 1773: 58.

*Melolontha occidentalis* (Linnaeus) Fabricius 1775: 32; Olivier 1789: 14; Herbst 1790: 72; Schonherr 1817: 169; Say 1824: 247; Erichson 1847: 659; Blanchard 1850: 161; Lacordaire 1856: 294.

*Polyphylla occidentalis* (Linnaeus) Burmeister 1844: 408; LeConte 1856: 231; LeConte 1863: 39; Crotch 1873: 61; LeBaron 1874: 86; Horn 1881: 73; Henshaw 1885: 92; Dalla Torre 1912: 260; Casey 1914: 351; Leng 1920: 257; Fall 1928: 31; Blatchley 1929: 70; Kuntzen 1933: 462; Leng and Mutchler 1933: 39; Brimley 1938: 204; Blackwelder 1939: 53; Cazier 1940: 138; Boving 1942: 175; Blackwelder and Blackwelder 1948: 33; Ritcher, 1949: 21; Ritcher 1966: 84; Young 1967: 282; Kirk 1969: 40; Kirk 1970: 40; Hatch 1971: 477; Blackwelder and Arnett 1974: R30.69; Hardy 1974: 5. (Neotype male, here designated, USNM 71423. Type locality:

NORTH CAROLINA: Southern Pines. See note below).

**Type.**—It was assumed that the name bearing type of *P. occidentalis* was deposited in the Linnaean Zoological Collections as held by the Royal Linnaean Society, London. With the extensive assistance of W.H.T. Tams and T. O'Grady, I was able to go through all of the coleopteran Linnaean material held by the Society. In the course of this search, Linnaeus' library, often containing his hand written notes in the margins, was extensively consulted as was much of his correspondence. Throughout this search no specimen bearing the name *occidentalis* was found. Furthermore, no material bearing this name is recorded from the Linnaean collections (Jackson 1913). Landin (1956) recorded 1 damaged specimen of the European *P. fullo* (Linn.) from the Linnaean collection, an observation which my search did not confirm. Finally, L. Hedstrom informs me (personal communication, 1968) there are no *occidentalis* specimens in the three boxes of Linnaean Coleoptera held by the University of Uppsala, Sweden (Museum Ludovicae Ulrica). To the best of my knowledge the Linnaean collections of Coleoptera contain no *Polyphylla*. On these bases the neotype male is here designated.

**Neotype Male.**—Elongate, narrow, parallel-sided. Head and pronotum dark brown, elytra a unique pale tan, becoming deep brown along anterior edge. Length 24.6 mm, width 10.9 mm. Clypeus squamate, lateral edges abruptly narrower basally. Head with deep, broad punctures, each puncture bearing a yellow hair-like squama, scales concentrated into an opaque mat around eyes. Prothorax broadly convex, one and one-half wider than long, entire surface with deep, broad punctures, covered with yellow hair-like squamae, becoming concentrated into a narrow vitta on depressed midline, without lateral vittae but scales concentrated over entire lateral one-third of surface. Elytra one and one-half longer than wide, edges parallel along entire length, very small narrow white scales forming vitta along suture, next lateral vitta broken posteriorly, second lateral vitta well formed as is line along lateral edge, interstitial areas covered with broadly spaced yellow hair-like scales. Pygidium covered with minute, yellowish scales. Protibiae weakly bidentate.



**Female.**—Showing sexual dimorphism in the normal characters of body size, antennal club, and clypeus. Like the male in other features to an unusual degree; protibiae deeply bidentate.

**Third Instar Larva.**—From Ritcher (1966). Based on one specimen collected at Holland, Virginia and seven specimens collected about sedge roots at Clayton, North Carolina and associated with reared adults.

"Larvae of this species may be characterized as follows: Maximum width of head capsule 6.5 mm. Head light reddish-brown in color, finely reticulate. Haptomerum of epipharynx with about 25 heli. Epipharynx with a pair of large, elliptical proplegmata each of which has more than 35 fine, curved proplegmata. Each plegmatium with 14 to 16 short plegmata. Haptolachus with about 6 crepidal punctures (microsensilla). Maxilla with a rather irregular, sparsely set row of 18 sharp-pointed stridulatory teeth. Abdominal spiracles progressively smaller in size.

Anal opening broadly V-shaped. Raster with 2 short palidia each sparsely set with 9 to 12 long, sharp, cylindrical pali. Tegilla extending in front of palidia for a distance equal to one half the length of the palidia. Preseptular, hamate setae about 25 to 40 in number. Tegilla occupying slightly less than the caudal half of the area between the lower anal lip and the anterior margin of the last abdominal segment."

**Distribution.**—Specimens examined: 298 males, 184 females for a male to female ratio in collections an unusual 1.62:1. *P. occidentalis* covers the largest geographic area of the eastern and southeastern species. It is distributed over all of Florida, where it occurs sympatrically with *P. gracilis*. Its range extends into the southern most coastal corner of Mississippi and covers the southern or eastern halves of Alabama, Georgia, the Carolinas, and Virginia. Its northern most record of occurrence is within the southern peninsular tip of Virginia (Fig. 9). There are no known records from as far inland as the Appalachian Mountains. This species is primarily a coastal one, restricted to the more equitable maritime areas. Assuming label data are correct it has been taken sympatrically with *P. comes* in the areas of Macon, Georgia and Jackson, Mississippi.

ALABAMA: *Baldwin Co.*: Fairhope. *Chilton Co.*: No data. *Lee Co.*: Auburn. *Mobile Co.*: Mobile, Theo-

dore. *Montgomery Co.*: Montgomery. *County Unknown*: Spring Hill, Storrsland.

FLORIDA: *Alachua Co.*: Gainesville, Micanopy (Fishe Prairie). *Baker Co.*: Olustee. *Columbia Co.*: Lake City. *Dade Co.*: Homestead, Miami. *Duval Co.*: Jacksonville. *Escambia Co.*: Pensacola. *Flagler Co.*: Marineland. *Franklin Co.*: Apalachicola, Ochlockonee River St. Park. *Gulf Co.*: Port St. Joe. *Hillsborough Co.*: Tampa. *Jefferson Co.*: Monticello. *Madison Co.*: No data. *Nassau Co.*: No data. *Orange Co.*: Orlando. *Palm Beach Co.*: Lake Worth. *Pinellas Co.*: Dunedin, St. Petersburg. *Putnam Co.*: Crescent City, Welaka. *Santa Rosa Co.*: Blackwater River St. Forest, Carr Lake, 4.5 mi. NW Holt. *St. Johns Co.*: St. Augustine. *County Unknown*: 7-Oaks, Yulee.

GEORGIA: *Berrien Co.*: Nashville. *Bibb Co.*: No data. *Charlton Co.*: Okefenokee Natl. Wildlife Refuge (Camp Cornelia). *Chatham Co.*: Savannah. *Clarke Co.*: Athens. *Clinch Co.*: Dupont, Fargo. *Coffee Co.*: Broxton, Douglas. *Emanuel Co.*: Swainsboro. *Liberty Co.*: St. Catherines Island. *Lowndes Co.*: No data. *McIntosh Co.*: Sapelo Island. *Mitchell Co.*: No data. *Thomas Co.*: Thomasville. *Tift Co.*: Tifton. *Turner Co.*: Rebecca. *Ware Co.*: Okefenokee Swamp, Billy's Island, Waycross, 6 mi. SE Waycross. *Wayne Co.*: No data.

MISSISSIPPI: *Hancock Co.*: Kiln. *Harrison Co.*: Gulfport, 9 mi. E. Saucier. *Jackson Co.*: Ocean Springs. *Rankin Co.*: 12 mi. S. Jackson. *County Unknown*: Ceaser.

NORTH CAROLINA: *Carteret Co.*: Beaufort. *Cleveland Co.*: Falston. *Columbus Co.*: Whiteville. *Cumberland Co.*: Fayetteville. *Edgecombe Co.*: Rocky Mount. *Johnston Co.*: Clayton. *Moore Co.*: Southern Pines. *New Hanover Co.*: Wilmington. *Scotland Co.*: Laurel Hill. *Wake Co.*: Raleigh.

SOUTH CAROLINA: *Barnwell Co.*: Blackville. *Beaufort Co.*: Coosawhatchie. *Charleston Co.*: Airport, Charleston, John Island, Seabrook Island. *Colleton Co.*: Yemasee. *Dillon Co.*: Dillon. *Dorchester Co.*: St. George. *Florence Co.*: Florence. *Horry Co.*: Myrtle Beach. *Richland Co.*: Columbia. *County Unknown*: Meredith.

VIRGINIA: *Hampton Co.*: No data. *King and Queen Co.*: No data. *Nansemond Co.*: Holland, Suffolk. *Newport News Co.*: Newport News. *Norfolk Co.*: Norfolk. *Northhampton Co.*: Cape Charles. *Prince George Co.*: Petersburg, Camp Lee. *Princess Anne Co.*: London Bridge, Virginia Beach. *County Unknown*: Beyer, Ocean View, Weith.

APRIL (15), MAY (90), JUNE (174), JULY (44), AUGUST (7), SEPTEMBER (1).

**Biology.**—Ritcher (1949, 1966) described the third stage larva based on specimens collected at Holland, Virginia and about sedge roots at Clayton, North Carolina. It is distinguished from the other three species of *Polyphylla* with described larvae (*P. decemlineata*, *P. modulata*, and *P. variolosa*) by the presence of proplegmatia which are always well developed.

Craighead (1950) recorded that under experimental conditions the larvae of this species fed heavily on the roots of pine seedlings, whereas they normally feed on the roots of sedge grass.

Dozier (1920) stated that *P. occidentalis* feeds on the foliage of pine. Blatchley (1929) also reported it taken on pine without specifically mentioning feeding activity. Kirk (1969) recorded it collected at black light and in golf greens; in 1970 he listed it taken at light and on pine. Label data show this species collected at light, at black light, at mercury vapor light, and on pine.

**Remarks.**—This species is readily distinguished from all others in the east and southeast by its relatively large size (20.20 mm long, 9 mm wide minimum), and, most significantly, by the elytral squamae forming well defined vittae. Of the southeastern species it is the only one which consistently shows these vittae. Overall length varies up to 25 mm and width up to 10.90 mm. The first elytral vitta laterad to the suture is most often broken and degenerate while the second and third lines laterad are clear and well defined in all specimens seen.

### *Polyphylla variolosa* (Hentz)

*Type Species of the Genus*

(Figs. 3d, 16, 18, 43)

*Melolontha variolosa* Hentz 1830: 256; Harris 1841: 30; Harris 1890: 33.

*Polyphylla variolosa* (Hentz) Harris 1841: 30; LeConte, 1856: 231; LeConte 1863: 39; Scudder 1869: 363; Crotch 1873: 61; LeBaron 1863: 86; Horn 1881: 73; Henshaw 1885: 92; Harris 1890: 33; Dalla Torre 1912: 261; Casey 1914: 251; Leng 1920: 257; Leonard 1926: 425; Fall 1928: 31;

Kuntzen 1933: 462; Leng and Mutchler 1933: 39; Blackwelder 1939: 53; Brown 1940: 186; Cazier 1940: 135; Heit and Henry 1940: 944; Boving 1942: 175; Blackwelder and Blackwelder 1948: 33; Ritcher 1949: 21; Ritcher 1966: 84; Young 1967: 284; Blackwelder and Arnett 1974: R30.69; Hardy 1974: 5; Hardy and Andrews 1978: 2. (Neotype male, USNM 71424. Springfield, Massachusetts, VII-2-1930, E.A. Chapin, collector. Hentz did not designate any type specimens when establishing this name in 1830; a fact confirmed by a search through all major collections in the United States. To properly fix the name of this type species of the genus the name-bearing neotype is here designated).

**Neotype Male.**—Short, broad, parallel sided. Head deep brown, approaching black, pronotum deep brown but lighter than head, elytra rich medium brown. Length 23.40 mm, width 10.50 mm. Clypeus gradually and evenly narrowing from apex to base, antennal club unusually small, one and one-fourth longer than combined length of head and clypeus, distal one-third slightly recurved outwardly. Prothorax with deeply depressed midline with narrow vitta of elongate white hairs, no true vittae laterally but hairs somewhat more concentrated, very fine hairs scattered randomly over surface, squamae absent. Elytra one and one-half longer than wide, all ornamentation composed of delicate white hair-like squamae, sutural vitta weakly formed, all other squamae scattered in random clumps except along lateral margins where a thin broken line is formed. Pygidium entirely clothed with extremely fine depressed hairs. Protibiae weakly bidentate.

**Female.**—Body larger, more robust. Head black around eyes. Protibiae broad, robust, deeply tridentate.

**Third Instar Larva.**—From Ritcher (1966). Based on ten specimens found injuring roots of California privet at Lawrence Harbor, New Jersey.

"Larvae of this species may be distinguished by the following characters: Maximum width of head capsule 6.2 to 6.6 mm. Head light reddish-brown in color, faintly reticulate. Haptomerum of epipharynx with 22 to 25 heli. Epipharynx without proplegmatia, the area covered instead with setae. Each plegmatium with 10 to 12 very short plegmata. Haptolachus

with 5 to 10 crepidal punctures (microsensilla). Maxilla with a row of 14 to 18 conical, sharp-pointed stridulatory teeth. Thoracic spiracles slightly larger than spiracles on abdominal segments 1 to 5 which are similar in size. Spiracles on abdominal segments 6 to 8 progressively smaller.

Anal slit curved, only feebly angulate. Raster with 2 short, nearly parallel, longitudinal paladia each sparsely set with 9 to 15 long, sharp, cylindrical pali. Septula narrow. Tegilla extending forward past the palidia for a distance equal to or slightly greater than the length of the palidia. Preseptular setae more than 50 (50 to 70). Tegilla occupying the caudal half or slightly more of the area between the lower anal lip and the anterior margin of the last abdominal segment."

**Distribution.**—Specimens examined: 967 males and 72 females. Male to female ratio ca. 13.4:1. *P. variolosa* is broadly distributed throughout the northeastern United States and portions of southern Quebec and Ontario. The southern most record for the species is Newport News, Virginia, where it is taken sympatrically with *P. occidentalis*. Moving northwards along the coast fairly continuous records are available through Maryland, Delaware, extreme southeastern Pennsylvania, New Jersey, and Long Island, New York. In this southern portion of its range *P. variolosa* is a distinctly maritime species, somewhat reminiscent of the more southern and western *P. occidentalis*. Based on the specimens seen for this work a disjunction is formed by the absence of any records from Connecticut. It is unlikely that *P. variolosa* does not exist there, at least in coastal areas. There is one record from Rhode Island (Providence). Continuing northwards this species is found throughout Massachusetts, the southern half of New Hampshire and southeastern Maine. The northernmost record for *P. variolosa* is Trois Rivières, Quebec; it has not been collected north of the St. Lawrence River.

To the west there are a few records from northwestern Vermont (being the only records from that state) and northeastern New York, clustering around Lake Champlain. There is a cluster of records from several localities within three counties in east central New York. Moving farther to the west to near the eastern tip of Lake Ontario one again finds records of this species occurrence. There are single records from the southwestern shore of Lake Ontario and the east-

ern tip of Lake Erie where Leonard (1926) recorded *P. variolosa* from Buffalo, New York. One male has been seen from this locality; it may be the same specimen recorded by Leonard. In short, the greater portions of New York state are without known occurrences of this species yet it is clearly established in the eastern and western extremes of the state. Surely these areas have been arduously collected for more than a century so I am inclined to believe that these interesting disjunctions are real. Endemism and disjunct distributions are fairly common in *Polyphylla*. Most likely local isolated demes occur around Lake Champlain, along the St. Lawrence River and along some portions of the shorelines of Lake Ontario and Lake Erie in association with sandy or sand dune areas and the sedge-like grasses needed for larval food.

*P. variolosa* also occurs on the north shore of Lake Ontario at Trenton, Ontario. Farther northwards on both sides of the Ottawa River there is a cluster of records from the areas of Chalk River, Ontario and Fort Coulonge, Quebec. The most western record on hand is from a single male specimen in the USNM collections labelled "Ontario, Georgian Bay, VI-26-1940." Though vague and nonspecific I accept this record as correct; *P. variolosa* does apparently occur along at least the eastern shores of Lake Huron (Fig. 18).

Overall the distribution of *P. variolosa* seems an anomaly. One would naturally expect deeper invasions inland in the more equitable southern areas and a more narrow restriction to the coastal northern areas. Just the reverse is true. I am speculating that the northern inland invasions are possible and associated with 1) the aforementioned sand/sedge habitat pockets and 2) the ameliorating effects on climatic extremes by the Great Lakes.

CANADA: ONTARIO: Chalk River, Georgian Bay, Petawa Res., Trenton. QUEBEC: Fort Coulonge, Norway Bay, Trois Rivières.

UNITED STATES: DELAWARE: *Sussex Co.*: Cape Henlopen, Dewey Beach, 6 mi. S. Dewey Beach, Fenwick Island, Georgetown, Lewes.

MAINE: *Cumberland Co.*: Cape Elizabeth, Chebeague Island, Portland. *York Co.*: Biddeford, Eliot, Ogunquit, Old Orchard, York Beach. *County Unknown*: Bedeford, Kamp, Prout's Neck.

MARYLAND: *Worcester Co.*: Assateague Island, Ocean City.

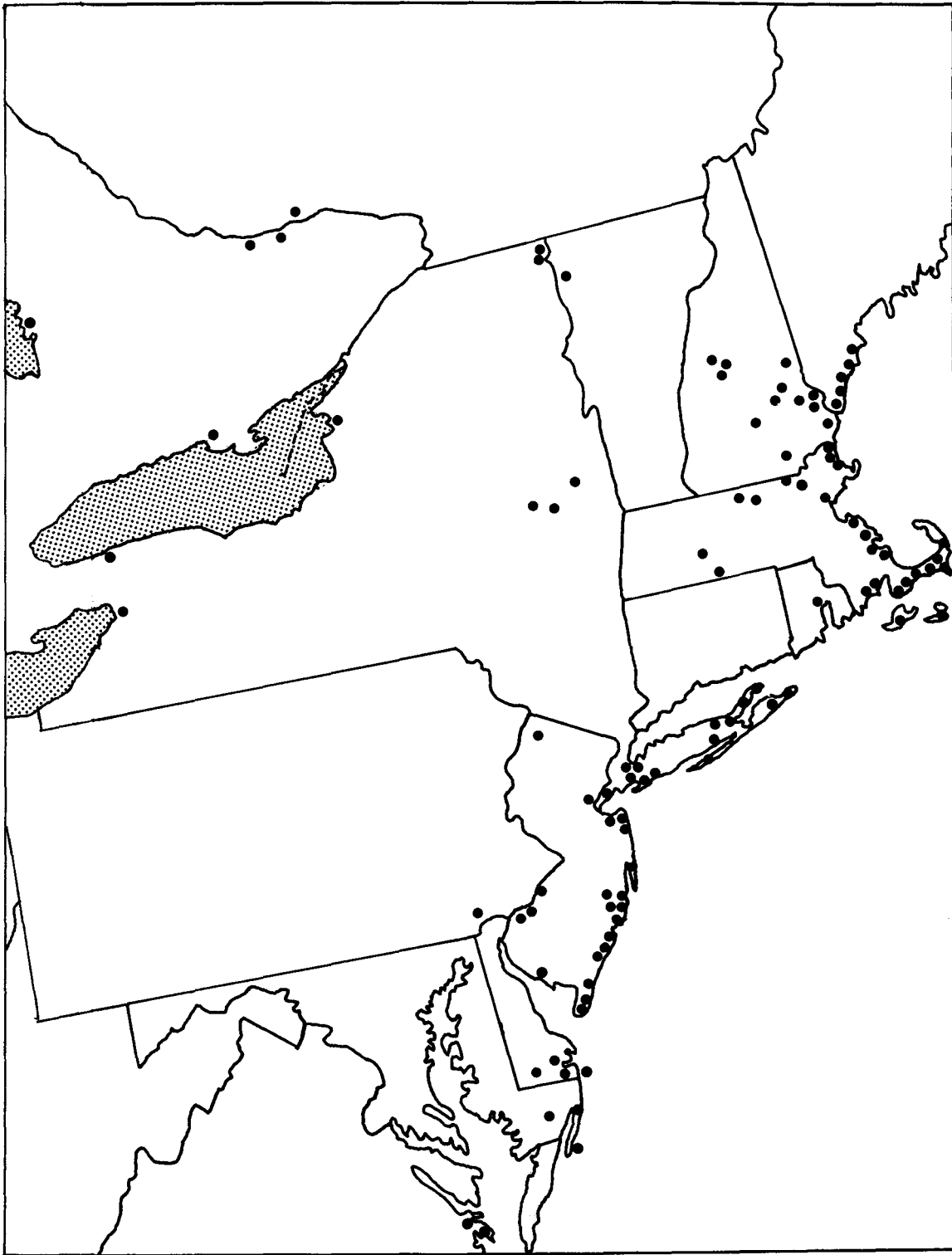


Fig. 18.—Distribution of *P. variolosa*.

MASSACHUSETTS: *Barnstable Co.*: Brewster, Cape Cod, Chatham, Dennis, Dennis Port, Eastham, Falmouth, Harwich, Harwich Point, Hyannis, Monomoy Point, Orleans, Woods Hole. *Dukes Co.*: Martha's Vineyard, West Chop. *Essex Co.*: Amesbury, Ipswich, Newburyport, Salisbury, Salisbury Beach. *Hampden Co.*: Springfield, West Springfield. *Hampshire Co.*: Amherst. *Middlesex Co.*: Lowell, Tyngsboro, Wilmington. *Nantucket Co.*: Nantucket, Nantucket Isle. *Norfolk Co.*: Cohasset. *Plymouth Co.*: Humarock, Humarock Beach, Monomet, Marion, Onset, Plymouth. *Suffolk Co.*: Boston. *Worcester Co.*: Phillipston, Templeton. *County Unknown*: Aganon, Long Pond, Walden.

NEW HAMPSHIRE: *Belknap Co.*: Alton, Barnstead. *Carroll Co.*: No data. *Grafton Co.*: Plymouth, Rumney, Squam Lake. *Hillsboro Co.*: Manchester. *Merrimack Co.*: Frankland. *Rockingham Co.*: Rye, Seabrook. *Strafford Co.*: Dover, Durham, Lee, Madbury.

NEW JERSEY: *Atlantic Co.*: Atlantic City. *Burlington Co.*: Riverside, Riverton. *Cape May Co.*: Cape May, Cape May Point, Wildwood. *Cumberland Co.*: Vineland. *Gloucester Co.*: Westville. *Monmouth Co.*: Highlands, Ocean Grove, Red Bank, Seabright. *Ocean Co.*: Beach Haven, Lakehurst, Wrangel Brook Road, Lavalette, Manahawkin, Point Pleasant, Seaside Heights, Seaside Park, Ship Bottom, Toms River. *Sussex Co.*: Hopatcong. *Union Co.*: Elizabeth. *County Unknown*: Angelsea, 5 Mile Beach, Lahaway, Longport, Midford Lakes, New Lisbon, Seashore, Spray Beach.

NEW YORK: *Clinton Co.*: Peru, Plattsburg. *Erie Co.*: Buffalo. *Jefferson Co.*: Watertown. *Kings Co.*: Brooklyn, Flatbush, Gerritsen Beach, Coney Island, Jamaica, Rockaway Beach. *Nassau Co.*: Jones Beach, Long Beach. *New York Co.*: New York, nr. New York City. *Queens Co.*: No data. *Richmond Co.*: Staten Island. *Saratoga Co.*: Saratoga, State Nursery. *Schenectady Co.*: Karner, Schenectady. *Suffolk Co.*: Bellport, East Hampton, Great Bend, Greenport, Montauk Point, Orient, Riverhead, Wading River, Yaphank.

PENNSYLVANIA: *Chester Co.*: Kennett Square.

RHODE ISLAND: *Providence Co.*: Providence.

VERMONT: *Chittendon Co.*: Colchester, Mallett's Bay.

VIRGINIA: *Accomack Co.*: Chincoteague. *Newport News Co.*: Ft. Monroe, Newport News.

MAY (4), JUNE (195), JULY (473), AUGUST (34).

**Biology.**—Harris (1841) first mentioned this species as an economic pest. He cited it as being injurious to fruit trees in the adult stage and as a heavy feeder on the leaves of various forest trees such as elm, maple, and oak. Heit and Henry (1940) recorded that larvae of this species caused extensive damage in a New York state forest tree nursery. Boving (1942) provided a key that will separate larval *P. variolosa* from *P. occidentalis* as well as a number of Melolonthini genera. Ritcher (1949, 1966) cited a collection record for ten third-stage larvae which were taken found injuring the roots of California privet at Lawrence Harbor, New Jersey, X-12-1941. This larval material was described by Ritcher (here included), and is deposited in the USNM.

Label data show *P. variolosa* collected at 300 ft. elevation, at light, at arc light, and in dune grass roots.

**Remarks.**—The following characters in combination will distinguish *P. variolosa* from the other three eastern species of the *occidentalis* complex: Elytral length greater than 20.2 mm, width greater than 9 mm, elytral squamae randomly scattered or at most concentrating into broken clumps in the normally vittate areas, vittae never well defined, and its northeastern distribution where it occurs to the exclusion of all other species. It is most easily confused with *P. comes*, from which it may be distinguished by its more northerly occurrence, the lack of sutural vittae in most cases, and the length of the male antennal club which varies from 3.20 mm to 5 mm (Fig. 16).

Variation in overall length 20.20 mm—23 mm; elytral width 9.30 mm—10.90 mm. Extreme variability in both shape and positioning is the most characteristic feature of the elytral scales of this species. Anteriorly the squamae tend to be very fine and hair like, while posteriorly they assume a more robust shape. Well defined vittae are never formed and a unicolorous brown specimen devoid of all scales is not uncommon. If present, the elytral scales often become more concentrated along the margins. Basal elytral color varies from a more common yellowish-brown to a deep, solid brown which may approach black on the humeral umbones.

**SPECIES PRIMARILY WEST  
OF THE MISSISSIPPI RIVER  
(THE *DECEMLINEATA*, *DIFFRACTA*,  
AND *HAMMONDI* COMPLEXES)**

THE *DECEMLINEATA* COMPLEX

***Polyphylla arguta* Casey**  
(Figs. 6a, 19, 44)

*Polyphylla arguta* Casey, 1914: 338; Leng 1920: 257; Fall 1928: 32; Kuntzen 1933: 462; Leng and Mutchler 1933: 39; Cazier 1938: 164; Blackwelder 1939: 53; Cazier 1940: 135; Blackwelder and Blackwelder 1948: 33; Young 1967: 282; Hatch 1971: 475; Blackwelder and Arnett 1974: R30.69. (Holotype male USNM 35635. Type locality: Provo, Utah. Also noted is one specimen in the USNM collections labelled "PARATYPE, *P. irregularis* Van Dyke." This is a specimen of *P. arguta*, the name *P. irregularis* has never been published, this note does not constitute publication, and the paratype label should be ignored).

**Holotype Male.**—Elongate, narrow. Length 23.5 mm, width 10.3 mm. Elytra deep brown, becoming black laterally; head black, pronotum like the elytra. Clypeus deeply concave, lateral edges gradually contracting posteriorly, covered with yellowish scales which become more concentrated along all margins; surface punctate, rugose between punctures. Head with deep, close punctures, covered with erect, yellow hairs throughout; broad white and yellow squamae concentrated laterally and along epistomal suture, also scattered sparsely over disc. Antennal club one and one-fourth longer than combined length of head and clypeus. Prothorax abruptly convex, just over one and one-half wider than long; disc randomly punctate, some punctures bearing unique, brown squamae the same color as the pronotal surface; midline depressed, especially posteriorly, midline and lateral vittae composed of small, white scales; devoid of hairs except along anterior and lateral margins. Elytra one and three-fifths longer than wide, slightly narrower posteriorly, sutural vitta absent, all other vittae broken and rough-edged, small white, interstitial squamae concentrated posteriorly. Pygidium densely covered with minute, white squamae. Protibiae weakly tridentate.

**Female.**—Heavy, robust, broad, narrowing slightly posteriorly. Sexual dimorphism normal in degenerate clypeus, larger size, and antennal club. Protibiae heavy, broad, tridentate.

**Distribution.**—Specimens examined: 274 males and one female. *P. arguta* is most common but apparently never abundant throughout Utah and the eastern three-fourths of Nevada. In addition to this primary area, records are on hand from the northern half of Arizona; NW Colorado; SE Idaho; Santa Fe, New Mexico, and the southern half of Wyoming. The eastern-most record for this species is Douglas, Wyoming (Fig. 19).

ARIZONA: *Coconino Co.*: Grand Canyon, 7 mi. E. Jacob Lake (6800 ft.). *Navajo Co.*: Heber (6500 ft.), 2 mi. W. Holbrook, 18 mi. WNW Kayenta.

COLORADO: *Moffat Co.*: 2.5 mi. E. Dinosaur, Maybell.

IDAHO: *Bingham Co.*: Springfield. *Cassia Co.*: Burley. *Minidoka Co.*: Acequia, Rupert (4157 ft.).

NEVADA: *Clark Co.*: Pine Creek (4000 ft.). *Lander Co.*: Austin Summit (7400 ft.), Elkhorn Summit (6870 ft.). *Lincoln Co.*: Cathedral Gorge St. Park. *Nye Co.*: 5 mi. S. Current (5000 ft.), Ichthyosaur St. Park (18 mi. E. Gabbs), Monitor Valley (6–7000 ft.). *White Pine Co.*: 8 mi. W. Baker, Lehman Creek (7000 ft.), Mt. Wheeler, Toquima Range (Pine Creek Canyon), White Pine Mts. (White River Canyon, 7100 ft.).

NEW MEXICO: *Santa Fe Co.*: Santa Fe.

UTAH: *Cache Co.*: 1 mi. N. Cornish, Logan. *Davis Co.*: Bountiful, Farmington, Syracuse. *Duchesne Co.*: Duchesne. *Grand Co.*: Moab (LaSalle Mts., Lake Oowah). *Kane Co.*: Kanab. *Salt Lake Co.*: Salt Lake City. *San Juan Co.*: 5 mi. W. Monticello (Dalton Springs Camp, 8500 ft.). *Tooele Co.*: Willow Springs. *Uintah Co.*: Myton Pocket. *Utah Co.*: Goshen, Granite (on dewberries), Provo, Spanish Fork, Vineyard. *Wasatch Co.*: Heber. *Washington Co.*: Leeds (Oak Grove Campground), Zion. *Weber Co.*: Hooper, Ogden.

WYOMING: *Converse Co.*: Douglas. *Lincoln Co.*: Border. *Natrona Co.*: Alcova. *Sweetwater Co.*: Rock Springs.

MAY (8), JUNE (50), JULY (188), AUGUST (5).

**Biology.**—Young (1967) established that the larvae of *Diogmites grossus* Brown (Diptera: Asilidae) are predacious on the immature stages of a species of *Polyphylla*, most likely *P. arguta* or *P. decemlineata*.

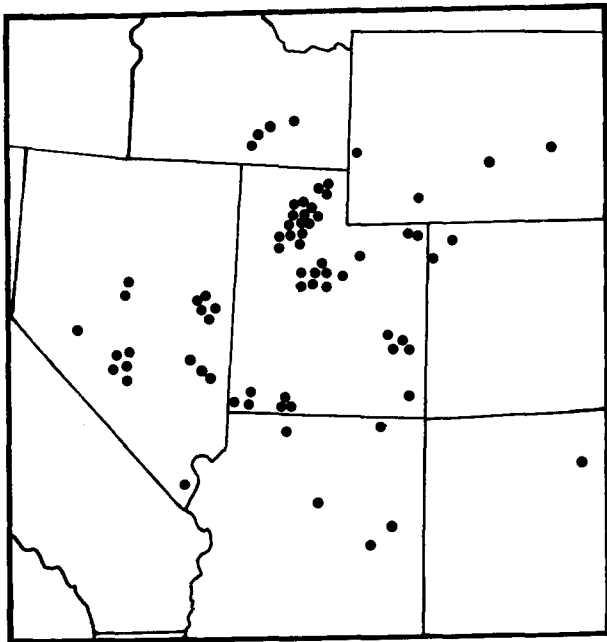


Fig. 19.—Distribution of *P. arguta*.

*ta*. A pupa of a female *Polyphylla* was recovered from the closely packed clay soil in the area of Delta, Utah in association with a nesting site of *Nomia* (Hymenoptera: Halictidae). Pupating immediately adjacent to the partially destroyed beetle pupa was a specimen of *D. grossus*. In another instance a pupal case of *D. grossus* was recovered adjacent to the scattered remains of a *Polyphylla* larva (determinations of Diptera by W.J. Hanson, Utah State University).

I have examined specimens collected by J.F. Emmel, M.D. from the following locality: Nevada: Nye Co.: T9N, R58E, Railroad Valley nr. NW base of the Grant Range, 5 road miles S. of Currant on road to Nyala, ca. 5000 ft. elv., VII-6-1969. In this sand dune and sand flats area, Dr. Emmel reports (personal communication, 1969) the diurnal activity of this species as follows:

"In late afternoon (approx. 3:30 or 4:00 PM) we saw numerous adults flying about the sand dunes and most were collected while flying. This activity appeared to cease near sunset. Interestingly, we camped here and blacklighted, but no *Polyphylla* came into the blacklight; this makes me think their peak activity is diurnal." Dr. Emmel further reports that he and his party collected this locality the next day until about 2:00 PM and saw no additional *Polyphylla* activity. Increasingly it is apparent that diurnal searching activity by male *Polyphylla* for females

is far more common than once thought. Hardy (1978) reported on the activity of *P. erratica* at dusk and the absence of its attraction to black light. I have seen similar activity at dusk of *P. hammondi* at a site near Douglas, Arizona and another near Canyon de Chelly, Arizona. Invariably this diurnal flight takes place in sandy grasslands or over actual sand dunes. From the 274 males and one female examined for this work, it is obvious that our common collecting techniques are about 50% inadequate. In these desert areas it is far too easy to enjoy good conversation around a light trap during the cool of the evening; in fact it might make better biological sense to discover how to sample these populations naturally, within their own biological rhythms. In at least some cases in *Polyphylla* those periods of flight activity are clearly diurnal.

*P. arguta* and its close relative *P. decemlineata* have been collected at the highest elevations recorded for the North American species. *P. arguta* is here recorded as high as 8500 ft. elv. near Monticello (San Juan Co.), Utah.

**Remarks.**—Distinguished from all other species at a glance by the lack of pronotal hairs combined with the elytral vittae not well formed but rough-edged and broken into squamal clumps. Overall length in males varies from an exceptionally small 20.90 mm to 31.00 mm. Basal elytral color varies from a light reddish-brown to the more usual black. No specimens examined have the pronotal hairs mentioned by Cazier (1938).

#### *Polyphylla decemlineata* (Say)

(Frontispiece, Figs. 6b, 20, 21, 45, Table 3)

*Melolontha decemlineata* Say 1824: 246; Hentz 1830: 256.

*Polyphylla decemlineata* (Say) Burmeister 1844: 407; LeConte 1854: 22; LeConte 1856: 230; LeConte 1863: 39; Crotch 1873: 61; Horn 1881: 73; Henshaw 1885: 92; Bates 1888: 215; Casey 1889: 169; Casey 1891: 17; Casey 1895: 607; Dalla Torre 1912: 257; Casey 1914: 344; Leng 1920: 257; Dawson 1922: 118; Essig 1926: 443; Fall 1928: 30; Kuntzen 1933: 462; Leng and Mutchler 1933: 39; Cazier 1938: 164; Blackwelder 1939: 53; Cazier 1939: 202; von Bloeker 1939: 149; Brown 1940: 185; Cazier 1940: 135; Boving 1942: 175; Blackwelder and Blackwelder 1948: 33; Ritcher 1949: 21; Johnson 1954: 717; Onsager 1966: 480; Ritch-

er 1966: 84; Young 1967: 284; Ritcher 1969: 872; Hatch 1971: 475; Lilly and Shorthouse 1971: 1757; Blackwelder and Arnett 1974: R30.69; Lago 1979: 65; Hardy 1981: 299. (Neotype male here designated; deposited in the Univ. Nebraska State Museum. See discussion below).

*Polyphylla comstockiana* von Bloeker 1939: 150. (Holotype male, Allotype female and six paratype males, LACM. Type locality: CALIFORNIA: Lassen Co.: Milford [nr. Honey Lake]). NEW SYNONYMY.

*Polyphylla decemlineata laticauda* Casey 1914: 345. (Holotype male USNM 35645. Type Locality: NEVADA.)

*Polyphylla decemlineata parilis* Casey 1914: 345. (Holotype male USNM 35644. Type Locality: WYOMING.)

*Polyphylla decemlineata reducta* Casey 1914: 346. (Holotype male and one paratype male USNM 35646. Type locality: WASHINGTON STATE.)

*Polyphylla matrona* Casey 1914: 350. (Holotype female USNM 35650. Type locality: ARIZONA: Oak Creek Canyon.) NEW SYNONYMY.

*Polyphylla potsiana* Casey 1914: 349. (Holotype male, four paratype males, and two paratype females USNM 35649. Type locality: MEXICO: San Luis Potosi.) NEW SYNONYMY.

*Polyphylla ruficollis* Casey 1914: 346. (Holotype female USNM 35642. Type locality: CALIFORNIA: Los Angeles County.)

*Polyphylla ruficollis castanea* Casey 1914: 347. (Holotype female USNM 35643. Type locality: CALIFORNIA: probably southern.)

*Polyphylla ruficollis oregona* Casey 1914: 348. (Holotype male and two paratype females USNM 35647. Type locality: OREGON: Corvallis.)

*Polyphylla squamotecta* Casey 1914: 343. (Holotype female USNM 35651. Type locality: CALIFORNIA.)

**Type.**—Say did not designate any type in his original description. There are some very questionable remnants in the MCZC but nothing that will fix this name. All the major North American collections have been checked for Say material, with negative results. For many years the name *P. decemlineata*, or “10-lineata” as Say first described it, has been a dumping ground for those specimens not clearly recognized. Over time the result has been, I fear, a gradual evolution of, or shift in, what organism this name spec-

ifies. Oddly enough this is the most commonly collected of the North American species while at the same time the name is subject to the most severe nomenclatural confusion. Under these conditions I believe a neotype designation is not only justified but badly needed. Say gave “Missouri” as the type locality for this species but in the 3,577 specimens on hand I have no record of this species from Missouri. Secondly he writes that he first saw this species “above the Pawnee villages on the Platte.” The Long Expedition to the Rocky Mountains, of which Say was a member, visited known Pawnee villages which are today fully identified historic sites (personal communication; Dr. Tom Myers, Curator of Anthropology, Univ. of Nebraska State Museum). They are located in the Loup River country of central Nebraska, where *P. decemlineata* is very common. I have selected a specimen from this area which most closely fits Say’s original description, type locality (see the Code, Art. 75B{f}) as follows: NEBRASKA: Thomas Co.: Halsey. Also labelled “VII-1969, U. of N. Coll. Trip.”

**Neotype Male.**—Elongate, robust, slightly broader posteriorly. Length 30 mm, width 14.5 mm. Elytra black, becoming rich brown laterally, pronotum black, becoming brown laterally at greatest width, head black. Clypeus deeply concave, anterior margin reflexed, edges narrowing posteriorly, narrow, yellow squamae set in large punctures centrally, becoming concentrated along anterior margin. Head with large setigerous punctures on disc, yellow hairs stiff, semi-erect, a few recumbant squamae scattered between, squamae becoming tightly packed around eyes. Antennal club one and two-fifths longer than combined length of head and clypeus, distal half deeply recurved. Prothorax broadly convex, one and two-fifths wider than long, disc with coarse punctures, as on clypeus; small, tightly packed, white squamae forming heavy vitta on depressed midline, lateral vittae only on posterior half except for a small clump of white squamae along anterior edge, interstitial squamae scattered randomly over surface except along edges where they become more concentrated, yellow, causing a distinct tricolorous appearance, a few erect yellow hairs along anterior middle. Scutellum slightly depressed, disc with solid mat of minute, white scales, naked shining brown laterally and posteriorly. Elytra nearly one and one-half longer than wide, umbones shining black with sparse small yellow squamae, three vittae on each side of



sutural midline composed of small, overlapping, white squamae, short humeral vittae also well formed, vittae 2 and 3 joining posteriorly, all vittae sharp-edged and distinct with shining, black naked band on each side; interstitial areas with small, yellow, squamae not nearly so numerous or concentrated, becoming slightly more whitish and concentrated posteriorly, overall appearance again tricolorous, hairs absent. Pygidium with dense but not packed small, white scales, most dense anteriorly, interspersed with short semierect yellow hairs, depressed midline much less squamate. Abdominal segments ventrally with dense minute white scales posteriorly, becoming less white and more scattered anteriorly, anterior-most portion of each segment naked, black and shining, especially centrally. Protibiae deeply bidentate.

**Measurements.**—Overall length 30.00 mm; length of antennal club 7.00 mm; combined length of head and clypeus 5.00 mm; length of pronotum 6.30 mm, width 10.30 mm; length of elytra 21.50 mm, width 14.50 mm.

**Female.**—Large, very robust throughout, much more rotund than male, slightly broader posteriorly. Sexual dimorphism normal in size, shape, clypeus, and antennal club. Protibiae broad, heavy, deeply tridentate.

**Third Instar Larva.**—From Ritcher (1966). Based on seven larvae, and exuvium of one larva reared to the adult stage. Specimens were dug from soil at Greenfield, California.

“Larvae of this species may be distinguished by the following characters: Maximum width of head capsule 7.8 to 8.66 mm. Head reddish-brown in color, reticulate. Haptomerum of epipharynx with 16 or more heli. Epipharynx with or without proplegmata; proplegmata, if present, poorly developed and consisting of numerous fine proplegmata. Each plegmatium with 11 to 15 very short plegmata. Haptolachus without crepidal punctures (microsensilla). Maxilla with a row of 16 to 18 conical, sharp-pointed stridulatory teeth. Thoracic spiracles slightly larger than spiracles on abdominal segments 1 to 4 which are similar in size. Spiracles on abdominal segments 5 to 8 progressively smaller.

Anal opening broadly V-shaped. Raster with 2 short, nearly parallel, longitudinal palidia each sparsely set with 7 to 12 long, sharp, cylindrical pali

whose tips frequently almost touch those of the opposite palidium. Tegilla extending in front of palidia for a distance equal to the length of the palidia. Pre-septular hamate setae more than 50 in number. Tegilla occupying the caudal half or slightly less than the caudal half of the area between the lower anal lip and the anterior margin of the last abdominal segment.”

**Distribution.**—Specimens examined: 2593 males, 984 females for a male:female ratio of 2.64:1. *P. decemlineata* is distributed discontinuously over the western U.S., small portions of southwestern Canada and possibly much of Mexico. The eastern boundary of its range is the eastern edge of North Dakota, central South Dakota, and northeastern to east central Nebraska. It is unrecorded in Minnesota, Iowa, and Missouri. In Nebraska it is not found south of the Platte River but is very common to the north. I have no record of *P. decemlineata* from Kansas; at first I thought this was simply insufficient data or a collecting artifact. I am now convinced, however, that this species does not occur south of the Platte River in Nebraska and in all of Kansas. I believe Hardy's 1981 citation of “known from Kansas to Washington” to be incorrect. I consider the records from central Oklahoma (Cleveland Co.), north central Texas (Baylor Co.), and east central Texas (Nacogdoches Co.) highly questionable. From this eastern boundary *P. decemlineata* is recorded from all western states and throughout each state. It is most common and abundant throughout Arizona, California, Nevada, and Utah.

In Canada demes are recorded from Vancouver and environs, and south central British Columbia. Areas on each side of the Alberta-Saskatchewan boundary just north of central Montana are also well represented.

From Mexico specimens of *P. decemlineata* are on hand from localities within the states of Baja California, Chihuahua, Hidalgo, and San Luis Potosi. I have little doubt that additional work on the Mexican and Central American species of *Polyphylla* will extend these few records considerably (Fig. 20).

CANADA: ALBERTA: Dunes, Lethbridge, Medicine Hat, Red Deer, Steveville, Writing-on-Stone. BRITISH COLUMBIA: Edgewood, Marysville, Oliver, Vancouver. SASKATCHEWAN: Cabri, Fox Valley, Pennant Station, Pike Lake, Riverhurst, (Great Sand Hills area).

MEXICO: BAJA CALIFORNIA: 14 mi. N. Laguna, San Pedro Martir (La Conia), Tijuana. CHIHUAHUA: Hidalgo (Guerrero Mill, 9000 ft.), Matachic. HIDALGO: 2 km. S. Metztilan. SAN LUIS POTOSI: San Luis Potosi. NOTE: Hardy (1981) cites the following uncorrelated Baja records: 14 mi. E. Meling Ranch, Corona Abajo, S. of El Rayo, 2 mi. S. Laguna Hanson, Arroyo Santo Tomas, 10 mi. S. San Matais Pass, San Jose Castillo.

UNITED STATES: ARIZONA: *Apache Co.*: Canyon de Chelly NM (7000 ft.), Lupton, Sanders. *Cochise Co.*: Chiricahua Mts. (Cave Creek Canyon @ 5800–8800 ft; S. Fork Cave Creek Canyon @ 5000 ft.), Huachuca Mts. (Garden City @ 5500 ft.), Madera Canyon, Oak Creek Canyon, Paradise, Portal, Rucker Canyon (5300 ft.), Southwestern Research Station (5400 ft.), Tombstone, Turkey Creek @ 6000 ft. (and E. Turkey Creek @ 6700 ft.-pine oak; Onion Saddle Rd. @ 6500 ft.), Wilcox. *Coconino Co.*: Flagstaff, Gonado Mission, Grand Canyon (Bright Angel Trail, Bright Angel Point, N. Rim), Oak Creek Canyon (3500 ft.), Painted Canyon Rd., Sedona. *Gila Co.*: Globe, Payson, San Carlos (Ash Hat), Star Valley. *Maricopa Co.*: Phoenix. *Pima Co.*: Madera Canyon, Tucson, Sec. 18 T19N R15E. *Mohave Co.*: Beaver dam. *Santa Cruz Co.*: Nogales, Patagonia. *Yavapai Co.*: Jerome, 4 mi. N. Prescott (Granite Dells), Rimrock. *Yuma Co.*: No data. *County Unknown*: Marsh Pass.

CALIFORNIA: *Alameda Co.*: Berkeley, hills back of Oakland, Oakland (Chobot Observatory), Piedmont. *Amador Co.*: Lone, Jackson, Sutter Creek. *Butte Co.*: Chico (190 ft.), Oroville, Paradise. *Calaveras Co.*: Arnold, Mokel Hill, Camp Wolfeboro. *Colusa Co.*: Arbuckle, Colusa. *Contra Costa Co.*: Lafayette, Pittsburg, Pleasant Hill, Walnut Creek, foot of Shell Ridge (Walnut Creek). *Del Norte Co.*: 6 mi. N. Klamath, Klamath. *El Dorado Co.*: N. side S. Fork American River, Bijou, Coma, Placerville, Snowline Camp, Stateline, Lake Tahoe (Lake Forest), Yosemite (3880–4000 ft.). *Esmeralda Co.*: Chiatovitch Creek. *Fresno Co.*: Fresno, 8 mi. W. Fresno (Kearney Park), Kerman, Pine Flat Res., Reedley, Selma. *Glenn Co.*: Greyhound Post Office (Orland). *Humboldt Co.*: Arcata, Eureka, 4 mi. S. Orick, Trinidad. *Inyo Co.*: Antelope Spring (8 mi. SW Deep Spring), Antelope, Big Pine, Bishop, Death Valley NM (Panamint Range, Wild Rose Canyon), Independence, Lone Pine, 9 mi. W. Lone Pine (8250 ft.), Lone Pine Creek (8250 ft.), Olancho, Owens Lake, Owens Range (High Sierra's, 7000 ft.),

Owens Valley, Panamint Range (Surprise Canyon), 7 mi. N. Parcher's Camp, Westgard Pass (7200 ft.), Whitney Portal to Mt. Whitney Trail (10,000 ft.). *Kern Co.*: Bakersfield, 7 mi. NW Frazier Park, Kernville, Oildale, Shafter, Wasco. *Lake Co.*: Anderson Springs. *Lassen Co.*: Amedu (3960 ft.), Hallelujah Jct., Milford (nr. Honey Lake), Angeles Natl. Forest (Sulphur Springs), Arcadia, Azusa, Beverly Hills, Buzzard Peak, Camp Baldy, Claremont, Crystal Lake, Glendale, Glendora, Griffith Park Observatory, Los Angeles, LaCanada-Tujunga (Foothill Blvd.), Mint Cyn., Monrovia, Monterey Park, North Hollywood, Pasadena, 3 mi. S. Pear Blossom, Redondo Beach, Santa Anita Cyn., Winter Creek, San Gabriel Mts. (Coldbreak Guard Station), Tanbark Flat, Valyermo, Whittier. *Marin Co.*: Corte Madera, Inverness, McClure Beach, Mill Valley. *Mariposa Co.*: Incline, Lake Tahoe, Oakhurst (Miami Ranger Station, nr. Sugar Pine, 5000 ft.), Yosemite Natl. Park, Yosemite, Yosemite Valley. *Mendocino Co.*: Mendocino, Purey. *Merced Co.*: Merced. *Modoc Co.*: 6 mi. NW Cedarville, Davis Creek (Wener Mts., 5600 ft.), Warner Valley (Plum Mts., 5800 ft.). *Mono Co.*: Benton, Benton Station, Bridgeport, Frying Pan Creek (E. Walker River), Grant Lake, 2 mi. SE Lee Vining, 5 mi. S. Lee Vining, Lee Vining, Lundy Creek (nr. Mono Lake), Mono Lake (Tioga Lodge), 5 mi. S. Mono Lake, 1 mi. W. Tom's Place, 1 mi. SW Tom's Place, White Mts. (Crooked Creek, 10,150 ft., 3 airline mi. N. Inyo Co., Crooked Creek Lab.). *Monterey Co.*: Carmel, Castroville, Chualar, Monterey, Salinas (Blanco District). *Napa Co.*: Pope Valley, St. Helena. *Nevada Co.*: Nevada City, Camp Celio nr. Nevada City, Trukee. *Orange Co.*: No data. *Placer Co.*: Auburn, Brockway, Colfax, Lake Tahoe, Penryn, Roseville. *Plumas Co.*: Johnsville, 4 mi. W. Quincey. *Riverside Co.*: Beaumont, Hemet, San Jacinto Mts. (Hurkey Creek, Idyllwild, NW Idyllwild), Magnesia Cyn., Palm Springs, Rancho La Sierra, Riverside. *Sacramento Co.*: Carmichael, North Frazier, Sacramento, Trange Vale, Watoma. *San Benito Co.*: 6 mi. SE Idria, head of Larious Creek SW of Idria (4380 ft.), Pinnacles Natl. Monument (Chalone Camp). *San Bernardino Co.*: Cajon Pass, Camp Angeles, Camp Baldy, Colton, Falls P.C. (?), Fawnskin, San Bernardino Natl. Forest (Hanna Flats), Lake Arrowhead, Miller Cyn., Redlands, San Bernardino, Toll Road P.C. (?), Upland, Wrightwood. *San Diego Co.*: Alpine (3600 ft.), Julian, Lakeside, La Mesa, Mt. Laguna, Mt. Palomar St. Park, Mt. Palomar, Ocean Beach, Poway, San Diego, Warmer Springs. *San*

*Francisco Co.*: San Francisco, north of San Francisco. *San Luis Obispo Co.*: Atascadero, Morro Bay. *San Mateo Co.*: Halfmoon Bay, San Bruno, Woodside. *Santa Barbara Co.*: Carpinteria Goleta, 6 mi. SW New Cuyama (Alliso Cyn.), 2 mi. S. Painted Cave, Santa Barbara, Sierra Madre Mts. *Santa Clara Co.*: Burbank, Los Gatos, Milpitas, Monte Vista, Morgan Hill, Mt. View, Palo Alto, San Antonio Valley, San Jose, San Jose St. College campus. *San Mateo Co.*: Menlo Park. *Santa Cruz Co.*: Ben Lomond, Felton, Mt. Herman, Santa Cruz, Waddell Creek, Watsonville. *Shasta Co.*: Hat Creek R.S., Hat Creek Post Office, Project City, Redding. *Sierra Co.*: Yuba Pass (6701 ft.). *Siskiyou Co.*: Fowlers Camp (5 mi. E. McCloud), Happy Camp, 7 mi. NW Pennent, Shasta City. *Solano Co.*: No data. *Sonoma Co.*: Bodega Bay, Cloverdale, Duncan Mills, Guerneville, Healdsburg, Mission Valley, Santa Rosa, Windsor. *Stanislaus Co.*: Salida. *Sutter Co.*: Live Oak, 3 mi. W. Liverdale. *Tehama Co.*: Aro Bluff, Red Bluff. *Trinity Co.*: Weaverville. *Tulare Co.*: Dinuba, Three Rivers, Sequoia Natl. Park, Visalia. *Tuolumne Co.*: Groveland, 4 mi. W. Pinecrest, Strawberry, Train-Harte (4000 ft.). *Ventura Co.*: Santa Paula, Saticoy, Ventura. *Yolo Co.*: Elkhorn Ferry, Esparto, Davis. *Yuba Co.*: Marysville. *County Unknown*: Black Lake, Brownsville, Davis Meadow RR Flat (2800 ft.), Hackmore, LaGrange, Laguna Mts., Paris, Peavine, Saugus, Tioga Pass (10,000 ft.), Westport.

**COLORADO**: *Alamosa Co.*: Great Sand Dunes NM. *Archuleta Co.*: Arboles (6000 ft.), Pagosa Springs (7100 ft.). *Baca Co.*: No data. *Boulder Co.*: Boulder, Lyons. *Costilla Co.*: Fort Garland (Mt. Home Lake @ 8300 ft.). *Chaffee Co.*: No data. *Delta Co.*: Paonia. *Denver Co.*: Denver. *El Paso Co.*: Colorado Springs (6000 ft.), Rock Creek Canyon, Manitou Peak, Manitou Springs. *Fremont Co.*: Canon City. *Garfield Co.*: Riverbottom (4 mi. W. Rifle), Rifle, Una. *Grand Co.*: Rocky Mt. Natl. Park. *Huerfano Co.*: Gardner. *Jefferson Co.*: Clear Creek (6–7000 ft.), Morrison, Pine. *La Plata Co.*: Durango. *Larimer Co.*: Big Thompson Canyon (6200 ft.), Estes Park, 21 mi. E. Estes Park, Fort Collins, 12 mi. NW Ft. Collins (Poudre River @ 5000 ft.), Loveland. *Logan Co.*: Sterling (4100 ft.). *Mesa Co.*: Grand Junction. *Moffat Co.*: Dinosaur NM (Castle Park), Maybell. *Washington Co.*: Cope. *Weld Co.*: Fort Lupton, Roggen. *County Unknown*: Alpine, Colorado Lake, Dixon Canyon, Dunes, Maysville.

**IDAHO**: *Ada Co.*: Boise. *Bingham Co.*: Springfield. *Blaine Co.*: 9 mi. NW Ketchum (North Fork Camp @

6200 ft.). *Boise Co.*: Horse Shoe Bend. *Bonner Co.*: Elmira, Priest Lake. *Bonneville Co.*: Idaho Falls, Ucon. *Butte Co.*: Craters of the Moon NM. *Canyon Co.*: Arena Valley, Melba, Notus, Parma, 4 mi. S. Roswell. *Caribou Co.*: Bancroft. *Cassia Co.*: Elba. *Fremont Co.*: Ashton. *Gooding Co.*: 3 mi. S. Tuttle. *Jefferson Co.*: Lorengo. *Kootenai Co.*: Coeur d'Alene, Garwood. *Latah Co.*: Moscow. *Lewis Co.*: Nez Perce. *Lincoln Co.*: Pagari (Littlewood River). *Minidoka Co.*: Ruper (4157 ft.). *Nez Perce Co.*: Lewiston. *Owyhee Co.*: Silver City (6179 ft.). *Shoshone Co.*: Murray. *Twin Falls Co.*: Twin Falls. *Valley Co.*: McCall. *County Unknown*: R'Dale.

**MONTANA**: *Big Horn Co.*: Lodge Grass. *Carbon Co.*: Crooked Creek. *Chouteau Co.*: Big Sandy. *Custer Co.*: Miles City. *Flathead Co.*: Big Fork (Flathead Lake), Kalispell. *Gallatin Co.*: Bozeman (Montana Exp. Station). *Garfield Co.*: nr. Snow Creek. *Lake Co.*: Lake Ronan, Ravalli. *Missoula Co.*: Missoula (3000 ft.). *Petroleum Co.*: No data. *Ravalli Co.*: Corvallis, Darby, Girds Creek, Hamilton. *Roosevelt Co.*: Poplar, Wolf Point (2000 ft.). *Rosebud Co.*: Rosebud. *Sanders Co.*: Thompson Falls. *Stillwater Co.*: Columbus. *Toole Co.*: Ethbridge. *Yellowstone Co.*: Billings. *County Unknown*: Menida.

**NEBRASKA**: *Antelope Co.*: Neligh. *Arthur Co.*: Arapaho Prairie, 4 mi. N. Arthur (on Chinese Elm), Arthur. *Boone Co.*: Petersburg. *Box Butte Co.*: No data. *Brown Co.*: No data. *Chase Co.*: No data. *Cherry Co.*: Valentine. *Cheyenne Co.*: Sidney. *Cuming Co.*: West Point. *Custer Co.*: No data. *Dawes Co.*: Chadron. *Deuel Co.*: Chappell. *Douglas Co.*: Omaha. *Garden Co.*: No data. *Grant Co.*: Hyannis, 1 mi. S. Hyannis. *Keith Co.*: Cedar Point Biological Station. *Lincoln Co.*: North Platte. *McPherson Co.*: Sandhills Ag. Lab. nr. Tryon. *Merrick Co.*: No data. *Morrill Co.*: Alliance, 10 mi. SW Alliance. *Scotts Bluff Co.*: Morrill, Scotts Bluff. *Sheridan Co.*: Gordon, 15 mi. S. Gordon. *Sioux Co.*: Agate, Glen (4000 ft.), Hat Creek Valley, Monroe Canyon, Sioux Canyon, Sioux City, Sowbelly Canyon, Warbonnet, Warbonnet Canyon. *Thomas Co.*: Halsey, Halsey Forest Reserve, Thedford. *Wayne Co.*: No data.

**NEVADA**: *Churchill Co.*: Fallon, 10 mi. N. Fallon, 8 mi. N. Fallon. *Clark Co.*: Corn Creek, Mt. Charleston (Kyle Canyon @ 7500 ft.), Mt. Springs Summit (5400 ft.), Pine Creek (4000 ft.). *Douglas Co.*: Clear Creek, Stateline, Zephyr Cove. *Esmeralda Co.*: Indian Creek (7700 ft.), Middle Creek. *Humboldt Co.*: Martin Creek (4800 ft.), 5 mi. W. Orovada, Winnemucca, 10 mi. N.

Winnemucca. *Lander Co.*: Austin, 5 mi. ESE Austin (Hwy. 50 @ 6750 ft.). *Lincoln Co.*: Alamo, Caliente, Charleston Mts. (Willow Creek Camp), Water Canyon (7500 ft.). *Lyon Co.*: Fort Churchill, Silver Springs, Wilson Canyon (4900 ft.), Yerrington. *Mineral Co.*: Alum Creek (6200 ft.), Hawthorn. *Nye Co.*: Beatty, McIntyre Summit (6940 ft.), Peavine Ranch, Sawmill Canyon (7600 ft.). *Ormsby Co.*: Carson City, nr. Carson City (Kings Canyon), 2 mi. W. Carson City. *Pershing Co.*: Rye Patch Dam. *Washoe Co.*: Pyramid Lake, S. Pyramid Lake, Reno, Reno Hot Springs, Wadsworth. *White Pine Co.*: Baker, 5 mi. W. Baker (7000 ft.), 8 mi. W. Baker, Mt. Wheeler.

NEW MEXICO: *Bernalillo Co.*: Albuquerque, Sandia Mts. nr. Albuquerque, Sandia Park. *Catron Co.*: 9.5 mi. NE Glenwood. *Grant Co.*: Mule Creek, 14 mi. N. Silver City (McMillan Camp @ 7000 ft.). *Hidalgo Co.*: Rodeo (4000 ft.). *Lincoln Co.*: Hondo, 2 mi. N. Ruidoso (Cedar Creek Camp @ 7000 ft.). *Los Alamos Co.*: Los Alamos. *Otero Co.*: Bent. *Sandoval Co.*: Bandelier NM (Frijoles Cyn. @ 6050 ft.), Battleship Rock Camp on upper Jemez River (6 mi. N. Jemez Springs), Jemez Mts. (6600 ft.), Jemez Springs (6400 ft.). *San Juan Co.*: Chico Cyn. *San Miguel Co.*: nr. Hot Springs (Las Vegas @ 7000 ft.), Las Vegas. *Santa Fe Co.*: Santa Fe, 6 mi. NE Santa Fe (8000 ft.). *Taos Co.*: Ojo Caliente, Taos. *County Unknown*: Watrous.

NORTH DAKOTA: *Billings Co.*: Medora, Th. Roosevelt St. Park. *Burleigh Co.*: Bismark. *Cass Co.*: No data. *Emmons Co.*: No data. *Grant Co.*: Heart Butte Dam. *McKenzie Co.*: Cannonball Crk., Th. Roosevelt Natl. Mem. Park (north unit). *Morton Co.*: Mandan. *Richland Co.*: No data. *Stark Co.*: Dickinson. *Slope Co.*: Burning Coal Vein, Chalky Buttes.

OKLAHOMA: *Cimarron Co.*: Kenton. *Cleveland Co.*: No data.

OREGON: *Baker Co.*: Baker (Pine Creek). *Benton Co.*: Corvallis. *Coos Co.*: No data. *Crook Co.*: No data. *Curry Co.*: Gold Beach, Port Orford. *Deschutes Co.*: No data. *Harney Co.*: 20 mi. S. Burns (4200 ft.). *Jackson Co.*: Gold Hill, Medford. *Josephine Co.*: Oregon Caves. *Klamath Co.*: Beaver Marsh, Klamath Falls. *Lane Co.*: Eugene, Oak Ridge. *Malheur Co.*: Ontario (2153 ft.). *Multnomah Co.*: Portland. *Umatilla Co.*: Milton. *Wasco Co.*: The Dalles. *County Unknown*: McMinnville, Rhododendron, Steamboat.

SOUTH DAKOTA: *Butte Co.*: Newell, Nisland. *Fall River Co.*: Hot Springs. *Hughes Co.*: Pierre. *Potter Co.*: Gettysburg. *Stanley Co.*: No data. *Sully Co.*: On-

dia. *Walworth Co.*: Mobridge, Selby. *Ziebach Co.*: Dupree. *County Unknown*: Edgerton.

TEXAS: *Baylor Co.*: Seymour. *Jeff Davis Co.*: Davis Mts. (Madera Canyon Park), Fort Davis (Limpia Cyn. @ 5000 ft.). *Nacogdoches Co.*: Nacogdoches.

UTAH: *Beaver Co.*: Beaver, 5 mi. E. Beaver (6300 ft.), Beaver Valley, Milford. *Box Elder Co.*: Snowville. *Cache Co.*: Hyde Park, Logan, Spring Hollow. *Carbon Co.*: Price. *Daggett Co.*: Manila, Palisade Park Camp. *Davis Co.*: Bountiful, Kaysville. *Duchesne Co.*: Duchesne, 7 mi. W. Duchesne (5900 ft.), Fort Duchesne, Myton, Roosevelt. *Emery Co.*: No data. *Garfield Co.*: 11 mi. SE Panguitch (Red Cyn. Camp @ 7200 ft.). *Grand Co.*: Moab (4000 ft.). *Iron Co.*: Cedar City, Iron Springs (5000 ft.). *Juab Co.*: Eureka. *Kane Co.*: Kanab, Orderville. *Millard Co.*: Delta, Fillmore, Hinckley. *Morgan Co.*: No data. *Piute Co.*: No data. *Salt Lake Co.*: Midvale, Salt Lake City, North Salt Lake City. *San Juan Co.*: Dun's Place, 5 mi. W. Monticello (Dalton Springs Camp @ 8500 ft.), Navajo Mt. Trading Post. *Sanpete Co.*: Gunnison, Sanpete. *Sevier Co.*: Big Rock Candy Mtn., Richfield. *Tooele Co.*: Johnson's Pass, Stockton, Tooele. *Uintah Co.*: Vernal, 22 mi. NNW Vernal (Kaler Hollow Camp @ 8900 ft.), 25 mi. N. Vernal (Iron Springs Camp @ 8700 ft.). *Utah Co.*: Benjamin, Delta, Dividend, Duquesne, Lindon, Pleasant Grove, Provo, Salem, Spanish Fork Canyon, Spanish Fork, Springville, Vineyard. *Washington Co.*: Leeds, Zion Natl. Park (Grotto Camp, Ciatio Camp, Oak Creek Canyon), St. George. *Weber Co.*: Hooper, Ogden Canyon, Ogden, Roy. *County Unknown*: Ballard, Granite, Hennifer.

WASHINGTON: *Chelan Co.*: No data. *Columbia Co.*: Dayton. *Douglas Co.*: Orondo. *Klickitat Co.*: No data. *Okanogan Co.*: Lake Okanogan. *Pierce Co.*: Puyallup. *San Juan Co.*: Friday Harbor, Orcas Island, San Juan Island. *Snohomish Co.*: Arlington, Everett. *Spokane Co.*: Spokane. *Stevens Co.*: Kettle Falls St. Park. *Walla Walla Co.*: College Place. *Whitman Co.*: Pullman. *Yakima Co.*: Toppenish, Yakima.

WYOMING: *Albany Co.*: Laramie, T15N R73W. *Bighorn Co.*: Buffalo Basin, Greybull, mouth of Shell Creek at Shell Canyon (4230 ft.). *Campbell Co.*: Gillette. *Converse Co.*: Douglas. *Crook Co.*: Aladdin, Devils Tower. *Goshen Co.*: 7 mi. NW Torrington. *Johnson Co.*: Buffalo. *Niobrara Co.*: 12 mi. NW Lusk, 40 mi. N. Lusk. *Park Co.*: 15 mi. S. Cody, Shoshone Natl. Forest (Horse Creek Camp), Morris Ranch nr. Cody (6700 ft.), Powell. *Platte Co.*: 11.5 mi. SW Ft. Laramie, Wheatland. *Sweetwater Co.*: Boars Tusk

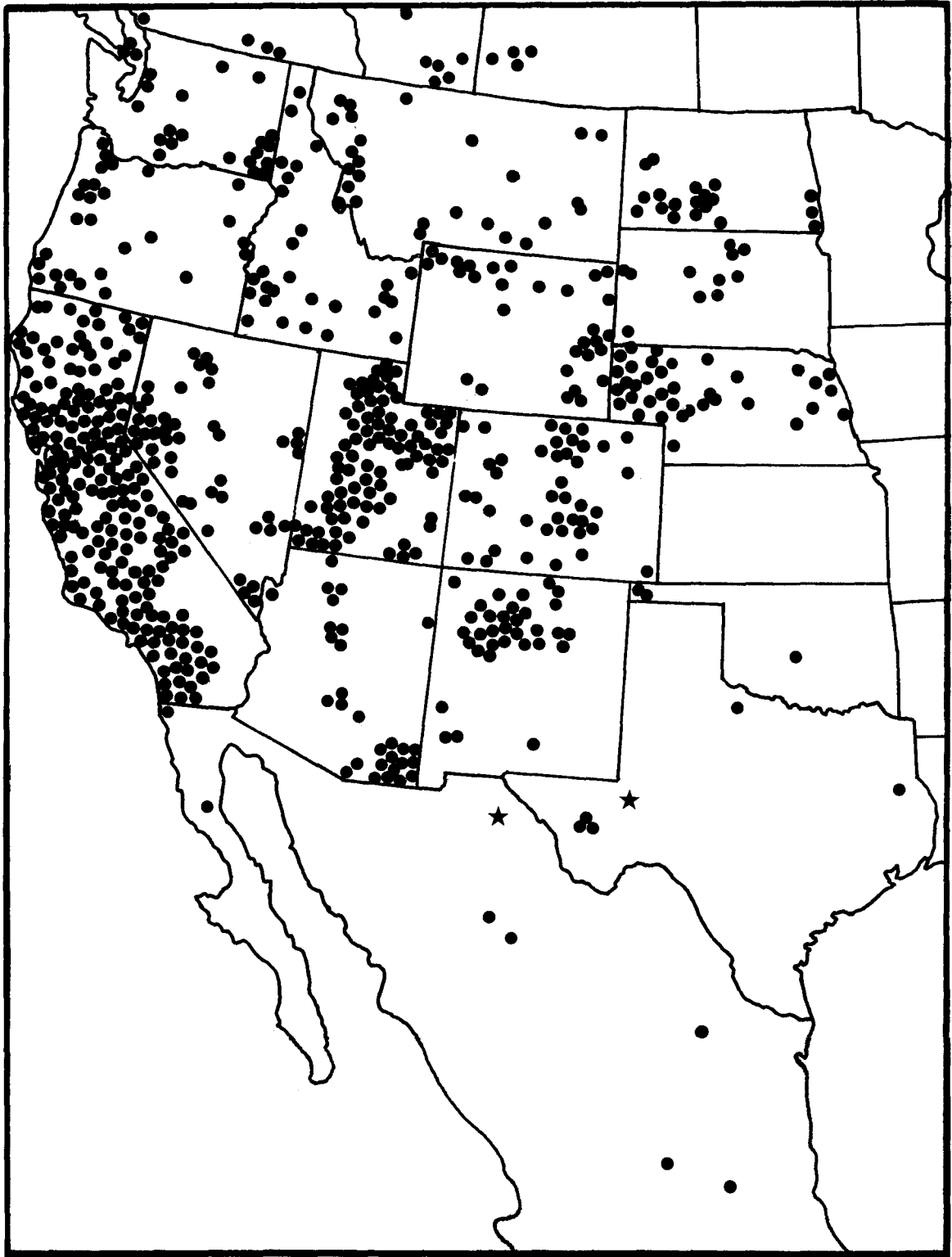


Fig. 20.—Distributions of *P. decemlineata* (●) and *P. monahansensis* (★).

Mtn., Old Ford on Green River (27 mi. S. LaBarge).  
*Teton Co.*: Yellowstone Natl. Park (Old Faithful area).  
*Washakie Co.*: Worland. *Weston Co.*: Newcastle.

MARCH (3), APRIL (0), MAY (56), JUNE (596),  
 JULY (1707), AUGUST (785), SEPTEMBER (53),  
 OCTOBER (4).

**Biology.**—Johnson (1954) recorded feeding activity of adult *P. decemlineata* at Spokane, Washington. They were found in considerable numbers during July, 1948 and 1949 feeding on the needles of ponderosa pine. The infestation was in natural pine stands with sparse grass and herbaceous cover. About one-half of all needles in lateral branch terminal clusters were eaten, with a single beetle present per cluster. The adults began their feeding distally and worked inwards towards the needle base consuming everything except the midrib. Many infested trees were the most luxuriant, with the greatest abundance of needles. Tree death did not result from this activity.

Onsager (1966) published a note on larval feeding activity in Washington state. A larval population at a density of four per square foot was found feeding in 40 acres of irrigated orchard grass near Winchester in Adams County. The population was 75% first instar with 30% of it feeding on the grass roots and the remainder found 4–9 inches below the soil surface.

J.A. Onsager (personal correspondence) has also observed marked differences in the relative numbers of each instar in wild populations at different seasons of the year. The life cycle in the Pacific Northwest seems to be a three year one with ca. one instar per year. New first instars are found during late August and September. All instars overwinter 12–30 inches below the soil surface and return to feeding level during April and May. After feeding for a short time the larvae moult or pupate during June and July.

In addition to describing the third instar larva, Ritcher (1966) recorded it in the sandy soils of western Oregon and Washington as feeding on strawberry plants, coniferous seedlings, roots of fruit trees, corn, table beets, hops, mint, potato tubers, and blueberry plants. Ritcher (1958) mentions that pupation takes place in early June from 5–8 inches deep with adults flying from early July until fall.

Lilly and Shorthouse (1971) published on the responses of male *P. decemlineata* to female sex pheromones. In Alberta, Seamans (1928, 1942) observed large numbers of adults on ca. 10,000 acres

of willows among sandy dunes at Manyberries, and on willows along the Oldman River at Lethbridge. The observations of Lilly and Shorthouse are from this Lethbridge locality. Larvae were found in sandy, sparsely-covered soil in clearings in mixed poplar groves (*Populus angustifolia* hybrid) bordering the river. Females emerged from the sandy soil at dusk and flew directly to the poplar trees. There they remained stationary on the branches and leaves until males flew in and initiated copulation. Mating pairs were found 8–18 ft. high in the trees. Incoming males had their antennal lamellae widely spread and were attracted to mating pairs as well as areas previously occupied by females.

Females (individuals and from mating pairs) were collected and quick frozen within three hours. As needed they were thawed and divided into (1) head plus thorax and (2) abdomen. Each portion was extracted separately for ca. three hours in a Soxhelt micro-extractor with 70% ethanol as the solvent. Extracts were diluted to 25 ml and stored. Cotton swabs soaked in either of the two extracts were secured to branches 6–9 ft. high in an isolated poplar tree earlier established as a favored aggregation site of the beetles. Males were not attracted to the head-thorax extract. Many were attracted to the abdomen extract. Their reactions seemed identical to those exhibited when approaching females. The males spread their antennal lamellae, hovered over the cotton swabs, and landed in apparent excitement to begin searching the site. Swabs soaked with the extract were placed in holes at two foot intervals along a 12 foot board which was erected vertically in the clearing. Counts for four evenings were as follows:

Height of extract above								
ground (ft.):	0	2	4	6	8	10	12	
No. of males attracted:								
	0	0	0	15	12	19	16	

Adults began emerging the second week of July and flight continued for one month. Largest flights were on clear, warm evenings when the air temperature at a height of three ft. was above 15 degrees C. Male flight to the extracted pheromone and to females in the trees began at 2117 hrs. but as the season advanced it started earlier, reaching 2025 hrs. late in the season. Time interval between sunset and flight initiation for 25 evenings averaged 39.7 minutes (range 30–53). Flight duration for the ten largest flights was 59.9 minutes (range 44–74). This corre-

lates reasonably well with my field observations in Arizona (Table 3). A heavy rainstorm disrupted flight as did a strong chinook wind. Erratic male flight three ft. above the ground without being attracted to samples of the extract at the same height suggested that wind hindered them from following the odor trails. Many flying males were eaten by bats.

In summary, Lilly and Shorthouse concluded that females of *P. decemlineata* fly directly to trees silhouetted against the sky, where emission of a pheromone supplemented by visual stimuli, promotes the mass mating flights of the males (see also summary of Fowler and Whitford, 1981 under biology of *P. diffracta*).

Stein and Kennedy (1972) wrote that *P. decemlineata* are solitary defoliators of white willow in the northern Great Plains, though they did not actually observe such feeding.

Lago (1979) observed large flights of this species in ponderosa pine stands in western North Dakota but recorded no adult feeding. Gut content analysis revealed no plant material. He was unable to discover a suitable explanation for the lack of North Dakota feeding records but suggested that adults feed only

under certain conditions of climate or stress. *P. decemlineata* is taken sympatrically with *P. hammondi* in western North Dakota, with *P. decemlineata* found in less sandy soils.

Data presented in the remainder of this section were collected by the author during the summer of 1967 which was spent collecting in the southwestern states, primarily Arizona and Utah (Table 3).

On July 17 an ultra-violet light was run at 8800 foot Rustlers Park, Cave Creek Canyon, Cochise Co., Arizona. It is within the douglas fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco)—yellow pine (*Pinus leiophylla* var. *chihuahuana* [Engelm.] Shaw) life zone, which, at this locality, runs from ca. 7300 to 9800 ft. elevation. I have used Little (1953) as a reference for tree species nomenclature and Martin (1963) refers to this area as pine parkland-forest. The vegetational complex includes in addition to the two species mentioned, ponderosa pine (*Pinus ponderosa* var. *ponderosa* Laws.), engelmann spruce (*Picea engelmannii* Parry), white fir (*Abies concolor* [Gord. & Glend.] Lindl.), and quaking aspen (*Populus tremuloides* Michx.). On a cold night (55 degrees F. dry bulb) just after heavy rains the first *P. decemli-*

**Table 3.** *P. decemlineata* flight activity at selected sites, July and August, 1967

Date	Elevation	Biotic Zone	Temp./RH	First	Last	Flight Duration
<i>Cave Creek Canyon, Arizona</i>						
July 17	8800	douglas fir-yellow pine	55 F. dry	9:50	10:10	20
July 19	7200	pinon-juniper	60 F. dry	9:25	9:55	30
July 29	7200	pinon-juniper	62 F. dry, 59 F. wet, 84% RH	9:30	10:05	35
July 19	6200	scrub oak-juniper	—	10:15	—	—
July 30	6200	scrub oak-juniper	—	9:45	—	—
July 20	5800	scrub oak-juniper	65 F. dry, 61 F. wet, 80% RH	9:35	9:55	20
July 28	5800	scrub oak-juniper	70 F. dry	9:20	10:10	50
August 3	5800	scrub oak-juniper	—	9:35	11:00	85
MEAN FLIGHT DURATION						40
<i>Rucker Canyon, Arizona</i>						
August 6	5300	juniper, yucca, sycamore	—	9:20	—	—
<i>Canyon de Chelly, Arizona</i>						
August 10	7000	pinon-juniper	—	9:10	—	—
<i>Zion National Park, Utah</i>						
August 17	4100	cottonwood	—	9:17	—	—

*neata* male was taken at 9:50 PM, with dusk falling at ca. 8:45 PM. Under these conditions there was a clear paucity of insect activity with only a few moths, one *Diplotaxis* and one *Orizabus clunalis* LeConte (Dynastinae) coming to the light. The last *P. decemlineata* was taken at 10:10 PM so adult flight, at least that induced by the lights, was limited to 20 minutes. Males were placed on young ponderosa pine but could not be induced to feed.

On July 19, a deme was sampled at 7200 feet in the same canyon, within the pinon pine (*Pinus edulis* Engelm.)—Rocky Mtn. juniper (*Juniperus scopulorum* Sarg.) life zone. Additional species were ponderosa pine, the endemic apache pine (*Pinus engelmannii* Carr.), blue spruce (*Picea pungens* Engelm.), shrub oak (*Quercus turbinella* Greene), barberry and rabbit brush. Dusk at ca. 8:50 PM triggered a swarming, feeding flight of *Phyllophaga vetula* (Horn) and *Orizabus clunalis* (LeC.) on the long-needled apache pine (Young, 1969). The first *P. decemlineata* was taken at 9:25 PM and the last at 9:55 PM, a 30 minute burst. This site was again sampled on July 29 with *P. decemlineata* taken from 9:30 to 10:05 PM, a flight period of 35 minutes (62 degrees F. dry bulb, 59 degrees F. wet bulb, 84% RH).

Also on July 19 a single male was taken at 10:15 PM at 6200 feet in an area dominated by Arizona white oak (*Quercus arizonica* Sarg.) and Rocky Mtn. juniper, with scattered ponderosa pine and douglas fir present in the wetter ravines. Dissected females on this date were heavily gravid. On July 30 *P. decemlineata* was again taken at this locality, around 9:45 PM.

A third site sampled within Cave Creek Canyon was at 5800 feet and forested primarily with the oak-juniper complex mentioned above but without the pine-fir association of higher, wetter sites. On July 20 the first *P. decemlineata* came into the lights at 9:35 PM (60 degrees F. dry bulb, 65 degrees F. wet bulb, 91% RH). Activity induced by the lights ended 20 minutes later. On July 28 flight activity at this locale lasted from 9:20 to 10:10 PM for an unusual duration of 50 minutes, probably due to the temperature being some 10 degrees F. warmer. One male was taken on alligator juniper (*Juniperus deppeana* Steud.) away from the lighted area where he had apparently been feeding. Another came to the light carrying a ponderosa pine needle between his mandibles where he consumed about half its length. A third sample taken here on August 3 yielded adults from 9:35 to 11:00 PM,

the longest activity period recorded. Unfortunately our temperature/RH equipment had been accidentally broken so I do not have climatic data for that evening. On August 5 this productive site was sampled from 11:00 PM to 2:00 AM with no *P. decemlineata* collected.

On August 6, Rucker Canyon 5 miles south of Apache, Arizona, was sampled. At ca. 5300 feet in a dry wash area dominated by alligator juniper, yucca, and Arizona sycamore (*Platanus wrightii* S. Wats.) a single female was taken at 9:20 PM.

On August 10 the 7000 foot plateau above Canyon de Chelly, Arizona was sampled. At the Spider Rock Overlook a single specimen was collected amid the pinon pine-Utah juniper (*Juniperus osteosperma* Torr. Little)—big sagebrush (*Artemisia tridentata* Nutt.) vegetation. The deme on this high plateau was effectively allotopically isolated from populations of *P. hammondi* occurring in this area at 5500 feet (see discussion of biology of *P. hammondi*).

On August 17 *P. decemlineata* was collected in Zion Natl. Park, Utah. Elevation was 4100 feet and the site was a sand flat area along a permanent river predominantly vegetated with fremont cottonwood trees (*Populus fremontii* var. *fremontii* S. Wats.). The only flight activity was recorded at 9:17 PM. This deme of *P. decemlineata* was evidently well isolated allotopically from *P. diffracta* populations in this same canyon which were sampled at 5200 feet (see biology of *P. diffracta*; see also Table 3).

I had the impression in Zion National Park that the last few stragglers of formerly more dense populations were being collected. This would seem illogical at first as the area is some 500 miles north of those sampled earlier in Arizona. One naturally would expect the more northerly populations to peak later in the season but the opposite seems to be true. Adult population density peaks for *P. decemlineata* and *P. diffracta* in Zion Natl. Park (from material collected by others) occur about the third week of July while the more southern populations peak a week or two earlier. The onset of the Arizona monsoon season around July 10 best explains this apparent discrepancy. This environmental factor, so critically important to much of the southern Arizona biota, is not present to such a degree in the deserts of southern Utah.

To summarize the data from Cave Creek Canyon, Arizona: *P. decemlineata* was collected from 4773 feet to 8800 feet. The sites ranged from the lower, formerly grassland areas which now support a desert



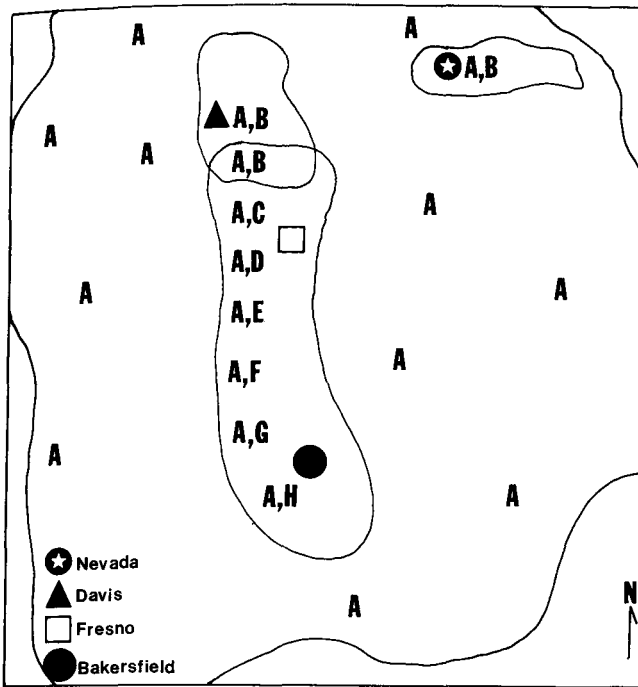


Fig. 21.—Schematic representation of north-south cline in basal elytral color of California and Nevada *P. decemlineata* demes. A = character state norm, B–H = character state variants.

*cemlineata*. I consider them as only local color phases of *P. decemlineata*. The color characters seem to be expressed in a north to south cline with the spectrum of variability increasing as one moves southwards through the central California valley. Fig. 21 shows this schematically with the homogeneous Davis deme overlapping morphologically (but not geographically) the heterogeneous Fresno-Bakersfield sample; both of which lie within the greater morphological expression of the *P. decemlineata* gene pool. The letters represent the relative degree of variation in color characters, with A equal to the norm. Another disjunct sample from Ormsby Co., Nevada, morphologically identical to that from Davis, is also represented.

The considerable list of Casey names synonymized by Fall (1928) under *P. decemlineata* is reaffirmed in this work, and lengthened. Repeated examinations of the Casey types clearly showed them to be individual variations. Each of the synonyms is represented by a type showing the clear cut vittae, large size, lack of pronotal hairs, aedeagal configuration, and coloration of the *P. decemlineata* norm. Among many workers, myself included, the tradition-

al idea that this name in fact covers a complex of species lingers on. However, there is no morphological, geographical, biological or ecological support for this concept. New synonyms of *P. decemlineata* here designated are *P. potsiana* Casey 1914, *P. comstockiana* von Bloeker 1939, and *P. matrona* Casey 1914. The name-bearing types of these three show all the essential features of *P. decemlineata* mentioned earlier. *P. comstockiana* was erected on the basis of its heavy dorsal white squamation, a character seen in many *P. decemlineata* from widely separated areas. *P. potsiana* was named because it came from a more exotic area (San Luis Potosi, Mexico) in a time when broad geographical areas remained poorly sampled if at all. The resulting geographical gaps in collections no doubt caused the naming of many demes which we now know are only samples of spatially continuous series of conspecific populations. *P. matrona* was apparently named on the basis of large size, as the name-bearing type is a large, robust *P. decemlineata* female. In summary none of these three names have any real basis for specific or subspecific standing and are herein newly synonymized with *P. decemlineata*.

#### *Polyphylla monahansensis* Hardy and Andrews (Figs. 6c, 20, 46)

*Polyphylla monahansensis* Hardy and Andrews 1978: 7. (Holotype male CASC 13100 and 137 male paratypes in AMNH, CASC, USNM, Howden, Nelson, Potts, Hardy. Type locality: TEXAS: Ward Co.: Monahans Sandhills State Park).

**Holotype Male.**—“Length 26 mm, width 8.5 mm, integumentary color testaceous to rufotestaceous except for piceous vertex, ocular canthi, clypeal suture, lateral clypeal margins. Apical clypeal margin reflexed; laterally, medially angulate. Reflexed clypeal margin, lateral margins, ocular canthi, lateral portions of front, vertex with close, recumbant elongate white scales. Medial portions of clypeus, front with few scattered white scales intermixed with long, erect testaceous hairs. Thorax trivittate basally; coarsely punctured, each puncture with a recumbant scale or single long erect testaceous hair. Punctures finer, closer anteriorly at midline. Elytra noticeably vittate, with scales smaller than thoracic scales. Pygidium without scales, with numerous short, semire-

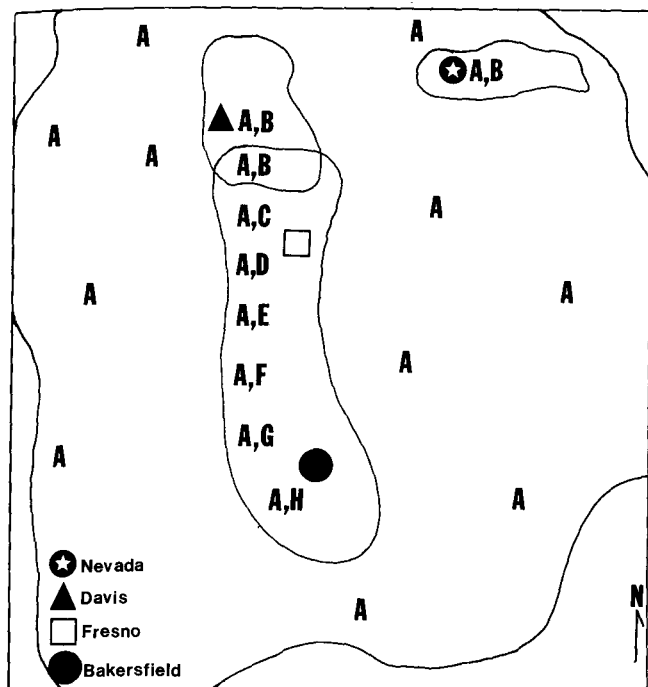


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***Polyphylla monahansensis* Hardy and Andrews**  
(Figs. 6c, 20, 46)

*Polyphylla monahansensis* Hardy and Andrews 1978:  
7. (Holotype male CASC 13100 and 137 male paratypes in AMNH, CASC, USNM, Howden, Nelson, Potts, Hardy. Type locality: TEXAS: Ward Co.: Monahans Sandhills State Park).

**Holotype Male.**—“Length 26 mm, width 8.5 mm, integumentary color testaceous to rufotestaceous except for piceous vertex, ocular canthi, clypeal suture, lateral clypeal margins. Apical clypeal margin reflexed; laterally, medially angulate. Reflexed clypeal margin, lateral margins, ocular canthi, lateral portions of front, vertex with close, recumbant elongate white scales. Medial portions of clypeus, front with few scattered white scales intermixed with long, erect testaceous hairs. Thorax trivittate basally; coarsely punctured, each puncture with a recumbant scale or single long erect testaceous hair. Punctures finer, closer anteriorly at midline. Elytra noticeably vittate, with scales smaller than thoracic scales. Pygidium without scales, with numerous short, semire-

cumbant testaceous hairs. Apical pygidial margin reflexed. Antennal club nearly three times length of basal segments (straight line measure). Maxillary palpi cylindrical in cross section, without flattened area. Anterior tibia bidentate. Thorax ventrally with dense, erect testaceous hairs. Ventral abdominal segments with sparse, recumbant, small white scales." (Hardy and Andrews 1978).

**Variation in Paratypes.**—"Length 21–27.5 mm, width 7.5–9.5 mm. Most conspicuous variation from the description above is in the shape of the reflexed anterior clypeal margin, which may lack the medial clypeal angulation, and have the lateral angles more rounded; and the anterior tibial teeth, which may be bidentate (as above) to strongly tridentate. The thoracic vittae may be more clearly developed than the type, and the elytral vittae occasionally may be faint, but are, in all specimens examined, clearly discernable throughout their length." (Hardy and Andrews 1978).

**Female.**—Unknown.

**Distribution.**—Specimens examined: 15. The holotype, ten paratypes, and three male topotypes (here designated) in the Ohio State University collections. Though they do not extend the distribution of this species, these three specimens are the first discovered other than the type series. They were collected by R.L. Berry (one specimen, VI–30–1972) and W.E. and C.A. Triplehorn (two specimens, VII–28–1973). Also one male from Mexico: Chihuahua, between Yepachic and Tomachic, large canyon bottom, VII–31–84, Doug Mullins. This is the first known specimen not from the type locality (Fig. 20).

JUNE (41), JULY (101).

**Remarks.**—Aedeagal configuration immediately places this species within the *decemlineata* complex, a conclusion entirely unexpected. In combination with this character the long, dense testaceous pronotal hairs distinguish it from all other species. Superficially *P. monahansensis* appears like the testaceous to rufotestaceous *P. sobrina*, a primarily California member of the *diffRACTA* complex, from which it may be distinguished by the aforementioned characters and its Texas and Mexican occurrence.

#### THE DIFFRACTA COMPLEX

##### *Polyphylla avittata* Hardy and Andrews

(Figs. 5a, 22, 47)

*Polyphylla avittata* Hardy and Andrews 1978: 1; Hardy 1981: 302; Young 1986: 49. (Holotype male CASC 13098 and 12 male paratypes in CASC, CA. Dept. Agr. Sacramento, Hardy, Howden, USNM. Type locality: UTAH: Washington Co.: 6 mi. S. Hurricane, Hurricane Dunes.)

**Holotype Male.**—"Length 22 mm, width 7.5 mm. Integumentary color of head piceous; thorax rufous; elytra rufo-testaceous; ventral surfaces (except abdomen), legs rufo-testaceous; abdomen rufo-piceous. Clypeal margin reflexed, outer apical angles well defined; reflexed margins with dense, close white scales; few scales medially on clypeal disc, along fronto-clypeal suture, scattered over front. Clypeus, front with close to contiguous large punctures, punctures with single scale or suberect hair. Vertex impunctate, glabrous, shining. Prothorax with close to contiguous punctures, with scales or hairs as above. Scales denser on midline and medio-laterally; prothorax appearing trivittate. Elytra lacking well defined punctures of thorax and head, but sparsely to densely covered with scattered scales, giving appearance of random clumping, without vittae, scales slightly smaller than on prothorax. Pygidium uniformly with scales and short recumbant hairs. Antennal club (measured in straight line, not along curve) twice length of three basal segments. Apical segment of maxillary palp slightly less than length of two basal segments; flattened on dorsal surface. Anterior tibia bidentate. Ventral surface of thorax with long grayish hairs." (Hardy and Andrews 1978).

**Variation in Paratypes.**—"Length 19.5–22 mm, width 7–7.5 mm. Most paratypes (9 of 12) have a faint indication of a third anterior tibial tooth, but this is never developed into more than just a slight flange on the tibial edge. Paratypes agree well in other respects." (Hardy and Andrews 1978).

**Female.**—Unknown.

**Distribution.**—Specimens examined: the holotype and three paratypes. Known only from the type

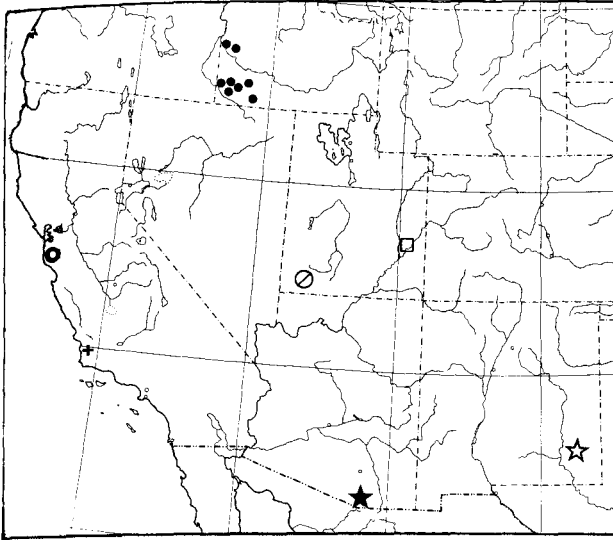


Fig. 22.—Distributions of *P. avittata* (ø), *P. barbata* (○), *P. devastiva* (●), *P. hirsuta* (★), *P. mescalerensis* (☆), *P. nubila* (+), and *P. ratcliffei* (□).

locality (Fig. 22). The type series was collected in July.

**Biology.**—*P. avittata* has only been collected at blacklight. Hardy and Andrews (1978) indicated that the type locality dunes may be derived from Navajo Sandstone and that they are vegetated primarily with *Artemesia filiformis*. Surrounding vegetation is *Larrea divaricata* Cav.

**Remarks.**—Hardy and Andrews (1978) distinguish *P. avittata* from *P. nubila* by its lack of elytral hairs. On very close examination however, I find a few scattered semi-erect elytral hairs on the holotype. This clusters *P. avittata* morphologically with *P. devastiva* Young from southwestern and southcentral Idaho. In addition I have on hand five male specimens collected 9 mi. NW Moab, Grand Co., Utah, which cannot be distinguished from *P. avittata* and *P. devastiva* based on external characters. These three samples form the points of a triangle with the points being southwestern Idaho (*P. devastiva*), southwestern Utah (*P. avittata*), and east central Utah (at this point, unnamed; Fig. 22). There are no specimens on hand bearing even the slightest resemblance to these three populations from intervening areas. To place all these specimens, named and un-

named, under *P. devastiva* seems wholly illogical to me, though one could perhaps construct an interesting argument on the fragmentation and isolation of populations via the waxing and waning of ancient Lake Bonneville. I extracted the aedeagus of the *P. avittata* holotype and the two paratypes available, with unexpected results. In the caudal view the left paramere of this species bears a translucent but clearly visible dorsal flange (and the right paramere a smaller dorsal flange), unlike anything else I have seen in the species west of the Mississippi River (Fig. 5a). This character is reminiscent of members of the eastern *occidentalis* complex (Young 1967), and it immediately removed *P. avittata* from *P. devastiva* and the Moab specimens. (See also *P. ratcliffei* Young).

***Polyphylla barbata* Cazier**  
(Figs. 5b, 22, 48)

*Polyphylla barbata* Cazier 1938: 161; Blackwelder 1939: 53; Cazier 1940: 135; Blackwelder and Blackwelder 1948: 33; Young 1967: 289; Blackwelder and Arnett 1974: R30.69. (Holotype male AMNH 23, and one female designated by Cazier [1940] as the allotype two years after original description of the species, a technical impossibility. It bears his metatype label, is deposited at the AMNH, remains today the only known female of the species, and is here first described. Type Locality: CALIFORNIA: Santa Cruz Co.: Mt. Hermon.)

**Holotype Male.**—“Relatively small, robust; head black, clypeus rufous, elytra dark blackish-brown; head, clypeus and pronotum densely clothed with long brown hair, elytra sparsely clothed with long brown hair. Head densely, shallowly punctate, punctures separated by one one-third to one-fifth their own widths; entire surface densely clothed with long brown hair; margins around eye and clypeal suture rather densely clothed with elongate, pointed squamae, middle of front devoid of squamae; clypeus densely, shallowly punctate, feebly concave, side margins narrowed at base, expanded to apical angles which are rounded, apical margin transverse, slightly prominent medially, surface densely clothed with long brown hair, margins somewhat densely clothed with uniform elongate, pointed squamae, middle portion devoid of squamae; maxillary palpi with third segment the same length as first, longer than second,

bluntly pointed on inner side, without impression; antennal club three times as long as funicle, about twice as long as head. Pronotum about twice as long as head, and about twice as wide as long; side margins serrate, obtusely angulate at middle; quite closely, shallowly punctate, punctures separated by about their own widths, a long brown hair arising from anterior side of each puncture; median depressed line densely clothed with elongate pointed white squamae; oblique sublateral basal vittae sparsely, irregularly clothed with elongate, pointed white squamae; side margins sparsely clothed with elongate, pointed yellow squamae, remainder of surface with only an occasional isolated elongate squama, basal margin densely clothed beneath with long yellowish-brown hair. Scutellum with median and lateral vittae composed of short, narrow squamae. Elytra three times as long as pronotum, widest at apical third; surface slightly rugose, ornamented with three irregular, more or less broken, discal vittae and sutural stripe, besides the short vittae which extend from the humeral umbones and are continued posteriorly in the form of disconnected spots; squamae of the vittae white, one-third as wide as long, those of the interspaces yellow, narrower, more pointed and less dense than those of the vittae; entire surface uniformly, sparsely clothed with long brown hairs which are most abundant on humeri. Anterior tibiae bidentate, all tarsi shorter than tibiae; thoracic sternites densely clothed with long brown hair; basal abdominal sternites black, apical one and one-half segments dark brown, sparsely clothed with white squamae except along posterior margin of each segment where they are most densely arranged; long brown hair uniformly, sparsely scattered over all segments; pygidium uniformly clothed with short brown hair. The slender yellow scales are more dense in the middle and at the base, sparse laterally. Male genital segment sinuate just posterior to the narrowly expanded tip, cleft for less than one-half its length. Length 20 mm, width 9.7 mm." (Cazier, 1938).

**Original Description of Female (Metatype).—**Length 22 mm, width 11 mm. Appearance diminutive but robust, hairy throughout. Clypeus castaneous, rectangular, nearly flat, margined edges slightly reflexed, barely emarginate medially, deep, dense punctures with long golden hairs, corners broadly rounded, lateral edges parallel to slightly expanded basally. Head black, becoming castaneous medially,

deep, close punctures hidden by long golden hairs, a few elongate white squamae on canthi and lateral edges. Pronotum one and two-thirds wider than long, lateral edges crenulate, widest at mid-length then abruptly, deeply, narrowing posteriorly; with broad, shallow punctures, especially along margins and antero-lateral corners, anterior median half with broad depression through which the depressed midline runs, midline bearing small white squamae, especially concentrated in anterior half, a few scattered along anterior margin and in lateral depressions, entire surface with long dense erect golden hairs. Scutellum one and one-quarter wider than long, minute white squamae packed centrally, line narrowing to a point posteriorly, lateral portions naked except for a few long hairs. Elytra just over one and one-third longer than wide, broadest at apical one-third; basal color castaneous with humeral and apical umbones much darker, suture with sparse, minute, white squamae barely forming vitta, first and second lateral vittae absent to barely formed anteriorly, becoming stronger posteriorly with broad asquamate band on each side; interstitial squamae yellow, narrow, entire surface with scattered erect hairs much shorter than on head and pronotum. Pygidium one and one-half wider than long, miniature white squamae most concentrated on anterior, scattered laterally and medially, with short fine semi-erect hairs. Ventral abdominal sternites black except apical one and one-half segments becoming castaneous, each segment with small white squamae most concentrated on posterior one-third, with short semi-erect hairs. Ventral thorax covered with dense hairs, all leg segments with long dense golden hairs, becoming less so on tarsi. Protibiae weakly tridentate, the first two teeth exceptionally long.

**Distribution.**—Specimens examined: 94 males and one female. Known only from the type locality and almost surely there restricted (Fig. 22).

JUNE (145), JULY (2), SEPTEMBER (1).

**Biology.**—Cazier (1938) noted that two of the paratypes were collected in the sand hills of the type locality. Cazier (1940) reported that the metatype series was collected with a series of *P. decemlineata*.

**Remarks.**—*P. barbata* is distinguished from *P. diffracta* and its immediate allies by the presence of relatively dense, long, erect hairs scattered randomly over the elytra. It is most similar to and easily con-

fused with *P. rugosipennis* from which it may be distinguished by the considerably longer, denser hair on the head, pronotum, and elytra, by the lateral margins of the clypeus contracting basally (in the male), and by the presence of short, erect hairs on the pygidium. This latter character is the most consistent of the three.

In one of the male paratypes the white squamae are continuous along the anterior margin of the head, not thinning out medially; the elytra is slightly more than three times as long as the pronotum, with the sutural vittae barely visible and composed of only a few scattered white squamae; the short vittae behind the humeral umbones are not continued posteriorly in disconnected spots, and the long erect hairs are least concentrated on the humeri. It agrees well with the holotype in all other characters.

Cazier (1938) stated that *P. barbata* could be separated from *P. rugosipennis* by the aedeagus which is cleft for less than half its length, implying that *P. rugosipennis* has the aedeagus cleft for half or more than half its length. This is not true in the specimens of *P. rugosipennis* on hand for this work; I have not used this character for species recognition.

Excepting the above noted variations, the paratypes and metatypes of this species show an unusual degree of morphological uniformity. Elytral color and vittae are subject of course to some variation but it is very slight compared to other species in the *diffRACTA* complex. Key characters, the diagnosis given above and its restriction to Mt. Hermon, California make identification of this species straight forward.

### ***Polyphylla crinita* LeConte**

(Figs. 5c, 23, 49)

*Polyphylla crinita* LeConte 1856: 230; Crotch 1873: 61; Horn 1881: 73; Casey 1891: 17; Fall 1908: 159; Casey 1914: 333; Leng 1920: 257; Essig 1926: 443; Fall 1928: 30; Leng and Mutchler 1933: 39; Blackwelder 1939: 53; Cazier 1939: 202; von Bloeker 1939: 148; Cazier 1940: 135; Downes and Anderson 1941: 5; Boving 1942: 175; Essig 1942: 579; Blackwelder and Blackwelder 1948: 33; Keen 1952: 29; Ritcher 1966: 85; Young 1966: 236; Young 1967: 305; Hatch 1971: 475; Blackwelder and Arnett 1974: R30.69; Hardy 1981: 299. (Lectotype female and two paralectotype females designated by Young 1966, in the LeConte cabinets, MCZC. Lectotype bearing holotype number 3793, holo-

type label placed on specimen previously by a museum assistant as a curatorial convenience, not meant to signify formal designation. Type locality: OREGON and CALIFORNIA).

*Polyphylla crinita mystica* Casey 1914: 334. (Holotype male USNM 35629. Type locality: OREGON).

*Polyphylla incolumis* Casey 1914: 335. (Holotype male and three male paratypes USNM 35630. Type locality: CALIFORNIA: Alameda Co.).

*Polyphylla ona* von Bloeker 1939: 148. (Holotype male and allotype LACM. Type locality: CALIFORNIA: Santa Barbara Co., Santa Cruz Island, Prisoners Harbor).

*Polyphylla pacifica* Casey 1895: 607. (Holotype female USNM 35641. Type locality: CALIFORNIA). NEW SYNONYMY, from *P. decemlineata*.

*Polyphylla ruficollis perversa* Casey 1914: 348. (Holotype and paratype males USNM 35648. Type locality: WASHINGTON State: Friday Harbor). NEW SYNONYMY.

*Polyphylla santarosae* von Bloeker 1939: 149. (Holotype male LACM. Type locality: CALIFORNIA: Santa Barbara Co.: Santa Rosa Island, Becher's Bay).

**Type.**—For the original description of *P. crinita*, LeConte (1856) had an unknown number of specimens before him representing both sexes. No type was designated. In the LeConte cabinets at the MCZC there are six specimens apparently of the original series, three males and three females. None of the males are *P. crinita*. Two are *P. modulata* Casey and the other is *P. sobrina* Casey. On this basis I designated the lectotype female and two paralectotype females in my 1966 paper.

**Lectotype Female.**—Broad, robust, color uniform medium brown. Length 29 mm, width 15 mm. Clypeus short, broad, flat except for weakly reflexed margins, especially the lateral ones, with shallow, regular punctures, each puncture bearing an elongate yellow squama, squamae becoming more concentrated along all edges, occasional squamae greatly elongated, somewhat hair-like in appearance but true erect hairs absent. Head with deep, broad punctures, each puncture in medial area bearing a long, fine, yellow erect hair, occasional yellowish squamae scattered between hairs, squamae becoming more concentrated in a broad band around eyes but not along anterior margin; occasional inter-

spersed erect hairs along lateral margins much shorter and stouter, punctures becoming smaller and more closely packed along lateral margins. Antennal club half as long as combined length of head and clypeus. Prothorax one and two-thirds wider than long, with deep, broad punctures on disc, punctures more concentrated along anterior and posterior margins, each puncture bearing a narrow, elongate, yellow squama or stout yellow hair, erect hairs more concentrated along anterior margin; elongate white squamae closely packed, forming distinct vittae on deeply depressed midline and 2 lateral areas, lateral vittae broken just anterior to mid-point of length, resumed just prior to anterior edge. Elytra one and one-third longer than wide, sutural vitta distinctly formed of white squamae but edges degenerate; all lateral vittae distinct and well formed, squamae of interstitial areas yellow, giving body a distinct tricolorous appearance. Pygidium covered with minute, elongate, white squamae except for naked midline on posterior half, scales more concentrated along posterior margin, extremely fine erect hairs randomly interspersed between squamae. Protibiae deeply tridentate. (Slightly modified from Young 1967.)

**Third Instar Larva.**—I have been able to identify one adult female as one of three Ritcher (1966) had in his rearing cage. The larva he described as *P. crinita* was that of typical *P. modulata*. Ritcher mentions that "Oregon specimens" were identified as *P. modulata* by O.L. Cartwright; my findings agree with those determinations. Ritcher, however, was using the nomenclature of Fall (1928), who placed *P. modulata* as a synonym of *P. crinita*. The demes in and around Sisters, Oregon compare most closely with the name-bearing type of *P. modulata*; they are so distinct that specimens from this locality may be separated from miscellaneous *Polyphylla* specimens at a glance. In short, I consider the larvae of *P. crinita* to be undescribed (see description under *P. modulata*).

**Distribution.**—Specimens examined: 927 males, 232 females; male to female ratio 3.99:1. *P. crinita* is distributed from southern California north to Quesnel, British Columbia at 53 degrees N. latitude. This is the northern-most occurrence of the genus in North America. It is also confirmed from Burnaby Island in the Queen Charlotte Islands, between 52 and 53 degrees N. latitude. In California and Oregon this species is primarily but not exclusively restricted to coastal

areas. It is found throughout Washington, the northern half of Idaho, and south of 53 degrees N. latitude in mainland British Columbia (Fig. 23).

An 1899 record from the CASC from what is now Yellowstone Natl. Park, Wyoming is questionable. Another singleton from CASC labelled "Mackenzie River, N.W.T., Canada, L.D. Townsend, July 14, 1947 is false (H.B. Leech, personal correspondence).

CANADA: BRITISH COLUMBIA: Agassiz, Buccaneer Bay, Christova, Colwood, Copper Mtn., Creston, Duncan, Edgewood, Enderby, Englewood, Invermere, Kamloops, Kelowna, Kingsgate, Lavington, Lillooet, Maillardville, Marysville, Nanaimo, Okanagan Lake, Oliver, Peachland, Pender Harbor, Penticton, Port Renfrew, Powell River, Quathiaski Cove, Queen Charlotte Islands (Burnaby Island, Burnaby), Quesnel, Raysian, Riondel, Saanich, Salmon Arm, Summerland, Sydney, Trail, Vancouver (University campus, Livingston), Vernon, Victoria, Wellington, Yulamen.

UNITED STATES: CALIFORNIA: *Alameda Co.*: Alameda. *Del Norte Co.*: Crescent City. *Humboldt Co.*: Orick, Samoa Beach, Samoa Sand Dunes. *Los Angeles Co.*: Burbank, Claremont, Monrovia. *Mariposa Co.*: Yosemite Valley, Yosemite (3880–4000 ft.). *Mendocino Co.*: Ukiah. *Monterey Co.*: Carmel, Pacific Grove. *Riverside Co.*: San Jacinto Mts. *Sacramento Co.*: Sacramento. *San Francisco Co.*: Pt. Lobos. *Santa Clara Co.*: Palo Alto. *Santa Cruz Co.*: Mt. Hermon. *Siskiyou Co.*: 6 mi. E. McCloud, Fowlers Camp. *Sonoma Co.*: Duncan Mills, 7 mi. E. Guerner, Hacienda, Mesa Grande. *Yolo Co.*: Clarksburg, Davis. *County Unknown*: Little Shasta River.

IDAHO: *Canyon Co.*: No data. *Kootenai Co.*: Coeur D'Alene. *Latah Co.*: Moscow. *Lemhi Co.*: Salmon, 4th of July Creek. *Nez Perce Co.*: Lewiston. *County Unknown*: Fort Sherman.

MONTANA: *Ravalli Co.*: No data.

NEVADA: *Washoe Co.*: Reno.

OREGON: *Baker Co.*: Baker. *Benton Co.*: Corvallis, 5 mi. NW Corvallis, McDonald Forest, Oak Creek Gate. *Clatsop Co.*: Necanicum Jct., Seaside. *Coos Co.*: Charleston. *Deschutes Co.*: Bend, LaPine. *Douglas Co.*: Sulphur Springs. *Jackson Co.*: Medford, Union Creek (3100–3500 ft.). *Josephine Co.*: Grants Pass. *Klamath Co.*: Crater Lake (7000 ft.), Klamath Falls. *Lane Co.*: Cobing, Eugene, Florence, 10 mi. NE Oakridge, Swisshome, Westlake, Middle Fork Willamette River. *Lincoln Co.*: Newport. *Wasco Co.*: No data. *Washington Co.*: No data. *County Un-*

(231), JULY (323), AUGUST (59), SEPTEMBER (20), OCTOBER (6).

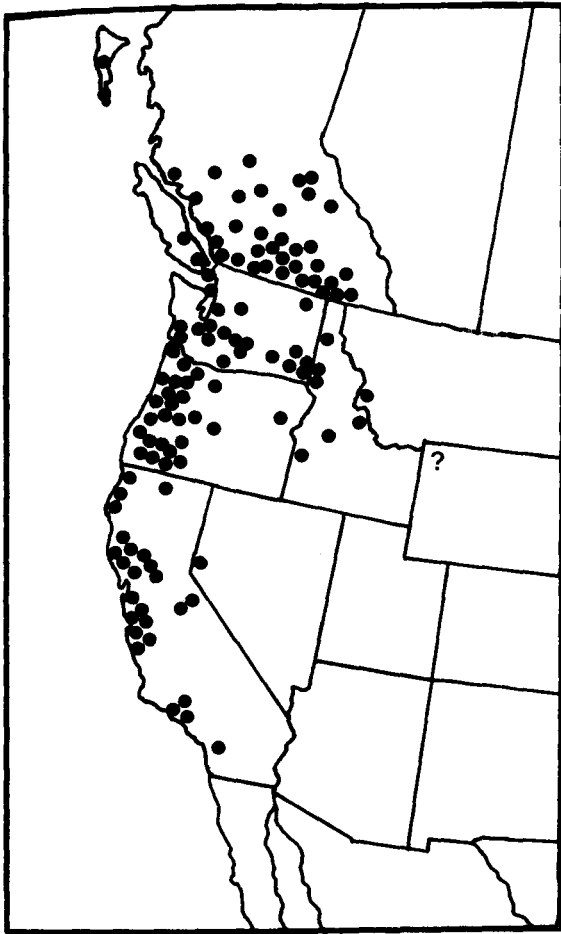


Fig. 23.—Distribution of *P. crinita*.

*known*: Ben Lomond, Santiam Natl. For., Troutdale.

WASHINGTON: *Chelan Co.*: Wenatchee. *Columbia Co.*: Dayton. *Garfield Co.*: 4 mi. NW Lower Granite Dam (Sand Dunes). *Grays Harbor Co.*: Westport. *Island Co.*: Island W. Deception Point, Whidbey Island. *King Co.*: Seattle (and Junita Point). *Klickitat Co.*: Spearfish. *Pacific Co.*: Tokeland. *Pierce Co.*: Fort Lewis, Puyallup, Tacoma. *San Juan Co.*: Eastsound, Friday Harbor. *Stevens Co.*: Northport. *Walla Walla Co.*: No data. *Whitman Co.*: Pullman. *Yakima Co.*: Granger, Yakima.

WYOMING: Yellowstone Natl. Park (questionable record).

TEMPORAL DISTRIBUTION CANADA: MAY (3), JUNE (62), JULY (207), AUGUST (186).

UNITED STATES: APRIL (10), MAY (10), JUNE

**Biology.**—Downes and Andison (1941) published a comprehensive study of *P. crinita*, under the name *P. perversa* which is here newly synonymized. It is the only such study for a North American species and is summarized below.

*P. crinita* has been in the past a significant pest species of the small fruits grown in the light sandy soil of southern Vancouver Island. Damage to strawberry fields is commonly heavy while many other crops in sandy soil are also attacked. Third instar larvae have caused economically significant injury up to and including the complete destruction of nursery stock of roses, apples, pears, plums, and cherries. Loganberries and raspberries are also subject to heavy root attack as are potatoes, with the larvae scooping out large cavities in the tubers. A single larva may move from plant to plant in corn cutting off the roots as it progresses. There are single damage records on broccoli, tulip, and crocus bulbs. Pratt (1943) records larval damage of commercial strawberry fields and Dutch iris bulb plantings on Whidbey Island, Washington.

The majority of damage is done by second and third instars (two and three years old). The main root of a strawberry plant is usually severed 2–4 inches below the surface or the main tertiary roots eaten away.

Eggs are commonly laid 8–12 inches deep; a maximum depth of 14 inches has been recorded in very loose sandy soil. Landing on the ground the female digs vertically to the desired depth and then moves horizontally, ovipositing as she tunnels. The usual number of eggs in one spot is 8–12 with 15 the maximum recorded. Dissected gravid females show a capacity of 60–70 eggs.

When first deposited the eggs measure ca. 2 mm wide by 3.4 mm long, but increase considerably in size within a few days. They are a dull creamy white color. Incubation is ca. 54 days. Field collected eggs reared in the lab hatched IX-2 while those kept outside hatched during the 3rd week of September.

Larvae are found only in sandy or gravelly soil with a permeable subsoil. The upper 6–8 inches generally hosts only mature larvae with younger stages occurring at greater depths where the finer roots are. Larvae move deeper into the soil in December and January and have been found as deep as 30 inches. A



few mature larvae may be found at such depths any time of the year—this is believed to be a function of nutrient searching rather than climatic stress. It is generally true, however, that mature larvae are found near the surface from February until pupation in May and throughout the summer. During Spring plowing of a one acre strawberry field in 1938 at Saanich, B.C., four gallons of larvae were unearthed.

The earliest record of pupation is V-10 (evidently 1938 or 1939). Pupal duration is estimated at five weeks. Most pupal cells formed were about four inches deep. Oblong in shape, the case measures ca. 0.75 inches wide by two inches long.

Adult emergence usually begins ca. the first week of July but it has been recorded as early as the third week of June in certain years. The first adults taken in 1939 were two males on VII-6. No females were collected before VII-10. Emergence holes are bored directly upwards from the pupal cells and are about 0.75 inch in diameter. They are often found in groups on hard packed soil as in pathways; firm soil may be actually preferred for pupation. The new adult does not necessarily fly at once but often remains in the emergence burrow until a favorable evening, with flight probably dependant on temperature. There is little or no flight below 54 degrees F. at 8:30 PM. Above this temperature activity increases with maximum flight at 60 degrees F. Flight starts ca. 8:30 PM and lasts ca. 30 minutes, with sporadic catches at light until 10 PM (see also biology of *P. decemlineata*, *P. diffracta*, and *P. hammondi*).

Adult females were not collected in any numbers until the males had been active for several days. Some were found in their emergence holes apparently waiting for a suitable evening for flight. The occupant of a hole may be detected by thrusting in a small stick or straw, which will cause the beetle to stridulate. This wheezing sound is produced by the expulsion of air as the elytra are raised and lowered over the abdomen.

Adult *P. crinita* feed on coniferous foliage. Under caged conditions they consumed douglas fir, norway spruce, and western hemlock, with apparent preference for the last. Lodgepole pine was taken only under hunger stress. Captive adults lived ca. three weeks. Males were taken at light as late as VIII-2. Adult life span in the wild is probably 4–5 weeks.

Adult *P. crinita* are subject to heavy attack by several predators. Elytra in considerable numbers have been found under douglas fir and western hemlock

where screech owls (*Otus asio kennicotti*) and bats have been seen to attack them in flight and eat them. Gulls, crows, hogs, and chickens all feed voraciously on the larval instars.

Adults are often parasitized by *Sarcophaga misera exuberans* Pandelle. *Muscina assimilis* (Fallen) and *M. stabulans* (Fallen) have also been reared from adult *P. crinita*. Larvae are heavily parasitized by at least one species of *Tiphia*.

Pratt (1943) also recorded predation. On Whidbey Island, Washington, *P. crinita* adults were pursued in flight by the asilid fly *Stenopogon inquinatus* Loew. One fly struck the beetle and knocked it to the ground while another attached itself to the beetle. Piercing the scutellum the fly fed for 65 continuous minutes and then flew away, its abdomen visibly distended. The *P. crinita* was killed by this predation. Under caged conditions the ground beetle *Carabus (Archicarabus) taedatus* F. actively fed on *P. crinita* larvae.

In addition to the usual records at black and white light, label data show *P. crinita* collected on or flying over sand dunes at 1) Humboldt Co., California (Samoa) and 2) Garfield Co., Washington (4 mi. NW Lower Granite Dam). A significant percentage of British Columbia specimens are labelled "flying" or "in flight"; I strongly suspect this indicates diurnal searching behavior in the males.

**Remarks.**—*P. crinita* is often confused with its distant relative *P. decemlineata*, probably because both are large, robust, vittate species. Its aedeagal configuration places it within the *diffracta* complex; these characters at once remove it from *P. decemlineata* and its sister species *P. arguta*. The aedeagus smoothly narrows from phallobase to apex without widening at the beginning of the cleft and the tip widens slightly (Fig. 5c). Female *P. crinita* may be separated at a glance from *P. decemlineata* by the setigerous pronotum (sometimes heavily so) in the former species. For both sexes the deep olivaceous basal color and tricolorous appearance of *P. crinita* will also distinguish it from *P. decemlineata*. Use of these two names has become increasingly broad (i.e., more meaningless) through time. In fact these two species are only distantly related and can be easily separated if the time is taken to extract aedeagi.

Within the *diffracta* complex, *P. crinita* is distinguished from *P. hirsuta* and its allies by the absence of elytral hairs. It is distinguished from *P. sobrina* and

*P. modulata* by the presence of pygidial hairs and is easily separated from *P. diffracta* by its generally much larger size, clear cut elytral vittae without a naked area on each side, and the deeply, broadly punctate pronotal disc. From its sister species *P. nigra*, male *P. crinita* may be separated by the lack of pronotal hairs, large (over 30 mm. length) body size, and deep olivaceous basal color.

Fall (1928) placed the names *P. crinita nigra*, *P. crinita mystica*, *P. modulata*, *P. incolumis*, *P. incolumis relictata*, and *P. incolumis robustula* in synonymy with *P. crinita*. I agreed with these conclusions in my 1967 paper with the exception of *P. modulata* (see discussion under *P. modulata*). Cazier (1940) first placed von Bloeker's four names as synonyms of *P. crinita*. In 1967 I also agreed with those conclusions.

Since then many more specimens have been seen and all the name-bearing types of Casey and von Bloeker have been re-examined. The two female paralectotypes designated by Young (1966) for *P. crinita* have also been examined again. Resultant nomenclatural changes are rather extensive and are summarized below.

*P. santacruzae* von Bloeker and *P. martini* von Bloeker have been removed from synonymy with *P. crinita* and placed as new synonyms of the resurrected *P. nigra* Casey (see remarks under that name).

The synonymy of *P. pacifica* Casey is herein changed. This name was first synonymized with *P. decemlineata* by Fall (1928). I am at a loss, as Fall was, to explain why or on what characters Casey established this name. The female name-bearing type is a very typical *P. crinita*; the pronotum is densely covered with long erect hairs, a character which immediately removes it from *P. decemlineata*. The body is heavy and robust with the elytra showing the deep olivaceous brown color so typical of *P. crinita* in the Pacific Northwest. It is here placed as a new synonym of *P. crinita*.

*P. ruficollis perversa* was originally described by Casey as another of the deeply colored populations from the Pacific Northwest. Fall (1928) also placed this name as a synonym of *P. decemlineata*. Brown (1940) raised the name to species status; his thoughts are summarized in the following quote:

"Study of Casey's descriptions and specimens show that this name may be applied to specimens from British Columbia, all of which differ in color from *decemlineata* as noted in the following key. I can detect no other differences, but the material on hand is

sufficient to establish the significance of the color character."

In his key which followed, Brown separated *P. perversa* from the other three Canadian species (*P. decemlineata*, *P. hammondi*, and *P. variolosa*) on the bases of vittate elytra, the deeply yellow interstitial scales, and the pronotal basal color usually not as dark as that of the elytra. The most significant point is that the name *P. crinita* is never mentioned in this paper. One cannot help but conclude that if Brown had had specimens under this name from the Pacific Northwest he would have synonymized *P. ruficollis perversa* with *P. crinita*. Other than sex both the holotype and paratype males of *P. ruficollis perversa* are alike in all characters with the lectotype I designated in 1966 for *P. crinita*. In summary, the large deeply colored *P. r. perversa* of the Casey type, so commonly collected throughout the American Pacific Northwest and parts of British Columbia, is no more than another name for the more northern demes of *P. crinita*.

### ***Polyphylla devestiva* Young**

(Figs. 5d, 22, 50, 51)

*Polyphylla devestiva* Young 1966: 233; Young 1967: 287; Hatch 1971: 475; Blackwelder and Arnett 1974: R30.70; Hardy and Andrews 1978: 1 (*Iapsus calami*); Young 1986: 49. (Holotype male USNM 68038. fifty-two paratype males: author, UCBC, UCDC, U. Idaho, USNM, USUC; three topotype males: J. Schuh, R. Woodruff, Cornell; 306 meta-types here designated: author, B.C. Ratcliffe, LACM, U. Idaho, UNSM; including the first three known females, in coll. author, LACM, U. Idaho. Type locality: IDAHO: Parma.)

**Holotype Male.**—"Body rather elongate and narrow, basal color of elytra light yellow-brown, head and pronotum slightly darker; head coarsely densely punctate, covered with dense erect hairs throughout, white squamae concentrated around eyes and epistomal suture; clypeus deeply concave, its margins reflexed but lateral edges not abruptly contracted at base, anterior half covered with closely packed elongate white squamae, posterior half coarsely punctate and covered with dense erect hairs as on head; antennal club one and one-third longer than combined length of head and clypeus; terminal segment of maxillary palpi twice as long as wide; prothorax weakly

convex, one and four-fifths broader than long, disc coarsely punctate, elongate white squamae forming vitta on midline, edges of lateral vittae deeply broken, lateral and posterior margins outlined with elongate, broadly spaced white squamae, erect hairs scattered throughout, becoming longer and more concentrated immediately anterior to disc; elytra one and a half times longer than wide, slightly broader posteriorly, sutural vitta highly degenerate, composed of a few scattered groups of squamae, haphazard groups of squamae scattered laterally, not forming true vittae, white squamae minute, often elongated into hairlike projections, extremely fine short erect hairs randomly interspersed among squamae; pygidium with minute broadly spaced white squamae, becoming more concentrated on lateral areas, coarse horizontal white hairs randomly interspersed among squamae; protibiae deeply tridentate." (Young, 1966). Length 23 mm, width 10 mm.

**Original Description of Female, Metatype.—**

Body elongate, narrow but more robust than male, elytra translucent, light yellow-brown, head shining black, pronotum deep shining brown. Clypeus parallel-sided, anterior angles strongly reflexed, produced, with broad, shallow punctures throughout, anterior and lateral edges with elongate white squamae, short erect hairs throughout. Head with shallow, smaller punctures, broader white squamae concentrated laterally, long erect hairs throughout. Prothorax one and two-thirds wider than long, elongate white squamae forming narrow vitta on depressed midline, broad lateral vittae broken anterior to midlength, squamae more concentrated along all margins, disc broadly punctate, with long erect hairs. Elytra 1.4 times longer than wide, slightly broader posteriorly, devoid of complete vittae, narrow white scales more concentrated along suture, laterally and in normally vittate areas, sometimes forming squamal clumps or patches, especially anteriorly; when not clumped then scattered very broadly, with or without short erect hairs, if present then most concentrated along anterior lateral margins and mesad to humeral umbones. Pygidium with small white scales concentrated along anterior and central portions, broadly scattered laterally and posteriorly, interspersed with a few short semi-erect hairs. Protibiae deeply tridentate. Length 21 mm, width 11 mm.

**Distribution.**—Specimens examined 377 males

and three females. This species, which I described some 20 years ago, remains known from only three counties in southwestern Idaho (Fig. 22). Most specimens come from the Arena Valley, in the area of Parma.

IDAHO: *Canyon Co.*: Arena Valley, Parma (2224 ft. elev.), 4 mi. SW Parma, 5 mi. S. Parma, 4 mi. SW Roswell. *Elmore Co.*: Glenn's Ferry (2562 ft. elev.). *Owyhee Co.*: 7 mi. W. Grandview, 3 mi. S. Grandview, Hot Springs, Sand Dune Lakes (7 mi. NE Bruneau), 17 mi. W. Silver City.

JUNE (12), JULY (361), AUGUST (3).

**Biology.**—Unknown. Nearly all specimens are taken at light. This species, like so many in the genus, is associated with sandy soils and sand dunes.

**Remarks.**—*P. devestiva* closely resembles the nonvittate phase of *P. diffracta* so common in Arizona. It can be distinguished from this color phase of *P. diffracta* by the presence of erect hairs on the elytra which, though very fine and short, are clearly visible in males under high magnification. Concentration and distribution of erect pronotal hairs is also helpful to separate these two taxa. While they are long, dense, and often concentrated in one given area in *P. devestiva*, they are clearly shorter, more widely spaced, and much more randomly scattered in nonvittate specimens of *P. diffracta*.

This is a highly variable species in general habitus (Figs. 50–51). Overall length varies from 17–23 mm. Color of the head, pronotum, and elytra varies widely. The vertex varies from dark brown to black, as does the pronotum. The elytra vary from the light yellowish-brown of the holotype to a considerably deeper reddish-brown. About one-third of the specimens on hand are without squamae on the elytra. The pronotal hairs may be heavily concentrated along the midline or they may be densely and randomly scattered over the entire pronotal surface. Male protibiae vary from weakly to very strongly tridentate.

***Polyphylla diffracta* Casey**

(Figs. 5e, 5f, 24, 52)

*Polyphylla diffracta* Casey 1891: 18; Dalla Torre 1912: 258; Casey 1914: 331; Leng 1920: 257; Fall 1928: 31; Leng and Mutchler 1933: 39; Van Dyke 1933: 116; Cazier 1938: 162; Blackwelder 1939: 53; Ca-

zier 1940: 137; Van Dyke 1943: 104; Van Dyke 1947: 161; Blackwelder and Blackwelder 1948: 33; Young 1967: 294; Blackwelder and Arnett 1974: R30.69; Hardy and Andrews 1978: 2; Fowler and Whitford 1981: 215. (Holotype male and one paratype male USNM 35626. Type locality: NEW MEXICO: "Probably near Las Vegas.")

*Polyphylla adusta* Casey 1914: 331. (Holotype male USNM 35625. Type locality: NEW MEXICO).

*Polyphylla alleni* Cazier 1939: 201. (Holotype male AMNH 25. Type locality: ARIZONA: Tube [should be Tuba] City). NEW SYNONYMY.

*Polyphylla diffracta arida* Van Dyke 1947: 161. (Holotype male CASC 5874. Type locality: UTAH: San Juan Co.: Navajo Mt., Duns Plc., alt. 5580 ft.)

*Polyphylla fuscula* Fall 1908: 161. (Lectotype male and one paralectotype male MCZC 24858, designated by Young 1966. Type locality: ARIZONA: Chiricahua Mts.)

*Polyphylla laevicauda* Casey 1914: 338. (Holotype male USNM 35634. Type locality: ARIZONA).

*Polyphylla opposita* Casey 1914: 330. (Holotype male USNM 35624. Type locality: OREGON: "the single specimen is so marked but perhaps erroneously").

*Polyphylla uteana* Tanner 1928: 276. (Holotype male BYUC 25. Type locality: UTAH: Kanab).

**Holotype Male.**—Elongate, narrow. Length 23.5 mm, width 10.75 mm. Dark brown, head and pronotum slightly darker than elytra. Clypeus concave, its anterior margin abruptly reflexed, lateral margins barely subparallel, not contracted basally, anterior three-eighths covered with closely packed, elongate, yellow squamae, posterior five-eighths with dense, deep punctures and covered with suberect white hairs. Head with similar punctures, covered throughout with dense, yellowish, erect hairs; patches of elongate white squamae on posteriolateral corners adjacent to eyes. Antennal club equal to length of head and clypeus. Prothorax weakly convex, one and three-fourths wider than long, with broad, deep punctures throughout which become gradually smaller in radius as lateral edges are approached; relatively large, white squamae forming vitta on depressed midline, similar squamae forming two lateral vittae on posterior half, on anterior half squamae clumped only adjacent to anterior margin, suberect, fine, yellowish hairs scattered over surface, becoming slightly more concentrated latero-anterior to disc. Elytra one and one-half longer than wide, slightly broader posterior-

ly, distinct sutural vitta composed of minute white squamae, lateral vittae somewhat broken especially on posterior one-third; each vitta with naked area on each side, width of vitta and one lateral naked area equal to width of band of hairs in interstitial area. Pygidium without well formed squamae, covered with randomly scattered, horizontal white hairs, a few suberect. Protibiae deeply bidentate.

**Female.**—Often smaller, less robust than male. Clypeus often rudimentary, short, exposing mouthparts. Elytra often asquamate, unicolorous brown, with or without erect hairs. Pygidium squamose, especially on anterior half. Protibiae deeply tridentate.

**Distribution.**—Specimens examined: 2,235 males and 36 females. The dominant feature in the distribution of this species is Arizona. *P. diffracta* also reaches into the western half of New Mexico, but most records come from the southwestern corner of this state. Scattered records are also present from southern (primarily desert) California and a few southern coastal localities. One series of a dozen specimens is recorded from Sonora, Mexico. The northern records from Alameda and Contra Costa counties shown in Young (1967) have turned out to be based on false data and are here eliminated (Fig. 24). *P. diffracta* is a truly southwestern, desert species.

MEXICO: SONORA: 86 km. NE Nacori Chico (Rancho Arroyo El Cocono, 1660 m.)

UNITED STATES: ARIZONA: *Apache Co.*: Lupton, 4 mi. E. McNary. *Cochise Co.*: Chiricahua Mts. (W. Turkey Creek), Huachuca Mts. (Cave Cyn. @ 1859 m.), Sunnyside. *Coconino Co.*: Flagstaff, S. of Flagstaff, 7.5 mi. NW Flagstaff (Fort Valley, 7350 ft.), 16 mi. SW Flagstaff (W. Fork Oak Creek), Grand Canyon, S. Rim Grand Canyon, Indian Wells, 8 mi. N. Sedona (Oak Creek Canyon), Upper Manzanita (Oak Creek Canyon), 8 mi. S. Williams (Lockett Spring, 7000 ft.), Williams. *Gila Co.*: Globe, 10 mi. S. Globe, 21 mi. NE Payson (6000 ft.), Payson, Meed's Ranch, Pinal Mts., base of Pinal Mts., Sierra, Sierra Ancha Mts. (Tonto Campground nr. Cohls Ranch; Workman Crk. @ 1779 m.; Aztec Peak @ 2109 m.), Star Valley, White Mts. *Graham Co.*: Geronimo. *Greenlee Co.*: 17 mi. N. Clifton (Blue Range of White Mts., Juan Miller Campground, 6400 ft.), White Mts. (6–8000 ft.). *Grant Co.*: Black Range (Gallinas Cyn @ 6650 ft.). *Mari-copa Co.*: Chandler, Phoenix, Tempe. *Navajo Co.*: Heber (6500 ft.), 15 mi. NW Kayenta, Lakeside, Na-

vajo Mt., Pinetop, 8 mi. S. Showlow, Whiteriver. *Pima Co.*: Bobaquivari Mts. (Sabino Cyn.). *Pinal Co.*: Pinal Mts., base of Pinal Mts. (4000 ft.). *Pima/Santa Cruz Co.'s*: Santa Rita Mts., (Madera Canyon, 4400–5000 ft.). *Santa Cruz Co.*: Nogales, Patagonia, Santa Rita Mts. *Yavapai Co.*: Hassayampa Lake (6520 ft.), 11 mi. N. Mayer (Valley High), Prescott. *Yuma Co.*: No data. *County Unknown*: Coulter, Hawley Lake.

CALIFORNIA: *Los Angeles Co.*: No data. *Monte-rey Co.*: Carmel. *San Bernardino Co.* (?): Mt. Wilson. *San Diego Co.* (?): Mexican Wells. *Santa Barbara Co.*: Santa Barbara.

NEW MEXICO: *Bernalillo Co.*: No data. *Dona Ana Co.*: No data. *Grant Co.*: Black Canyon (40 mi. NE Silver City), 14 mi. N. Silver City, 13 mi. N. Silver City (6800 ft.). *Lincoln Co.*: No data. *McKinley Co.*: Canyon N. Side Satan Pass, between Thoreau and Crown Point, Thoreau. *San Juan Co.*: Aztec, Farmington. *Socorro Co.*: Magdalena Mts. (Water Canyon, 7000 ft.). *Valencia Co.*: El Morro, El Morro Natl. Monument. *County Unknown*: Datil, Continental Divide.

UTAH: *Kane Co.*: Coral Pink Sand Dunes, Kanab. *San Juan Co.*: Bridge Cyn. 42 mi. W. Kayenta, AZ.; Dun's Place (Navajo Mtn.). *Washington Co.*: Hurricane, Leeds, Leeds Canyon (Oak Grove Camp), 9 mi. NW Leeds, Zion Natl. Park (Grotto Camp, Wylle Camp, 4200 ft.).

JUNE (100), JULY (1709), AUGUST (375), SEPTEMBER (24).

**Biology.**—A series of *P. diffracta* was taken at UV lights on July 24 and 25, 1967, near the Santa Rita Lodge, Madera Canyon, AZ. Collected syntopically with the *P. diffracta* was one male avittate *P. hammondi*, an unusual occurrence in my experience. This

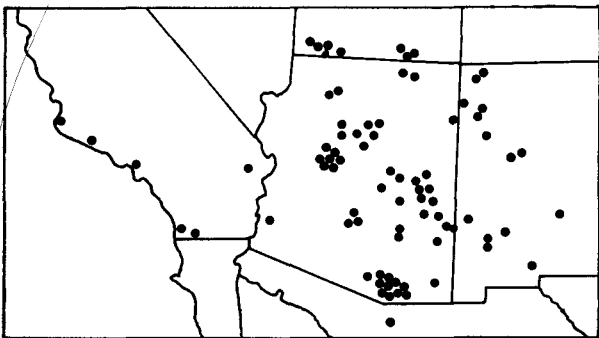


Fig. 24.—Distribution of *P. diffracta*.

area is a 5400 ft. Arizona white oak (*Quercus arizonica* Sarg.)— Rocky mtn. juniper (*Juniperus scopulorum* Sarg.) vegetational zone within the Savanna Biochore; during this time and in this zone no other species were collected. By moving out of the canyon onto a 4500 ft. bajada (Martin, 1963) covered with mesquite, yucca, and cactus species, vittate *P. hammondi* but no *P. diffracta*, could be readily taken at black light. This site was of the desert or mesquite grassland type within the Grassland Biochore. These data suggest that although shown as sympatric on our maps, in this instance at least, breeding demes of *P. diffracta* and *P. hammondi* (vittate phase) are allotopic and quite effectively isolated from each other. Furthermore the last *P. hammondi* was taken at 10:15 PM, while at the higher location, *P. diffracta* males were active until 12:30 PM.

A second deme of this species was sampled in Zion National Park, Utah, during August of the same year. The collecting site was at 5400 ft., with Utah juniper (*J. osteosperma* [Torr.] Little), pinon pine (*Pinus edulis* Engelm.), prickly pear cactus (*Opuntia* sp.), yucca, and shrub live-oak (*Quercus turbinella* Greene) growing in deep sand. Adult males were taken at UV light from 9:30 to 10:40 PM (dusk at 8:40 PM). Again, this species was collected to the exclusion of all others. *P. decemlineata* was taken in a lower cottonwood zone but the two were never taken together.

Fowler and Whitford (1981) published a note on the mating behavior of *P. diffracta*. On VII-26-1969 adults were observed emerging from an open park nr. Las Cruces, New Mexico between 1800–2000 hrs. MST. Males flew in a zig-zag pattern, 10–50 cm. above the ground, antennal lamellae fully extended. In three of 22 observed copulations males helped the female dig her way out of the soil. Females emerged, mated, and disappeared down their emergence burrows. None came to light. On 16 occasions more than one male was attracted to an emerging female. Once a male achieved copulatory success other males dispersed. Caged females attracted males within five minutes. The authors concluded that these observations suggest the presence of sex pheromones in *P. diffracta* and that females mate only once (see also discussion of Lilly and Shorthouse, 1971 under the biology of *P. decemlineata*). It is here noted that these authors refer to Travis (1939) and cite imagos as using sex pheromones for mate finding; later in their note they cite *Polyphylla lanceolata*. This citation and name is wrong, there is no such species. Travis' pa-

per is on *Phyllophaga lanceolata*; the only confirmed case of pheromones in *Polyphylla* is the aforementioned paper by Lilly and Shorthouse (1971).

**Remarks.**—*P. diffracta* falls within the cluster of species of the *diffracta* complex which is characterized by the absence of elytral hairs. This character separates it from *P. hirsuta* and its allies. *P. diffracta* varies in a random manner, as far as I have been able to determine, from unicolorous brown to distinctly vittate. I find no correlation of this variation with latitude, longitude, or elevation, unlike similar variation in *P. hammondi* which does show an east to west and north to south cline (see remarks under that species). Any given deme may show avittate to vittate individuals; in 1928 Tanner named an avittate specimen *P. uteana*. These unicolorous brown *P. diffracta* specimens are most easily confused with *P. hirsuta* but may be separated from it by the absence of elytral hairs. It may sometimes be confused with *P. barbata*, from which it may be separated by the same character, the distinctly smaller elytral squamae and the pronotal hairs which are much less dense in *P. diffracta*.

Throughout its range *P. diffracta* is subject to broad variation in external characters, especially so in the peripheries of its distribution. Fall (1928) used the bidentate male protibia as a distinguishing character in his treatment of the genus. However, Cazier (1938) has shown that this character does not hold true in the species *P. arguta* and *P. hammondi*. It clearly is of no value in *P. diffracta*, as samples seen from throughout the range of this species show variation in this character ranging from unidentate to deeply tridentate. As has been mentioned earlier in this work, this character holds true only if the numerical or geographic sample size is small.

Fall's character concerning the presence or absence of pronotal hairs does effectively separate *P. diffracta* and its allied species from other complexes within the genus. Cazier (1938) questioned the validity of this character, especially for *P. rugosipennis*, in which the pronotal hairs may be present or absent. However, he further stated that it seems to hold true in those species within the *diffracta* complex characterized by a dense cover of erect hairs on the pronotum, namely *P. hirsuta* and *P. barbata*. The key to species in this work does not use pronotal hairs alone as a distinguishing character. It is a very useful character but only when used in association with others.

*P. alleni* is here placed as a new synonym of *P.*

*diffracta*. The holotype has been examined since publication of Part I of this work (Young, 1967). The following characters are noted from the holotype (AMNH No. 25): small overall size, elytral basal color yellowish-brown (as in *P. sobrina*), vittae clear cut but broken posteriorly, pronotal hairs short and sparse, no elytral hairs, antennal club exceptionally small and barely recurved, protibiae bluntly tridentate. This specimen is somewhat smaller and more distinctly colored than many *P. diffracta* samples but its external morphology falls well within the range of variation of the species.

### ***Polyphylla hirsuta* Van Dyke**

(Figs. 5g, 22, 53, 54)

*Polyphylla hirsuta* Van Dyke 1933: 116; Cazier 1938: 163; Blackwelder 1939: 53; von Bloeker 1939: 149; Cazier 1940: 137; Blackwelder and Blackwelder 1948: 33; Young 1967: 286; Blackwelder and Arnett 1974: R30.69. (Holotype male and two paratype males CASC 3740. Type locality: ARIZONA: Santa Cruz Co.: near Nogales, Mt. Washington, 6000 ft.).

**Holotype Male.**—Length 20 mm, width 10 mm. Elytra pale reddish-brown, head and pronotal disc shining black. Clypeus parallel-sided, frontal margin nearly straight, outer angles rounded, with short semierect hairs throughout. Head with broad, deep, close punctures; hairs long, dense, and semierect. Antennal club nearly equal to combined length head and clypeus, distal third barely recurved. Pronotum one and one-half wider than long, lateral margins irregularly subserrate, disc with large, deep, regular punctures, depressed midline narrow and shallow, with long, dense hairs throughout. Elytra very slightly widening posteriorly, just under one and one-half longer than wide, randomly punctured and rugose throughout; vestiture entirely of semierect to erect hairs, hairs becoming more concentrated in normally vittate areas, lightly scattered in interstices, without squamae throughout. Pygidium with fine, minute punctures; fine hairs throughout. Protibiae bidentate.

**Female.**—Unknown.

**Distribution.**—Specimens examined: six males. Known only from the type locality and Patagonia Mountain (also Santa Cruz Co.), Arizona (Fig. 22). Collected in July (5) and August (1).

**Remarks.**—*P. hirsuta* is most easily confused with *avittate*, unicolorous brown specimens of *P. diffracta*. The character of elytral hairs, present in *P. hirsuta* and absent in *P. diffracta*, readily separates these two species. It is distinguished from *P. barbata* and its allies by the complete lack of elytral and pronotal squamae.

*P. hirsuta* is the only species in the *diffracta* complex having suberect elytral hairs and a complete lack of pronotal and elytral squamae. Configuration of the aedeagus (Fig. 5g) clearly places it within this complex of species and I do not agree with Van Dyke's statement (1933) that it is not closely related to any of the previously described species. Label data (not personally confirmed by field data) indicates that this species is sympatric with *P. diffracta*. Considering the morphological uniqueness of the few specimens available, I strongly suspect that *P. hirsuta* is allotopically or allochronically isolated from *P. diffracta*.

***Polyphylla mescalensis* new species**

(Figs. 5h, 22, 55, 56)

**Holotype Male.**—Elongate, narrow. Length 25 mm, width 11.3 mm. Clypeus and head black, pronotum and elytra rich medium brown. Clypeus twice as wide as long, much wider anteriorly, corners rounded, anterior third abruptly reflexed, anterior margin smoothly produced in middle; with elongate, white, recumbant scales. Head with large, close punctures, vertex asquamate, scales only along anterior and lateral margins; with long, dense, erect hairs throughout, canthi asquamate, with shorter, stout, erect hairs. Antennal club equal to combined length of head and clypeus, distal half deeply recurved. Pronotum 1.7 wider than long, widest just anterior to midlength; with broad, shallow, close punctures, especially on disc, median vitta on depressed midline composed of elongate, white scales, lateral vittae present but broad and diffuse; exceptionally long, erect (and recumbant) hairs scattered over surface. Elytra 1.4 longer than wide, barely broader posteriorly; with rare, short, erect hairs. Without formed vittae except for fine line along suture a few scales wide, small, white scales scattered individually over surface except concentrated into clusters and portions of vague, heavily broken lines in first and second normally vittate areas, also concentrated laterally on anterior half and on

posterior angles. Pygidium narrow, elongate, evenly covered with recumbant, stout hairs and scales, without naked midline. Protibiae deeply tridentate, all three teeth acute.

**Measurements.**—Length clypeus 2 mm, width 4 mm; length antennal club 5 mm, combined length head and clypeus 5 mm; length pronotum 5 mm, width 8.5 mm; length elytra 16 mm, width 11.3 mm.

**Female.**—Unknown.

**Types.**—Holotype male Univ. Nebr. State Museum: New Mexico: Chavas Co.: Mescalero Dunes, T12S R30E Sec. 24, 4029 feet elevation, ultra-violet light, VII-14-1985, S. McCleve, P. Jump, Collectors (Fig. 22). Eighteen male paratypes, same data, deposited in the following collections: AMNH (2), B.C. Ratcliffe (1), CASC (2), CNC (1), H.F. Howden (1), R.M. Young (2), S. McCleve (6), Univ. Nebraska State Museum (1), USNM (2).

**Etymology.**—From the Nahuatl language of the classical Aztecs, *mexcalli*; as used by the Spanish in *mescal*, *mezcal* to designate certain Apache peoples as the mescal-eaters, the Mescalero Apache. A cactus species of Mexico and the southwestern U.S., commonly called "peyote."

**Remarks.**—I am indebted to Scott McCleve of Douglas, Arizona, who collected all the specimens in the type series and called them to my attention. This is apparently another *Polyphylla* species endemic to specific sand dune habitat islands like those described by Young (1966) and Hardy and Andrews (1978). At the type locality it has been collected sympatrically with *P. pottorum*. This general area appears on most maps as the Mescalero Sands, ca. 40 mi. E. of Roswell, New Mexico on U.S. Highway 380 (McCleve, personal communication). McCleve continued east ca. 6 more miles and turned south on state highway 172 which runs along an escarpment called the Mescalero Ridge. He turned west 10.6 mi. south of U.S. 389 on a dirt road which runs toward and down the escarpment. The type series was collected at light in an active dune area ca. 4.3 road miles west of New Mexico highway 172. The dominant plant species at the type locality is shinnery oak, *Quercus havardii* Rydb., which seldom grows over 3 ft. in height at this site.

This very distinctive species belongs to that cluster of species within the *diffracta* complex having elytral hairs and at least a suggestion of vittae on the elytra. It clusters morphologically with *P. rugosipennis* and *P. barbata* by having long, dense pronotal hairs. It is separated from *P. rugosipennis* by having white interstitial scales which are broadly scattered, and barely suggested to broken elytral vittae, much less distinct than the clear white vittae of *P. rugosipennis*. In *P. barbata* the elytral hairs are very long and obvious, in *P. mescalerensis* they are short and few.

The paratypes vary in length from 22–26.75 mm, in width from 9.4–12 mm. Clypeal angles are rounded to acute. They all show long, erect hairs on the head and pronotum. The elytra have, at most, suggestions of two broken vittae between the suture and humeral umbones on the anterior half. Protibiae are tridentate.

***Polyphylla modulata* Casey**

(Figs. 5i, 25, 57)

*Polyphylla modulata* Casey 1914: 333; Leng 1920: 257; Fall 1928: 31; Blackwelder 1939: 53; Cazier 1939: 202; Cazier 1940: 135; Blackwelder and Blackwelder 1948: 33; Young 1967: 302; Hatch 1971: 476; Blackwelder and Arnett 1974: R30.69; Young 1986: 50. (Holotype male and one paratype male USNM 35627. Type locality: OREGON: Graham).

*Polyphylla decemlineata modulata* sensu Cazier 1939: 202.

**Holotype Male.**—Broad, blunt. Length 26.4 mm, width 12 mm. Head and elytra black, pronotum shining brown. Clypeus with deep, irregular punctures, on posterior half each puncture bearing a fine but stout yellow erect hair, yellowish squamae dense and closely packed over entire anterior half and along lateral edges, gently concave, anterior margin gradually reflexed, lateral edges parallel. Head with shallow, dense punctures, each puncture bearing an unusually long, fine, yellow, erect hair; a few pale yellowish squamae interspersed between hairs on disc, scales becoming closely packed along anterior margin and around eyes. Antennal club just over one and one-third longer than combined length of head and clypeus, distal half recurved. Pronotum just under one and two-thirds wider than long, irregularly punctate, the punctures of unequal diameters; each puncture

bearing a long, erect, yellow hair, a broad white scale, or some structure intermediate between the two; white squamae densely packed to form distinct vitta on depressed midline and on lateral areas, lateral vittae on posterior half only, squamae scattered randomly in interstitial areas, becoming more concentrated along margins, long, erect, yellow hairs most concentrated just anterior to disc. Elytra just less than one and one-half longer than wide, all vittae well formed from white squamae, edges very slightly broken, interstitial squamae distinctly yellow; becoming considerably broader posteriorly. Pygidium covered with randomly mixed, yellow squamae, and short, blunt, suberect hairs; hairs slightly more concentrated along anterior margin and on disc. Protibiae deeply bidentate.

**Third Instar Larva.**—These specimens were described by Ritcher (1966) as *P. crinita*. Adults had been identified as *P. modulata* by O.L. Cartwright (determinations which I agree with) but Ritcher was using the nomenclature of Fall (1928), which placed *P. modulata* as a synonym of *P. crinita* (see also discussion under *P. crinita*).

Taken from Ritcher (1966) with the above proviso, this description is based on the following material: Three third instar larvae reared from eggs layed in a rearing cage containing three males and three females. These adults were dug from beneath nests of the harvester ant *Pogonomyrex owyhei* Cole on VI–27–1961, 10 mi. SE Sisters, Deschutes Co., Oregon.

“Larvae of this species may be distinguished by the following characters: Maximum width of head capsule 6.3–6.7 mm. Head yellow to reddish-brown, reticulate; with transverse ridges on either side of anterior part of frons. Haptomerum of epipharynx with 14 to 20 heli, mostly arranged in 2 irregular semicircles. Acroparia well developed: area between base of haptomerum and anterior margin of epipharynx rather uniformly covered with long, slender setae. Epipharynx with or without proplegmata; proplegmata, if present, vague and poorly developed, consisting of about 12 fine proplegmata. Each plegmatium with 12 or 13 short, slightly curved plegmata. Haptolachus without crepidial punctures (microsensilla). Maxilla with a row of 14 to 16 conical, sharp-pointed stridulatory teeth. Respiratory plate of thoracic spiracle with arms only slightly constricted; thoracic spiracle similar in size to spiracles of first four abdominal segments. Spiracles on abdominal segments 5 to 8 progressively smaller in size.



Anal opening broadly V-shaped. Raster with two short, rather sparsely set, longitudinal palidia, each sparsely set with 8 to 12 long, slender palia whose tips meet on the midline of the septula. Tegilla extending past palidia for a distance equal to the length of the palidia. Preseptular tegillar setae 20 to 35 in number on each side. Tegilla extending about half the distance between the lower anal lip and the anterior margin of the last abdominal segment."

**Distribution.**—Specimens examined: 206 males and 17 females for a male: female ratio in collections of ca. 12:1. This species has a much broader distribution than recorded by Young (1967). Additional specimens have shown that *P. modulata* reaches as far south as central coastal California. Two records from much further south, Idyllwild (Riverside Co.), I consider questionable. This is primarily a Pacific northwestern species. It is recorded throughout most of Oregon and Washington, with a few scattered records from western and northern Idaho. Oddly enough I have no records from British Columbia (Fig. 25).

Throughout its range *P. modulata* is recorded sympatrically with *P. crinita* and *P. decemlineata*. In northern California it occurs sympatrically with *P. sobrina* and is rarely so with *P. nigra*. The deme at Sisters, Oregon compares most closely with the name-bearing type; examples may often be picked out at a glance.

CALIFORNIA: *Fresno Co.*: Kearney Park (8 mi. W. Fresno). *Mendocino Co.*: S. Fork Eel River. *Monterey Co.*: No data; *Riverside Co.*: Idyllwild. *Shasta Co.*: Hat Creek (Post Office), Lassen Natl. Park (Manzanita Lake). *Sonoma Co.*: Sebastopol.

IDAHO: *Canyon Co.*: Parma. *Lewis Co.*: Nez Perce. *Nez Perce Co.*: Lewiston. *Owyhee Co.*: Indian Cove. *Shoshone Co.*: Wallace.

OREGON: *Benton Co.*: Corvallis. *Deschutes Co.*: Bend, 6 mi. SW Bend (in ground), Sisters, 10 mi. SE Sisters (in soil nr. ant nest). *Douglas Co.*: Castle Creek, Diamond Lake. *Jackson Co.*: Union Creek. *Klamath Co.*: 10 mi. N. Beatty, 12 mi. NE Chiloquin. *Lake Co.*: 24 mi. SE LaPine. *Lane Co.*: Eugene, Junction City. *Marion Co.*: Santiam Natl. Forest. *Umatilla Co.*: Hermiston. *County Unknown*: Beaver Marsh, Graham.

WASHINGTON: *Douglas Co.*: Rock Island. *Franklin Co.*: Pasco. *Kittitas Co.*: Whiskey Dick Canyon (5 mi. N. Vantage). *Okanogan Co.*: Okanogan. *Spokane Co.*: Spokane. *Stevens Co.*: Kettle Falls St. Park.

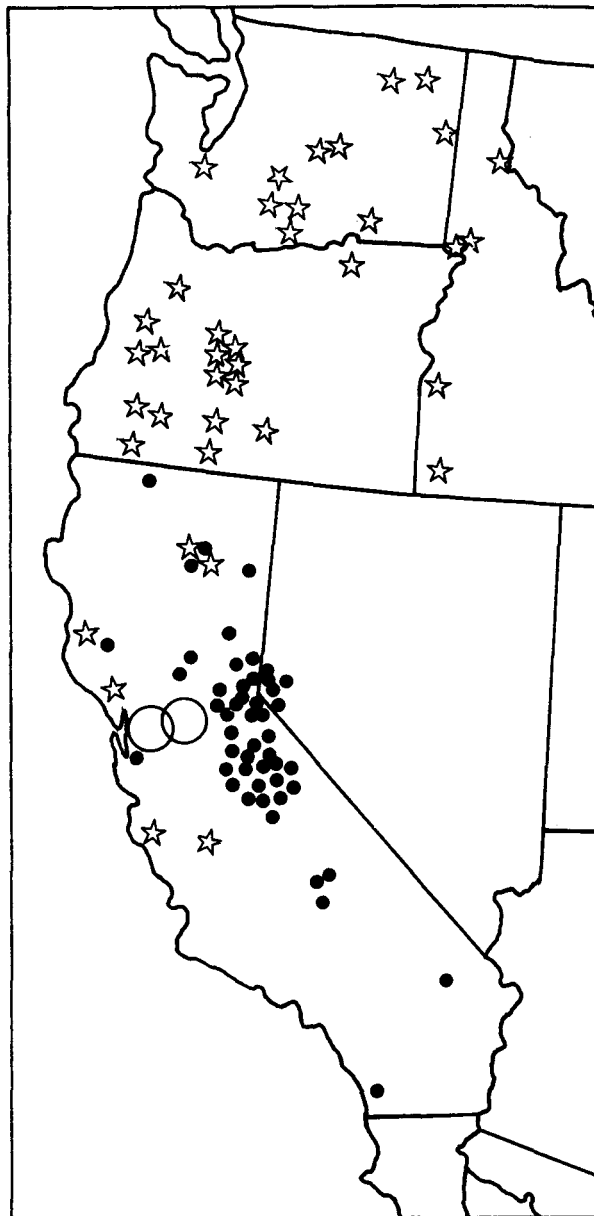


Fig. 25.—Distributions of *P. modulata* (☆), *P. sobrina* (●), and *P. stellata* (○).

*Thurston Co.*: Rochester. *Yakima Co.*: Granger, Toppenish, Yakima.

JUNE (23), JULY (188), AUGUST (12).

**Biology.**—Collected at 2231 ft. elv. at Parma, Idaho, "in ground" 6 mi. SW Bend, Oregon, and beneath harvester ant nests as recorded by Ritcher (1966) and detailed above.

**Remarks.**—As Ritcher (1966) commented, *P. modulata* typically looks like “small specimens of *P. decemlineata*.” Its setigerous pronotum and aedeagal configuration (Fig. 5i), however, separates it from that species at once. The absence of elytral hairs distinguishes it from *P. hirsuta* and its allies. It may be separated from *P. diffracta* and *P. crinita* by the absence of pygidial hairs, or if present, they are short and blunt. Its basal dark brown to black color and hard-edged vittae distinguish it from *P. sobrina*, which is always a reddish to yellow-brown color and very distinctive.

Fall (1928) originally synonymized this name, under *P. crinita*. I do not agree with this, as *P. modulata* is effectively separated from *P. crinita* by its consistent and much smaller overall size and absence of pygidial hairs. Cazier (1939) placed *P. modulata* as a subspecies of *P. decemlineata* and stated that it was commonly found with that species, thereby disproving his nomenclatural decision. Moreover, the morphological evidence to separate *P. modulata* from *P. decemlineata* is very clear. The presence of heavy, dense hairs on the pronota of the type series removes *P. modulata* from *P. decemlineata*. More important is the distal broadening of the *P. modulata* aedeagus; a character of the *diffracta* complex. In 1940 Cazier raised this name back to its original specific standing and placed *P. comstockiana* von Bloeker as its synonym. *P. comstockiana* is a synonym of *P. decemlineata* in this work.

***Polyphylla nigra* Casey**  
(RESURRECTED NAME,  
RAISED TO SPECIES STATUS)  
(Figs. 5j, 26, 58)

*Polyphylla crinita nigra* Casey 1914: 334; Leng 1920: 257; Fall 1928: 31; Kuntzen 1933: 462; Blackwelder 1939: 53; Cazier 1940: 137; Blackwelder and Blackwelder 1948: 33; Young 1967: 305; Hatch 1971: 477; Blackwelder and Arnett 1974: R30.69. (Holotype male USNM 35628. Type locality: “labelled Texas, but certainly in error and probably from WASHINGTON State.”)

*Polyphylla incolumis relicta* Casey 1914: 336. (Holotype male and paratype female USNM 35631. Type locality: CALIFORNIA). NEW SYNONYMY, from *P. crinita*.

*Polyphylla incolumis robustula* Casey 1914: 336. (Holotype male USNM 35632. Type locality: CAL-

IFORNIA: Los Angeles Co.). NEW SYNONYMY, from *P. crinita*.

*Polyphylla martini* von Bloeker 1939: 150. (Holotype male LACM. Type locality: CALIFORNIA: Santa Barbara Co.: Santa Rosa Island: Becher’s Bay). NEW SYNONYMY, from *P. crinita*.

*Polyphylla santacruzae* von Bloeker 1939: 149. (Holotype male, allotype female, 55 male paratypes, and two female paratypes LACM; two male paratypes USNM 54042. Type locality: CALIFORNIA: Santa Barbara Co.: Santa Cruz Island: Prisoners Harbor). NEW SYNONYMY, from *P. crinita*.

**Holotype Male.**—Robust, rotund, becoming markedly broader posteriorly, body abruptly truncated posteriorly. Length 28 mm, width 13 mm. Clypeus with lateral edges essentially parallel. Head shining black, pronotum the same except becoming deep brown centrally, elytra similar except lateral edges becoming a lighter brown, pygidium shining black. Antennal club just over twice as long as stem, slightly recurved. Pronotum with long erect hairs throughout but especially so along anterior edge, strongly depressed midline bearing hard-edged vitta composed of delicate hair-like scales, lateral vittae formed but only along posterior half. Elytra without hairs, all vittae including sutural one clear and well formed, composed of fine, thin, white scales; the dense vittae reminiscent of *P. crinita* or *P. decemlineata*. Pygidium covered with minute white scales and randomly scattered short semierect hairs. Abdominal segments heavily covered with squamae like those of elytral vittae, especially on posterior two-thirds of each segment. Protibiae outwardly bidentate but not broad or robust anywhere along length.

**Female.**—Taken and preserved *in copula* in two cases on hand. Heavier, more robust throughout. Normal sexual dimorphism in degenerate clypeus, 5-segmented antennal club. Diagnostic characters: combination of setigerous pronotum and clear, hard-edged elytral vittae. There may be a slight tendency for vittae to be rougher and more broken than in the male.

**Distribution.**—Specimens examined: 493 males and 27 females. About 70% of the specimens seen are from extreme southern California and Baja California Norte. To the north it is recorded throughout California but with most records being coastal. It is

also recorded from scattered localities in Oregon and Washington, but not nearly as commonly. Also on hand is what appears to be a disjunct record from Nye Co., Nevada (Fig. 26).

MEXICO: CALIFORNIA BAJA NORTE: Bocade Santa Maria, Colonia Guerrero, 4.7 mi. upstream of Hamilton Ranch, Norte Arr (Del Rosario), 3 mi. N. Rosario.

UNITED STATES: CALIFORNIA: *Alameda Co.*: Alameda, Oakland. *El Dorado Co.*: Lake Tahoe. *Humboldt Co.*: Ferndale. *Kern Co.*: Arvin, Mt. Pinos. *Los Angeles Co.*: Angeles Natl. Forest (Sulphur Springs, Crystal Lake, Mt. Wilson), Los Angeles. *Madera Co.*: Northfork. *Mendocino Co.*: S. Fork of Eel River. *Monterey Co.*: Carmel. *Orange Co.*: Anaheim, Laguna Mts. *Riverside Co.*: Idyllwild (San Jacinto Mts.), Palm Springs, Santa Rosa Park (8000 ft.). *San Bernardino Co.*: Lake Arrowhead, Barton Flats, Bear Valley, Big Bear Lake, Fawnskin, Seven Oaks. *San Diego Co.*: Mission Valley, Palomar Mtn. (4700 and 5260 ft.), 8 mi. N. San Diego, San Diego. *San Francisco Co.*: San Francisco. *Santa Barbara Co.*: Santa Cruz Island (Prisoners Harbor), Santa Rosa Island (Becher's Bay). *Santa Cruz Co.*: Ben Lomond, Santa Cruz. *Shasta Co.*: Hat Creek Ranger Station, Lassen Natl. Park (Manzanita Lake). *Siskiyou Co.*: 5 mi. E. McLoud, Mt. Shasta. *Sonoma Co.*: Duncan Mills, Healdsburg, Mesa Grande, nr. Monte Rio, Russian River. *Tehama Co.*: 1 mi. SW Harrison (Basin Gulch Camp, Gulch Research Station). *Tulare Co.*: Visalia. *Ventura Co.*: Upper Cuyama (Camp Ozena). *Yolo Co.*: Davis. *County Unknown*: Paraiso Hot Springs (1400 ft.), San Marcos Valley (Little Anne), Stewart's Point.

NEVADA: *Nye Co.*: Monitor Valley.

OREGON: *Douglas Co.*: Diamond Lake. *Harney Co.*: 20 mi. S. Burns (4200 ft.). *Hood River Co.*: Hood River. *Klamath Co.*: Klamath Falls.

WASHINGTON: *Pierce Co.*: Puyallup. *San Juan Co.*: Friday Harbor. *Yakima Co.*: Toppenish, Yakima. *County Unknown*: Entrat.

MARCH (3), APRIL (2), JUNE (229), JULY (195), AUGUST (89).

**Biology.**—Label data show *P. nigra* collected from offshore California islands up to 8000 ft. elevation. Specimens collected 10 mi. S. Vantage, Grant Co., Washington are "ex sage."

**Remarks.**—Distinguished from *P. hirsuta* and its allies by the lack of elytral hairs and from *P. stellata*

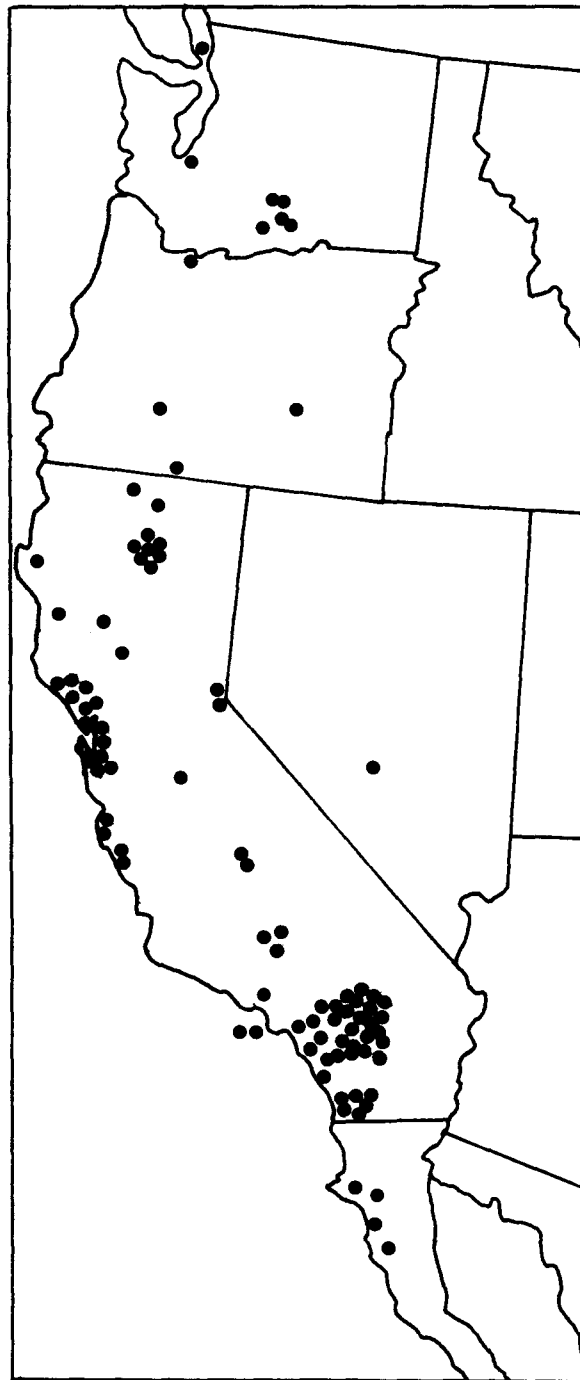


Fig. 26.—Distribution of *P. nigra*.

by the presence of well defined vittae. This character in combination with a more heavily setigerous male pronotum and overall larger size separates it from *P. diffracta*. *P. nigra* is most commonly confused with *P. crinita*. These two species may be separated by the

larger size of *P. crinita* combined with its unique olivaceous brown to black basal color.

In working through long series of California specimens, samples collected at Idyllwild (central Riverside Co.) emerged as a distinct morphological entity, distinguished from all others by the combination of well defined elytral vittae (as in *P. decemlineata*) and the densely hairy pronotum. Similar samples from several localities in the SW corner of San Bernardino Co. also emerged from the material on hand (Big Bear Lake, Fawnskin, Lake Arrowhead, Running Springs, Seven Oaks). These two collecting sites, in Riverside and San Bernardino counties, respectively, are labelled 8000 and 6300 ft. in elevation. Like *P. modulata* (but on a much larger scale), this species looks like *P. decemlineata* in external features, except for the setigerous pronotum which leads one to suspect an affinity with the *diffRACTA* complex. Aedeagal configuration confirms that suspicion (Fig. 5j). These various specimens were set aside, awaiting further examinations of various name-bearing types.

*P. santacruzae* von Bloeker was described in 1939 and synonymized under *P. crinita* by Cazier (1940). I am unable to tell what characters induced von Bloeker to establish this taxon. One also cannot discern why Cazier placed it as a synonym of *P. crinita*; his 1940 paper so listed it without discussion or comments. My first examination of the type series of this name caused me to affirm Cazier's decision, based on overall large size, well formed elytral vittae, coloration, and presence of pronotal hairs. A great deal of additional material seen since my 1967 paper has, however, changed that decision. Forty-three male paratypes of *P. santacruzae* have been directly compared with the paralectotypes of *P. crinita* designated by Young (1966). This material is very dissimilar in several characters believed to be significant. Not only the type material of *P. crinita*, but many comparable specimens, are much larger than *P. santacruzae* samples. The often mentioned tricolorous appearance of *P. crinita* type specimens is not seen in those of *P. santacruzae*, as the interstitial scales are densely packed, obscuring the elytral basal color. This lack of harsh coloration in the *P. santacruzae* type series makes it most similar superficially to *P. decemlineata*, but as mentioned above, the hairy pronotum at once separates these two. The *P. santacruzae* paratype series was set aside until I realized that it "fit" with the earlier discussed material from S. California. The S. California specimens and the *P. santacruzae* paratypes were alike in those two characters considered

most significant in this case, the pronotal hairs and the hard-edged elytral vittae. It is emphasized that these two characters *in combination* is the significant point. At this point I felt that *P. santacruzae* should be resurrected.

At a later date the Casey types were re-examined. The holotype of *P. crinita nigra* immediately emerged, showing an array of characters like the various samples discussed above. On these bases, *P. nigra* is revived with *P. santacruzae* as one of its new synonyms.

*P. martini* was first described (von Bloeker 1939) because the short humeral vittae connected mesad with the next vittae, forming a Y-shaped pattern. This character has been seen in every vittate species of the *diffRACTA* complex. Re-examination of the *P. martini* type and its direct comparison with the type material of *P. crinita* led to conclusions the same as for *P. santacruzae* above.

Finally, a re-examination of all of Casey's types showed *P. incolumis relictata* and *P. incolumis robustula* to compare favorably throughout with the name-bearing types just discussed.

### ***Polyphylla nubila* Van Dyke**

(Figs. 5k, 22, 59, 60)

*Polyphylla nubila* Van Dyke 1947: 160; Hardy and Andrews 1978: 2. (Holotype male CASC 5879 and three male paratypes CASC. Type locality: CALIFORNIA: San Luis Obispo Co.: Atascadero).

**Holotype Male.**—Short, robust. Length 22 mm, width 10 mm. Reddish-brown elytra, head and pronotum darker. Clypeal margins reflexed; with dense, shallow punctures, lateral margins contracted basally. Head with coarse, dense punctures, punctures giving rise to long, light brown hairs. Antennal club barely longer than head, distinctly recurved. Pronotum convex, disc with coarse, irregular punctures, depressed midline bearing a vitta composed of white scales, scales more concentrated along lateral and posterior margins; with long, light, brown hairs throughout. Elytra one-third longer than wide, with irregular, shallow punctures; rugose, shining where not scaled; without well defined vittae, instead white scales densely joined into random clumps not limited to normally vittate areas, single scales scattered between clumps; with fine erect hairs throughout. Pygidium densely clothed with white scales and fine,

short hairs except for naked midline. Protibiae strongly bidentate. (Modified from Van Dyke, 1947).

**Female.**—Unknown.

**Distribution.**—Specimens examined: the type series of four males and one male labelled "S. Luis Obispo P.C." collected V-15-1956. This latter specimen, now in my collection, was attained in a trade with Delbert A. La Rue of Riverside, California. It, and others in his collection, are the only specimens known other than the type series. This species was described 40 years ago at this writing and remains known only from Atascadero and San Luis Obispo (Fig. 22). The type series was collected at light May 23.

**Remarks.**—Distinguished from *P. diffracta* and its allies by the presence of elytral hairs. Distinguished from *P. barbata* and *P. rugosipennis* very readily by the elytral squamae randomly clustered, not forming a striped pattern. Some specimens of *P. barbata* show vittae heavily broken but never with random clumps of scales as in *P. nubila*. This is the only Pacific Coast species with this very distinctive elytral pattern.

***Polyphylla pottsorum* Hardy and Andrews**  
(Figs. 5L, 27, 61)

*Polyphylla pottsorum* Hardy and Andrews 1978: 6. (Holotype male CASC 13101 and 329 male paratypes: AMNH, CASC, Hardy, Nelson, Potts, USNM. Twelve male homotypes here designated, LACM, and private collections. Type locality: TEXAS: Ward Co.: Monahans Sandhills State Park).

**Holotype Male.**—"Length 20 mm, width 7 mm. Integument of head, prothorax, scutellum piceous; elytra, antennal club, ventral body surfaces pale testaceous; pygidium, basal segments of antennae, legs testaceous. Clypeus widened apically, anterior margin reflexed, nearly linear, angles sharp, not produced above anterior margin. Clypeus, front with elongate, pointed white scales, intermixed with semi-erect gray hairs. Prothoracic disc with few erect hairs close to anterior margin; with elongate white scales closely to densely (scattered?) over surface; scales intermixed with recumbant white scale-like hairs medially. Prothorax appearing faintly trivittate. Elytra

sparsely covered with small, elongate, pointed white scales, faintly vittate at elytral base. Pygidium sparsely scaled. Antennal club approximately 2 (linear) to 2.5 times (along curve) length of basal segments. Ventral abdominal segments glabrous basally near suture, densely scaled apically; covered with sparse to dense, long, fine pubescence. Ventral surface of thorax densely covered with long, white hairs, except glabrous patch at midline of metasternum. Anterior tibia distinctly tridentate, not as strongly as previous species." (Compared to *P. erratica* of the *hammondi* complex. Quoted from Hardy and Andrews 1978).

**Paratypes. (Variation).**—"Length 16–22 mm, width 5.5–7.6 mm. There is some variation in the development of the third (basal) tooth, but in all cases, there is clearly a third tooth present. Variation in scale density varies the elytral appearance from that of glabrous (although scales are present) to distinctly vittate, with vittae extending nearly to the elytral apex." (Hardy and Andrews 1978).

**Female.**—Unknown.

**Distribution.**—Specimens examined: The holotype, ten paratypes, and the 12 homotypes here designated. While they have no validity or standing under the provisions of the Code, I believe the use of homotypes (designated by someone other than the author of the species) and metatypes (designated only by the author of the species) remains a constructive and helpful technique, as they tell future investigators that the designated specimens have been directly compared with the name-bearing type. The 12 homotypes are the first specimens I am aware of other than the type series, and they are the first known specimens not from the type locality (Fig. 27).

NEW MEXICO: *Chaves Co.*: Mescalero Dunes (T12S R30E Sec. 24, 4029 ft. elev.).

TEXAS: *Ward Co.*: Monahans Sandhills State Park. *Winkler Co.*: Rest Area (Junction Highways 115 and 874).

MAY (29), JUNE (146), JULY (167).

**Biology.**—Unknown. Taken at ultraviolet light and directly associated with sand dunes. The New Mexico specimens were collected sympatrically with *P. mescalerensis* new species. Texas specimens from the type locality were collected sympatrically with *P. monahansensis*.

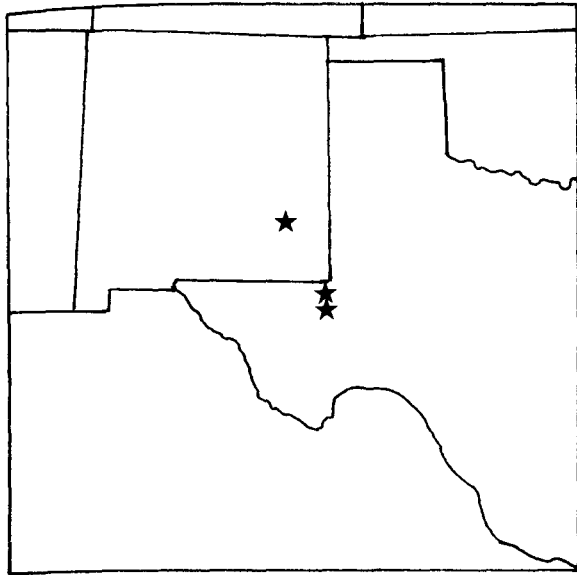


Fig. 27.—Distribution of *P. pottorum*.

**Remarks.**—This very distinctive species is distinguished from *P. hirsuta* and allied species by the lack of elytral hairs. From *P. diffracta* and its allies it is readily distinguished by overall size not exceeding 22 mm, the unique pale yellow elytral color and its apparent restriction to west-central Texas and southeastern New Mexico (Fig. 27). I do not agree with Hardy and Andrews' conclusion (1978) that it is closely related to *P. squamiventris*, which is of a similar size. *P. squamiventris* is a member of the *hammondi* complex of species by aedeagal configuration (Fig. 8g) and is very distant from *P. pottorum* (Fig. 5L). In diminutive overall size and loss of vittae these two species probably represent a case of convergent evolution, but they are widely distanced by aedeagal characters.

***Polyphylla ratcliffei* Young**  
(Figs. 5m, 22, 62–63)

*Polyphylla ratcliffei* Young 1986: 49. (Holotype male, CASC. Type locality: UTAH: Grand Co.: 9 mi. NW Moab. Four male paratypes, same locality, deposited as follows: author [1], University of Idaho [1], University of Nebraska State Museum [1], USNM [1].)

**Holotype Male.**—“Body narrow, small, overall length 21 mm, width 9.5 mm. Elytra light brown, pron-

otum darker brown, head black. Clypeus moderately reflexed apically, lateral margins continuously narrowing posteriorly, anterior one-third with narrow, elongate, yellowish, suberect to recumbant squamae, squamae continuing laterally and along epistomal suture, disc with a few scattered scales interspersed with suberect hairs. Head with large, dense, shallow punctures, scaled along lateral margins and on canthi, disc shining black, with long golden suberect hairs throughout. Antennal club barely longer than combined length of head and clypeus, distal two-thirds recurved. Prothorax broadly convex, widest just anterior to midlength, one and two-thirds wider than long, with dense, large, shallow punctures; vitta on depressed midline degenerating on posterior half; lateral vittae broad, strongest posteriorly; squamae concentrated along all margins except middle quarter of front, with long, golden, suberect hairs throughout. Elytra just under one and one-half longer than wide, parallel-sided, with sparse, short, fine, erect hairs; narrow sutural vitta weakly formed of small, white squamae, squamae broadly and randomly scattered to clustered over surface, without defined vittae (but squamae somewhat more clustered in anterior third of normally vittate areas). Pygidium with small, white scales evenly distributed (except along midline) and with short, fine, recumbant hairs. Prothorax strongly tridentate.” (Young, 1986).

**Measurements (Holotype male).**—Length antennal club 4 mm, combined length head and clypeus 3.5 mm; length pronotum 4.5 mm, width 7.5 mm; length elytra 14 mm, width 9.5 mm.

**Female.**—Unknown.

**Distribution.**—Specimens examined, five males. *P. ratcliffei* cannot be distinguished by external characters from *P. devastiva* and *P. avittata*. As mentioned in my remarks on *P. avittata*, these three demes form the points of a triangle with the points being southwestern Idaho (*P. devastiva*), southwestern Utah (*P. avittata*), and east central Utah (*P. ratcliffei*; Fig. 22). There are no intervening morphologically similar demes. *P. devastiva* is endemic to three counties in southwestern and south central Idaho and it seems entirely illogical to me to place the Utah demes under this name. I extracted the aedeagi of Hardy and Andrews' holotype and two paratypes of *P. avittata*, and the types series of *P. ratcliffei*. In caudal view, the

parameres of *P. avittata* are clearly unequal, the left one bearing a translucent dorsal flange with a lesser flange on the right paramere (Fig. 5a). The parameres of *P. ratcliffei* do not bear these flanges and are equal (Fig. 5m; see also remarks under *P. avittata*).

***Polyphylla rugosipennis* Casey**  
(Figs. 5n, 28, 64)

*Polyphylla rugosipennis* Casey 1914: 337; Leng 1920: 257; Fall 1928: 32; Leng and Mutchler 1933: 39; Cazier 1938: 163; Blackwelder 1939: 53; Cazier 1940: 137; Blackwelder and Blackwelder 1948: 33; Young 1967: 291; Blackwelder and Arnett 1974: R30.69; Hardy 1981: 299. (Holotype male USNM 35633. Type locality: ARIZONA: Grand Canyon of the Colorado).

*Polyphylla peninsularis* Van Dyke 1943: 103. (Holotype male and seven paratype males CASC 5338. Type locality: BAJA CALIFORNIA: San Pedro Martir Mts., La Brulla, 7000 ft.).

**Holotype Male.**—Short, broad. Length 22.33 mm, width 10.75 mm. Elytra brown, becoming black at humeral umbones, deeper brown posteriorly, pronotum deep brown. Clypeus flat except for weakly reflexed lateral margins and abruptly reflexed anterior margin, lateral margins contracted just anterior to base; anterior half and lateral margins covered with closely packed, broad, yellowish scales, posterior half with deep wide punctures, each puncture bearing a squama, occasional squama elongate and thin, hair-like. Head black, with deep close punctures between eyes, each puncture bearing a long, coarse, erect hair in medial area and a broad, yellowish squama on anterior margin; squamae becoming concentrated along entire anterior margin. Antennal club barely longer than head, barely recurved. Prothorax one and one-half wider than long, with deep broad punctures throughout, punctures smaller and more packed towards lateral margins; oval white squamae forming distinct vitta on depressed midline, similar squamae forming lateral vittae which are broken just posterior to their origin on anterior margin; very broadly scattered, stout, white hairs along lateral edges of midline vitta and anterior margin of pronotum. Elytra one and one-half longer than wide, sutural vittae well formed of very minute, closely packed, oval, white squamae;

lateral vittae distinct but with somewhat broken edges, especially posteriorly. Pygidium shining brown, covered with white squamae varying from hair-like to broad, most concentrated along anterior margin, without erect hairs. Protibiae bidentate, proximal tooth weakly formed.

**Female.**—Unknown.

**Distribution.**—Specimens examined, 48 males. This poorly known species is recorded from northwestern New Mexico, northern Arizona in the vicinity of Grand Canyon National park, Inyo Co., California, and ca. the northern half of the Baja peninsula (Fig. 28). It is rare in collections; only a few additional specimens have been seen since my 1967 paper. The mapped distribution of this species does not yet make much sense; I suspect the discontinuous pattern to be an artifact of collecting and the fact that most investigators do not correctly identify this species.

MEXICO: BAJA CALIFORNIA NORTE: El Rayo, 9 mi. SE El Rayo, La Grulla, Laguna Hanson, 3.2 mi. S. Laguna Hanson, 18 mi. E. Meling Ranch, San Pedro Martir Mts. (7000 ft.), Vallecitos, V. Trinidad.

UNITED STATES: ARIZONA: *Coconino Co.*: De-



Fig. 28.—Distribution of *P. rugosipennis*.

sert View (Grand Canyon), Grand Canyon (S. Rim), N. Rim Grand Canyon.

CALIFORNIA: *Inyo Co.*: Deep Springs.

NEW MEXICO: *San Juan Co.*: Farmington.

JUNE (10), JULY (36), SEPTEMBER (2).

**Biology.**—Unknown.

**Remarks.**—*P. rugosipennis* is a member of that species group within the *diffracta* complex characterized by having elytral hairs. It is most easily confused with *P. barbata* from which it may be distinguished by the absence of interspersed hairs on the pygidium and by the lateral edges of the clypeus which are parallel, rather than gradually narrowing basally as in *P. barbata*. The presence of continuous elytral vittae distinguish it from *P. nubila*.

#### ***Polyphylla sobrina* Casey**

(Figs. 5o, 25, 65)

*Polyphylla sobrina* Casey 1914: 339; Leng 1920: 257; Fall 1928: 32; Leng and Mutchler 1933: 39; Cazier 1938: 163; Blackwelder 1939: 201; Cazier 1940: 137; Blackwelder and Blackwelder 1948: 33; Young 1967: 300; Blackwelder and Arnett 1974: R30.69; Young 1986: 50. (Holotype male USNM 35636. Type locality: CALIFORNIA: El Dorado Co.).

**Holotype Male.**—Broad, elongate. Length 26.5 mm, width 11.5 mm. Uniform ferrugino-testaceous. Clypeus deeply and abruptly concave with anterior margin perpendicular to disc, punctures with radiæ greater than those on head, spaced regularly, each puncture bearing an unusually large, broad, yellowish squama; squamae more concentrated along anterior and lateral margins, without interspersed hairs on disc but occasional stout suberect hairs in lateral and posterior portions, lateral edges gradually narrowing posteriorly. Head with deep, unevenly scattered punctures of dissimilar sizes, pattern highly irregular, each puncture in medial band bearing a stout, yellow, erect hair; widely scattered, yellowish squamae randomly interspersed in same area; fairly regular line of squamae on anterior margin, erect hairs generally replaced by large, white squamae around eyes, a few long, stout hairs interspersed but much more dense in medial area. Antennal club one and one-third longer than combined length of head and

clypeus. Prothorax one and three-fourths wider than long, with shallow, irregular punctures throughout, punctures more concentrated along all margins; elongate, white squamae forming distinct vitta on depressed midline and lateral vittae on posterior half; widely scattered yellow squamae in interstitial areas becoming more concentrated along posterior margin; stout yellowish hairs scattered randomly along anterior and lateral margins, lateral edges abruptly reflexed. Elytra one and one-half longer than wide, becoming slightly broader posteriorly, lateral edges sharply reflexed; sutural vitta present but broken, with randomly alternating areas of white squamae and naked patches, lateral vittae distinct but with rough edges, interstitial areas with broadly spaced, distinctly yellow squamae which are smaller than those composing vittae. Pygidium densely covered with elongate, yellowish squamae, naked midline, without hairs throughout. Protibiae bidentate.

**Female.**—Consistently larger than male, more robust throughout. Color of pronotum and elytra uniform deep brown. Clypeus and head devoid of squamae except for a few along anterior margin of clypeus, variable erect hairs scattered throughout. Prothorax devoid of hairs except for extreme anterior margin, vittae variable, especially the lateral ones. Elytra with vittae greatly degenerated, often approaching unicolorous brown. Pygidium squamose, especially anteriorly, without hairs. Protibiae tridentate.

**Distribution.**—Specimens examined, 1130 males and 23 females. This number has more than doubled since my 1967 paper. Several cases of false data and incorrect determinations have been established, resulting in some changes in the mapped distribution of this species. This very distinctive species occurs in the greatest numbers from the Lake Tahoe area south to and including Yosemite National Park. About one-half of the examined specimens come from these two areas. There are scattered records from northern California, but none from northwestern Nevada or Oregon. The Utah record shown in Part I (Young 1967) is based on false labelling and is rejected. This species also occurs occasionally in California south of Yosemite National Park (Fig. 25).

CALIFORNIA: *Alameda Co.*: Piedmont. *Alpine Co.*: Crystal Springs Campground, Hope Valley, Pleasant Valley (Markleville). *Butte Co.*: Chico. *Calaveras Co.*:



Camp Wolfboro. *El Dorado Co.*: Eldorado, Lake Tahoe (Bijou, Biton, Globins, Lakeside, Tahoe Valley), Myers, Pollock Pines, Snowline Camp, nr. Whitehall. *Fresno Co.*: Fresno, Huckleberry Meadow, Kings Canyon Natl. Park (Cedar Grove, 4600 ft.), Kings River Canyon, Mono Hot Springs, Riverton. *Lake Co.*: Fallen Lake. *Lassen Co.*: Doyle, Hallelujah Junction, Manzanita Lake, Milford, Sussanville. *Madera Co.*: Northfork, Placer Ranger Station. *Mariposa Co.*: Miami Ranger Station (4700 ft.), Yosemite National Park (3880–5000 ft. and Miguel Meadows @ 5200 ft.), Wawona. *Nevada Co.*: Donner Lake, Truckee, Lake Ver- (illegible). *Placer Co.*: Auburn, Brockway. *Plumas Co.*: Vinton. *San Bernardino Co.*: No data. *San Diego Co.*: Jacumba. *Shasta Co.*: Hat Creek Ranger Station, Lassen National Park. *Siskiyou Co.*: McCloud, Mt. Shasta City. *Tulare Co.*: Camp Sierra, Kaweah (1000 ft.), Three Rivers, Tipton, Visalia. *Tuolumne Co.*: Camp Wolfe, Dardanelles, Mather, 8 mi. S. Mather, Pinecrest, 4 mi. W. Pinecrest, Sonoro, Strawberry, Twain-Harte (4000 ft.), Upper Baker Camp. *Yuba Co.*: Oroville. *County Unknown*: Bass Lake, Diamond O'Mather, Lower Hot Springs (6000 ft.), Mohawk, Pacific, Pacific House, Sand Flat (5500 ft.).

NEVADA: *Douglas Co.*: Camp Galilee, Clear Creek (5700 ft.), 1 mi. from Glenbrook, Stateline, Zephyr Cove. *Ormsby Co.*: No data. *Washoe Co.*: Lake Tahoe.

MAY (6), JUNE (16), JULY (968), AUGUST (161), SEPTEMBER (2).

**Biology.**—Unknown. Often taken at black, UV, and white light. Recorded from elevations of 1000–6000 ft.

**Remarks.**—*P. sobrina* is a very distinctive species; its unusual yellow to yellowish-brown basal color distinguishes it from all other species within its geographic range. Large samples examined show a degree of morphological cohesiveness not often seen in this genus. Elytral vittation varies more widely than any other character, ranging from hard-edged lines to nearly unicolorous brown, especially in some females. Nonetheless, the basic color of this species will normally enable the investigator to pick it out at a glance.

### ***Polyphylla stellata* Young**

(Figs. 5p, 25, 66–67)

*Polyphylla stellata* Young 1986: 50. (Holotype male and two paratype males UCDC, two paratype males USNM, one paratype male author's collection. Type locality: CALIFORNIA: Sacramento Co.: Carmichael).

**Holotype Male.**—Body narrow, parallel-sided. Length 24 mm, width 10.4 mm. Elytra deep brown along all margins, becoming lighter centrally; head and pronotum deep brown marginally, black centrally. Clypeus with only anterior margin reflexed, punctures large, with areas between punctures rugose; white squamae concentrated on lateral and anterior margins, scattered widely on disc. Frons with similar punctation and rugosity, a suberect, yellow hair rising from each puncture, broad white squamae concentrated along eye margin, less concentrated along epistomal suture. Antennal club equal in length to combined length of head and clypeus, barely recurved at distal tip. Pronotum gradually convex, one and three-fifths wider than long, with deep, broad punctures, especially on disc; broad white squamae forming narrow vitta on slightly depressed midline, lateral vittae formed only on posterior half, more elongate, yellowish squamae broadly scattered over rest of surface; elongate, recumbent hairs only on central third of width, hairs scattered between squamae. Elytra one and one-half longer than wide, vittae (or any suggestion of vittae) lacking over entire surface; fine, minute, white squamae scattered randomly over surface, becoming concentrated in a few small spots, erect hairs absent. Pygidium with scattered, minute, white squamae, squamae more concentrated each side of midline. Protibiae weakly tridentate.

**Female.**—Unknown.

**Distribution.**—Specimens examined: the type series of six males. Known from the type locality and Antioch, Contra Costa Co., California (Fig. 25). Collected from July 3 through July 30.

**Remarks.**—This very distinctive species may be placed within the *diffRACTA* complex at a glance by the presence of pronotal hairs. The absence of elytral hairs removes it from *P. hirsuta* and allies. Within the

species cluster not having elytral hairs it is the only species exceeding 22 mm length which is deep brown to black and devoid of formed vittae.

The paratypes range in overall length from 22.1–23.3 mm, in width from 10.1–11.0 mm. Elytral length ranges from 14.3–15.7 mm. Overall they show very little variation in external morphology. In two paratypes the pronotal disc is devoid of squamae, having only a light covering of recumbent hairs. In another the elytral squamae are missing centrally, giving the animal a simple deep brown appearance. Protibiae vary from barely to deeply tridentate. Once seen, this distinctive species should be easy to recognize. The spotted or speckled aspect of the elytra (hence the name *stellata*), with each spot being a single isolated white scale, is most unique.

#### THE HAMMONDI COMPLEX

##### *Polyphylla anteronivea* Hardy and Andrews (Figs. 8a, 29, 68)

*Polyphylla anteronivea* Hardy and Andrews 1978: 2. (Holotype male CASC 13097. Thirty-five male paratypes in CASC, Ca. Dept. Agriculture, USNM and private collections of Cicero, Howden, Nelson, Potts, Rulien. Type locality: CALIFORNIA: Inyo Co.: Saline Valley Dunes).

**Holotype Male.**—“Length 26 mm, width 8.8 mm. Integumentary color of head piceous to rufo-piceous; thorax rufo-piceous; elytra, ventral body surfaces, appendages testaceous. Clypeal angles well defined; reflexed margin, disc, front with close to contiguous round to oval, cream to white scales. Front with few semierect cream colored bristle-like hairs. Vertex smooth, glabrous, thorax with close to contiguous to densely overlapping oval white scales, which obscure virtually entire thoracic integument. Few scattered erect hairs at anterior margin of prothorax. Scutellum contiguously covered with oval white scales. Elytra anteriorly, along suture, lateral margin and apically, with scattered to contiguous oval white scales. Ventral thoracic segments with sparse, medium, gray to white erect hairs, less dense than in most *Polyphylla*. Apical segment of maxillary palp short (.7 times length of basal two segments), stout

(length 3.2 times width), with small, slightly concave area dorsally. Antennal club 2 (linear measurement) or 2.8 (along curve) times length basal segments. Anterior tibiae strongly tridentate.” (Hardy and Andrews 1978).

**Female.**—Unknown.

**Distribution.**—Specimens examined: the holotype male and one paratype male. Known only from the Saline Valley Dunes (Fig. 29).

MAY (7), JUNE (25), JULY (3), AUGUST (1).

**Biology.**—Directly associated with a sand dune complex and taken at blacklight.

**Remarks.**—*P. anteronivea* is distinguished very easily from all its congeners by the snowy white pronotum and scutellum; the covering composed of solid white scales. Hardy and Andrews (1978) note that overall length ranges from 21–29 mm., and width from 7–10 mm. They also record that elytral scalation may be reduced or not appear vittate.

This species is very closely related to *P. erratica*, so closely in fact that I doubt that both names represent biological species. This matter is discussed more fully under *P. erratica*.

##### *Polyphylla brownae* Young (Figs. 8b, 30, 69–70)

*P. brownae* Young 1986: 47. (Holotype male ANSP 8395, paratype males CASC, MCZC. Type locality: ALABAMA: Washington Co.: Calvert).

**Holotype Male.**—Long, narrow. Length 29.3 mm, width 12.1 mm. Elytra light brown, head and pronotum deeper, richer brown. Clypeus moderately concave, lateral margins contracted for posterior one fourth; surface entirely, deeply punctate, each puncture giving rise to a broad, yellowish, suberect hair, hairs becoming erect in postero-lateral corners. Head with large, dense, shallow punctures, covered with widely spaced, erect hairs throughout, hairs becoming shorter and more concentrated along epistomal suture; scales lacking. Antennal club one and one-third longer than combined length of head and clypeus, distal one-third gradually curved outwards.

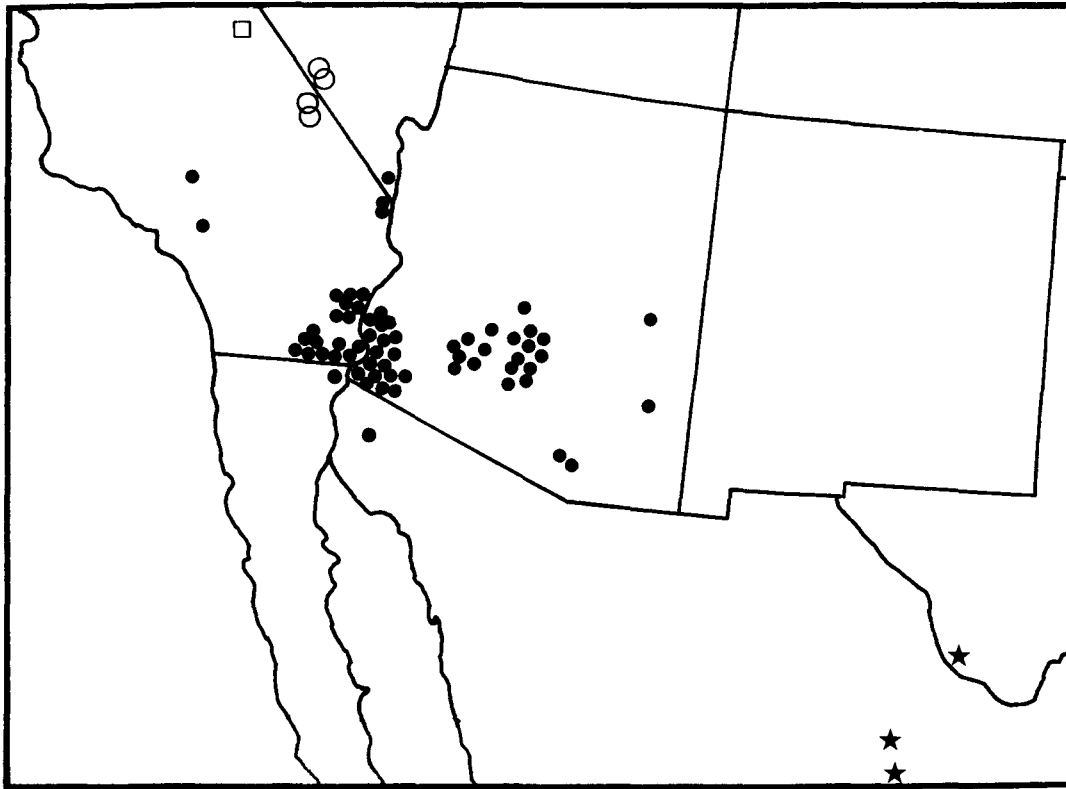


Fig. 29.—Distributions of *P. anteronivea* (□), *P. cavifrons* (●), *P. erratica* (○), and *P. squamiventris* (★).

Prothorax abruptly convex, just over one and one-half wider than long, disc mostly rugose, with variably sized, random punctures laterally; midline suddenly and deeply depressed just anterior to middle, bearing a swirl of fine, recumbant hairs; lateral one-third with dense, recumbant hairs, without scales throughout. Elytra one and one-half longer than wide, slightly narrower posteriorly, entire surface clothed with short, recumbant, randomly scattered hairs; hairs becoming slightly more concentrated marginally. Abdomen devoid of scales, clothed with fine hairs. Pygidium the same, hairs a bit longer than those on elytra. Prothorax weakly tridentate.

**Female.**—Unknown.

**Distribution.**—Specimens examined: The holotype male from Alabama: Calvert, VII-4-1923, no collector's name. Calvert is in extreme southern Washington Co., bordering on Mobile Co. which borders on the Gulf of Mexico. Also one paratype male:

Alabama: Calvert, VII-4-1921, no collector's name, from the CASC and there deposited. One paratype male: Alabama: Calvert, VII-4-1923, no collector's name; also labelled "H.C. Fall Collection" and "Liebeck Coll.," from the MCZC and there deposited (Fig. 30).

**Male Genitalia.**—Aedeagal structure finely formed, elongate and very narrow throughout; basal plate unusually narrow but abruptly curved in cross section; parameres viewed from above abruptly narrowing basally, majority of length parallel-sided and narrow; centrally fused for just over half their length leaving the remaining distal portion centrally cleft, distal tip truncate viewed from above, in lateral aspect sharply turned downwards but smoothly so, no dorsal ridge present; unquestionably most similar throughout to *P. hammondi* and related species, characters not diagnostic to species (Fig. 8b).

**Remarks.**—This species was named in honor of

my wife, Nova Brown Young, whose unyielding support over the years has made completion of this work possible.

The three specimens on which this description is based emerged from the thousands of *Polyphylla* examined for this monograph, from institutional collections on opposite coasts of the United States. It seems likely that H.C. Fall collected these three and they have been subsequently separated. Externally *P. brownae* looks like a member of the *hammondi* complex but its occurrence in the Alabama panhandle causes one to look again. Configuration of the aedeagus, however, immediately confirms the first suspicion (Fig. 8b). This species is yet another eastern relict of the *P. hammondi* lineage as I discussed in my 1972 paper but in this case the isolation has resulted in a clear speciation event. Recognition of this species includes, I think, a fairly high level of predictability that the type locality is some type of a sandy refugium or that additional collecting will show it distributed southwards to the Gulf Coast.

*P. brownae* may be distinguished from all other species of the genus by its distribution and unique lack of squamae over its entire body above and below. Vestiture is composed entirely of hairs. The two paratypes are slightly smaller and darker than the holotype; other than this character they are very much like the holotype.

### ***Polyphylla cavifrons* LeConte**

(Figs. 8c, 29, 71)

*Polyphylla cavifrons* LeConte 1854: 222; LeConte 1856: 229; Crotch 1873: 61; Horn 1881: 73; Henshaw 1885: 92; Bates 1888: 215; Dalla Torre 1912: 257; Casey 1914: 323; Leng 1920: 257; Fall 1928: 31; Kuntzen 1933: 464; Leng and Mutchler 1933: 39; Cazier 1938: 163; Blackwelder 1939: 53; Cazier 1939: 200; Cazier 1940: 135; Blackwelder and Blackwelder 1948: 33; Young 1967: 285; Blackwelder and Arnett 1974: R30.68; Hardy and Andrews 1978: 4; Hardy 1981: 299. (Holotype male MCZC 3768. Type locality: Not clearly stated. LeConte mentions "on the San Diego trip" and "on the Rio Grande").

**Male.**—(California: Riverside Co.: Blythe). Elongate, narrow, parallel-sided. Length 26 mm, width 10.5 mm. Reddish-brown throughout, pronotum darker than elytra. Clypeus concave, spatulate, anterior and

lateral edges abruptly reflexed, scattered minute hairs over surface, especially anteriorly. Head with similar fine hairs, more dense than on clypeus. Pronotum just under twice as wide as long, widest at midlength, centrally depressed midline bearing closely placed, minute, white squamae which form a vague vitta; without hairs, vestiture composed only of minute, white squamae randomly scattered over disc except for midline, scales more concentrated along all margins, especially postero-lateral corners. Antennal club barely as long as combined length of head and clypeus, distal one-third barely recurved. Elytra one and one-half longer than wide, surface with apparently random, slightly raised, linear ridges; vestiture composed of only minute, white squamae scattered over surface, scales slightly more concentrated in normally vittate areas but no clear-cut vittae formed; appearing pruinose; scales slightly more concentrated along posterior third of midline and posterior edges. Pygidium with similar vestiture, central linear depression on posterior half. Protibiae deeply tridentate.

**Female.**—Broader, more robust than male. Without vittae and often without scales throughout, appearing unicolorous brown. Protibiae deeply tridentate, like the male.

**Distribution.**—Specimens examined, 336 males and 33 females. *P. cavifrons* is restricted to the deep southwestern deserts of the United States; in Mexico it is recorded from Sonora and the extreme northern Baja (Fig. 29).

MEXICO: BAJA CALIFORNIA NORTE: Algodones. SONORA: No data.

UNITED STATES: ARIZONA: *Graham Co.*: No data. *Maricopa Co.*: Dendora Valley, Agua Caliente, Gila Bend, Gillespie Dam, nr. Mesa, Phoenix, Tempe, Waddell, Wickenburg. *Navajo Co.*: Lakeside. *Pima Co.*: Tucson. *Yuma Co.*: Ehrenburg, 1 mi. N. Ligurta, 5 mi. N. San Luis, 1 mi. E. Somerton, 1 mi. E. Wellton, Wellton, Yuma. *County Unknown*: Cibola, Goldwater, Granite Reef, S. Mtn. Park.

CALIFORNIA: *Imperial Co.*: El Centro, Fort Yuma, Holtville, Laguna Dam, Palo Verde (254 ft.), Winterhaven. *Kern Co.*: No data. *Riverside Co.*: Blythe. *San Bernardino Co.*: Needles. *Tulare Co.*: Tulare. *County Unknown*: Mtn. Springs.

NEVADA: *Clark Co.*: Mesquite. *County Unknown*: Circle City.

APRIL (2), MAY (47), JUNE (68), JULY (71), AUGUST (161), SEPTEMBER (4) OCTOBER (2).

**Biology.**—A species of the true xeric desert, often attracted to lights.

**Remarks.**—*P. cavifrons* is distinguished from all others by its southwestern distribution in combination with its pruinose, avittate appearance. It should not be confused with samples of small, avittate *P. hammondi*, which have deeply yellow elytral squamae.

***Polyphylla erratica* Hardy and Andrews**  
(Figs. 8d, 29, 72)

*Polyphylla erratica* Hardy and Andrews 1978: 4. (Holotype male CASC 13099, and 65 male paratypes in CASC, LACM, USNM and private collections Hardy, Howden. First known female here discovered, homotype, UCDC. Type locality: CALIFORNIA: San Bernardino Co.: Death Valley National Monument, Saratoga Springs).

**Holotype Male.**—“Length 26.5 mm, width 9.7 mm. Integument of head rufous, except piceous vertex, anterior, lateral clypeal margins and angles. Thoracic integument rufous. Elytra, ventral surfaces, pygidium, appendages rufotestaceous; antennal club testaceous. Clypeus quadrate, margins strongly reflexed, anteriorly bisinuate, outer angles sharp, nearly spinose. Clypeal disc with close to contiguous oval white scales; front with close to contiguous to “shingled” oval white scales, with semierect to erect testaceous hairs; vertex shining, impunctate, glabrous. Prothorax with close, to “shingled” oval white scales, slightly denser medially, medio-laterally, forming trivittate prothoracic pattern normal for genus; few erect to semierect white to testaceous hairs at anterior margin. Scutellum “shingled” with oval white scales. Elytra with oval white scales, which are dense and “shingled” anteriorly; becoming scattered laterally, posteriorly; forming broken “vittae.” Elytra lacking hairs. Pygidium with close white oval scales. Ventral surfaces nearly completely covered (except sutures) with oval white scales. Thorax ventrally with erect white hairs. Antennal club 2 (linear) to 3.3 (along curve) times length basal segments. Anterior tibiae strongly tridentate” (Hardy and Andrews 1978).

**Female.**—This homotype, the first and only known female of this species, is so labelled and deposited at UCDC.

Broad, robust, much wider posteriorly. Length 26.5 mm., width 8.5 mm. Pronotum deep reddish-brown, elytra medium brown. Clypeus, head, and pronotum totally devoid of squamae except for a few minute, white scales in posterior pronotal angles; clypeus, head, and pronotum with extremely deep, dense punctures, nearly rugose. Elytra unicolorous brown to the naked eye except for a few very widely scattered scales, scales more concentrated lateral to humeral umbones and posterior to apical umbones. Pygidium with a sparse covering of minute, white squamae and semierect, yellowish, stout hairs.

**Paratypes. (Variation).**—Length 23–27 mm, width 8–9.5 mm. Scaled vestiture on the pronotum and elytra varies from nearly absent to semivittate. It is noted in the above description of the holotype that the oval white scales are closely enough packed on the pronotum, scutellum, and anterior elytra to be characterized as “shingled.” This character brings *P. erratica* very close indeed to *P. anteronivea*.

**Distribution.**—Specimens examined, 71. This number includes the holotype, 55 paratypes, and 15 homotypes here designated. The homotypes include the only known female, described above, and the first specimen from other than the type locality. (See also remarks below and Fig. 29).

CALIFORNIA: *Inyo Co.*: Tecopa. *San Bernardino Co.*: Death Valley (Death Valley National Monument), Saratoga Springs.

NEVADA: *Nye Co.*: Ash Meadows, Fairbanks Springs, Pahrump.

APRIL (5), MAY (70), JUNE (5), JULY (1).

**Biology.**—Hardy and Andrews (1978) recorded that some specimens from Saratoga Springs were taken at dusk flying low over *Distichlis* grass in the salt encrusted bottom of the Amargosa River. These specimens were not attracted to blacklight after dark

**Remarks.**—Based on a series of 14 specimens, this taxon was recognized as new in 1968. The holotype, allotype and several paratypes were deposited at UCDC in 1969, where they originally came from. Paratypes were also deposited in the USNM. Due to a complex of intervening factors, my description of this new species was never published. Hardy's original description of this species in 1978 was based

on additional specimens collected during his contract work on the fauna of western sand dune habitats. I do not know if he had seen my material in the collections at Davis, California. I have now removed all type labels from my original series of 14 specimens and replaced them with homotype labels; I have also so labelled one additional male in the AMNH.

As Hardy and Andrews (1978) noted, *P. erratica* and *P. anteronivea* are closely related. They are most readily separated by the snowy-white pronotum, scutellum and anterior elytra of *P. anteronivea* used in combination with the collecting locality. Both species occur in Inyo Co., California (Fig. 29), with *P. anteronivea* recorded from the north (Saline Valley), and *P. erratica* from the south (Death Valley). At this very early stage in our knowledge of these demes, we have no collecting records between these points. The heavily scaled (in some specimens) pronotum, scutellum, and anterior elytra of *P. erratica* is clearly grading towards the solid white covering of *P. anteronivea*. Though I have not seen any *P. erratica* which is so fully scaled as to give an opaque white appearance, there certainly are gradations between the two which can only be clearly identified by the collection locality. In his descriptions of these two species, Hardy did not extract aedeagi. I have done so and find no differences considered significant. In sum, we have at this writing, insufficient data to decide whether these two names represent valid, somewhat cryptic species, or a single, perhaps clinal, taxon. As the nomenclatural history of this genus is one of extreme fragmentation, I have tried throughout this work to be conservative with names. In this case, for now, I believe these two names are best left standing as we do not have enough field data to justify a change.

Hardy and Andrews (1978) distinguish *P. anteronivea* from *P. erratica* as follows: "*P. anteronivea* has slightly less well developed clypeal angles, an apically broadened clypeus (quadrate in *erratica*), less elongate and apically less pointed scales, and an anterior elytral impression which results in a transverse carina from the scutellum towards the humeral area. Additionally, *anteronivea* lacks any trace of a pattern of vittae in the posterior half of the elytra (*erratica* usually displays at least some evidence of fragmented vittae posteriorly)."

### ***Polyphylla hammondi* LeConte**

(Figs. 8e, 8f, 30–32, 73–75, Table 4)

*Polyphylla hammondi* LeConte 1856: 228; LeConte 1863: 39; Crotch 1873: 61; Horn 1881: 73; Henshaw 1885: 92; Bates 1888: 215; Casey 1891: 18; Dalla Torre 1912: 259; Casey 1914: 325; Leng 1920: 257; Dawson 1922: 118; Fall 1928: 31; Kuntzen 1933: 463; Leng and Mutchler 1933: 39; Cazier 1938: 163; Blackwelder 1939: 53; Cazier 1939: 200; Brown 1940: 185; Cazier 1940: 135; Blackwelder 1944: 227; Blackwelder and Blackwelder 1948: 33; Young 1967: 284; Young 1972: 31; Blackwelder and Arnett 1974: R30.68; Hardy and Andrews 1978: 2; Lago 1979: 63; Young 1986: 49. (Holotype male and four paratype males MCZC 3792. Type locality: KANSAS: Fort Riley).

*Polyphylla diffusa* Casey 1914: 329. (Holotype and paratype males USNM 35622. Type locality: ARIZONA).

*Polyphylla latifrons* Casey 1914: 340. (Holotype male USNM 35637. Type locality: NEW MEXICO: Jemez Springs). NEW SYNONYMY.

*Polyphylla oblita* Casey 1914: 326. (Holotype and two paratype males USNM 35618. Type locality: TEXAS: near El Paso).

*Polyphylla oblita impigra* Casey 1914: 326. (Holotype and two paratype males USNM 35619. Type locality: NEW MEXICO).

*Polyphylla oklahomensis* Hatch 1926: 145. (Holotype female originally in Hatch's personal collection. As of late 1985-early 1986, it is not in the collections of the University of Oklahoma [personal communication, H.P. Brown], Oregon State University [personal communication, G.L. Parsons], Washington State University [personal communication, R.S. Zack], CASC [personal communication, N.D. Penny] or USNM (personal communication, R.D. Gordon]. Not located. Type locality: OKLAHOMA: Choctaw Co., 4 mi. S. of Grant along Red River, on grass).

*Polyphylla pimalis* Casey 1914: 330. (Holotype and paratype males USNM 35623. Type locality: ARIZONA: probably southern).

*Polyphylla proba* Casey 1914: 329. (Holotype male USNM 35621. Type locality: ARIZONA).

*Polyphylla rufescens* Tanner 1928: 276. (Holotype male BYUC. Type locality: UTAH: Saint George). NEW SYNONYMY.

*Polyphylla sejuncta* Casey 1914: 328. (Holotype and two paratype males USNM 35620. Type locality: NEW MEXICO: Albuquerque).

*Polyphylla speciosa* Casey 1889: 168. (Holotype female USNM 35638 and paratype male same number. Type locality: COLORADO). NEW SYNONYMY.

*Polyphylla speciosa acomana* Casey 1914: 342. (Holotype female, three paratype females, and two paratype males USNM 35639. Type locality: NEW MEXICO: Jemez Springs). NEW SYNONYMY.

*Polyphylla squamicauda* Casey 1914: 324. (Holotype and two paratype males USNM 35614. Type locality: TEXAS: El Paso).

*Polyphylla squamicauda molesta* Casey 1914: 324. (Holotype male USNM 35615. Type locality: NEW MEXICO).

*Polyphylla subvittata* LeConte 1856: 229. (Holotype male, not in the LeConte cabinet at the MCZC and probably lost. Type locality: TEXAS: on the Rio Grande). A synonym by page priority.

*Polyphylla subvittata bisinuata* Casey 1914: 327. (Holotype male and paratype [not allotype] female USNM 35617. Type locality: TEXAS: near El Paso).

*Polyphylla verecunda* Casey 1914: 325. (Holotype male USNM 35616. Type locality: NEW MEXICO).

**Topotype Male.**—Narrow, elongate. Length 31 mm, width 10.9 mm. Shining deep brown throughout. Clypeus radically narrowing basally, clothed with heavy, semierect hairs. Pronotum with depressed midline and lateral areas vittate, vittae composed of fine, white scales; interstitial areas with randomly scattered, deeply yellow squamae, entire surface without hairs. Antennal club barely as long as combined length of head and clypeus, apical half slightly recurved. Elytra without hairs, vestiture composed of minute, yellow squamae scattered over surface, scales becoming slightly more concentrated in normally vittate areas but no vittae formed (in this color phase). Pygidium and venter of abdominal segments with minute, white scales. Protibiae deeply bidentate.

**Female.**—Heavy, robust, much broader posteriorly. Clypeus flat, degenerate. Vestiture throughout like the male, elytra with a scattering of minute, yellow scales, no hint of formed vittae. Protibiae exceptionally wide and heavy, deeply tridentate.

**Distribution.**—Specimens examined, 1,742 males (1,199 avittate and 543 vittate), and 102 females (48 avittate and 54 vittate). The eastern-most extension of this species is marked by a series of five geographically disjunct demes recorded from sandy environmental refugia in (1) Anoka Co., Minnesota [Fridley Sand Dunes] (2) Sauk Co., Wisconsin, an area known locally as the “Wisconsin desert” (3) Union Co., Illinois (4) Mason Co., Illinois [Sand Ridge State Forest] and (5) Posey Co., Indiana. Young (1972) discussed this relictual pattern in detail; it is summarized below (Fig. 30).

On the bases of these disjunct demes of entirely typical northern avittate *P. hammondi* as characterized by the holotype, it was and is proposed that this species (1) invaded as far east as Wisconsin and Indiana via the dry Pliocene Steppe formed by the uplift of the Sierra Nevada-Cascade and Peninsular massifs of southern California (2) retreated westwards and southwards in response to the environmental rigors of the Pleistocene (3) secondarily invaded as far east as Indiana via the postglacial xerothermic prairie peninsula and (4) secondarily retreated westwards and southwards in response to the postglacial destruction of the xerothermic prairie and spread of the more mesic forest, with western relicts left in relatively dry, sandy, eastern environmental refugia.

On a larger scale the discovery of *P. brownae* Young 1986 in the Alabama panhandle, clearly a member of the *hammondi* lineage, supports the above hypothesis. *P. brownae* is, I believe, yet another disjunct deme in an environmental refugium, but one which is very distinct morphologically, unlike the five more northern demes just discussed. In short, I believe it “achieved” isolation via the framework given above and in its case, that isolation has been complete enough and/or long enough to realize reproductive isolation.

Moving to the west to the next tier of states, *P. hammondi* is recorded from scattered localities in Iowa, Missouri, Arkansas, Louisiana, and Mississippi. West of these states the species is commonly found from southern Manitoba (with a single disjunct record from southeastern Alberta) straight south through all states to (and well beyond) the Mexican border, and west through the prairies of eastern Colorado, and all of New Mexico, and Arizona. It also occurs in the deserts of southern Utah, the southern tip of Nevada, and southern California. The line drawn at the Mex-

ican border is entirely artificial, as this species has been seen from a number of Mexican localities (Fig. 30).

Throughout the great majority of its range, *P. hammondi* is sympatric (but not necessarily syntopic) with *P. decemlineata* and in the far west, with *P. diffracta* as well, where all three occur.

CANADA: ALBERTA: Medicine Hat. MANITOBA: Aweme.

MEXICO: AGUASCALIENTES: Calvillo. COAHUILA: Rio Bravo at San Vicente, Parras. DURANGO: Durango. JALISCO: Guadalajara. HIDALGO: Guerrero Mill (9000 ft.), 2 km. S. Metztlán, nr. Zimapan at Pasada del Ray Motel. MORELOS: Cuernavaca. OAXACA: No data. PUEBLA: Puebla. STATE UNKNOWN: Baranca, Gomez Palacia, Sonita.

UNITED STATES: ARIZONA: *Apache Co.*: Chinle, nr. Chinle at Canyon de Chelly (camp below Ranger Station, 5500 ft.). *Cochise Co.*: Benson, Douglas, 32 mi. E. Douglas (Peloncillo Mts. at entrance to Guadalupe Canyon at 4200 ft.; 0.4 mi. NE entry; 1.3 mi. NE entry at 4300 ft.), Huachuca Mts. (Huachuca Canyon), 5 mi. W. Portal, Portal (4700 ft.), nr. Portal (Southwestern Research Station), Puebla del Sol, San Bernardino Ranch (3750 ft.), 2 mi. W. Sierra Vista (5300–5400 ft.), 10 mi. S. Sierra Vista, 6 mi. SE Willcox, 65 mi. N. Willcox (Deer Creek Ranch). *Cocconino Co.*: 9.5 mi. SE Flagstaff, Fredonia, Grand Canyon (Phantom Ranch on River at 2500 ft.), Sedona, Supai (3500 ft.), Vail Lake Road (6500 ft.). *Gila Co.*: Globe, Payson, 7 mi. N. Payson, 4 mi. ESE Pine (Control Road at 5400 ft.), Star Valley. *Graham Co.*: Safford, Thatcher. *Green Lee Co.*: White Mts. *Mari-copa Co.*: Falcon Field, Mesa, nr. Mesa, Phoenix, Tempe, Wickenburg. *Mohave Co.*: Littlefield. *Navajo Co.*: Holbrook, Joseph City, Winslow. *Pima/Santa Cruz Co.*: Madera Canyon (Santa Rita Mts.: Santa Rita Lodge at 5400 ft.), mouth of Box Canyon at bridge (4340 ft.). *Pima Co.*: Continental, Tucson, mouth of Madera Canyon (Proctor Ranch Road at 4500 ft.). *Pinal Co.*: Florence, Oracle, Sacaton. *Santa Cruz Co.*: Bear Canyon Bridge on Lochiel-Bisbee Road at 5300 ft., nr. Nogales (Oro Blanco Mts.), 4 mi. N. Nogales, Patagonia (Senoita River), 5 mi. SW Patagonia at 3700 ft., 2 mi. SW Patagonia, Patagonia Mts. *Yavapai Co.*: Prescott, Skull Valley, Verde Valley. *Yuma Co.*: Yuma. *County Unknown*: Sasaton, Satorra.

ARKANSAS: *Arkansas Co.*: Arkansas River. *Lee*

*Co.*: Marianna. *Marion Co.*: Buffalo River State Park. *Washington Co.*: No data.

CALIFORNIA: *Imperial Co.*: No data. *Kern Co.*: Bakersfield. *Los Angeles Co.*: Angeles National Forest (Sulphur Springs). *Riverside Co.*: Blythe. *Tulare Co.*: Tipton.

COLORADO: *Arapahoe Co.*: No data. *Denver Co.*: Denver. *El Paso Co.*: Cold Springs (Rock Creek Canyon). *Jefferson Co.*: No data. *Larimer Co.*: Estes Park. *Logan Co.*: Sterling. *Otero Co.*: Rocky Ford. *Prowers Co.*: No data. *Pueblo Co.*: Pueblo. *Rio Blanco Co.*: Meeker. *Weld Co.*: Fort Lupton, Greeley. *Yuma Co.*: Wray (3500 ft.). *County Unknown*: Lemar.

ILLINOIS: *Mason Co.*: Havanah, Sand Ridge State Forest. *Union Co.*: Reynoldsville.

INDIANA: *Posey Co.*: No data.

IOWA: *Louisa Co.*: Columbus Junction. *Pottawattamie Co.*: Council Bluffs. *Woodbury Co.*: Sioux City. *County Unknown*: Hastings.

KANSAS: *Butler Co.*: Butler. *Clark Co.*: Ashland. *Douglas Co.*: Lawrence. *Ellis Co. (?)*: Fort Hays. *Finney Co.*: Garden City. *Ford Co.*: Dodge City. *Graham Co.*: at 2130 ft. *Harper Co.*: No data. *Kiowa Co.*: Belvidere. *Logan Co.*: at 3322 ft. *McPherson Co.*: McPherson. *Meade Co.*: 13 mi. S. Meade. *Ness Co.*: at 2260 ft. *Osborne Co.*: at 1557 ft. *Rawlins Co.*: at 2850 ft. *Reno Co.*: Medora (Sand Dunes), Sylvania. *Riley Co.*: Fort Riley, Manhattan, Riley. *Rooks Co.*: Stockton. *Sedgewick Co.*: Wichita (1291 ft.). *Shawnee Co.*: Topeka. *Stafford Co.*: Salt Flats Area. *Trego Co.*: at 2450 ft. *Wallace Co.*: Wallace (3000–3440 ft.).

LOUISIANA: *Caddo Co.*: Shreveport. *Natchitoches Co.*: Natchitoches.

MINNESOTA: *Anoka Co.*: Fridley Sand Dunes.

MISSISSIPPI: *Warren Co.*: Vicksburg.

MISSOURI: *Buchanan Co.*: Missouri-Kansas Bridge. *Stoddard Co.*: Sikeston.

MONTANA: No other data.

NEBRASKA: *Antelope Co.*: Neligh. *Arthur Co.*: Arapahoe Prairie. *Boyd Co.*: Lynch, Spencer. *Brown Co.*: Ainsworth, Springview Bridge. *Cass Co.*: Weeping Water. *Cherry Co.*: F. Crowe Ranch 25 mi. S. Valentine, Hackberry Lake, Niobrara Wildlife Refuge. *Cheyenne Co.*: No data. *Custer Co.*: Arnold, Milburn. *Dakota Co.*: S. Sioux City. *Dawson Co.*: No data. *Dodge Co.*: Dead Timber State Recreation Area, Fremont. *Douglas Co.*: Omaha (Carter Lake). *Dundy Co.*: Haigler. *Frontier Co.*: No data. *Furnas Co.*: Cambridge. *Gage Co.*: No data. *Hall Co.*: Grand Island,



Mormon Island Refuge (in Platte River). *Holt Co.*: Chambers, Lynch, Spencer Dam. *Keith Co.*: Cedar Point Biological Station, Ogallala. *Keya Paha Co.*: Carns. *Knox Co.*: Niobrara, Niobrara State Park. *Lancaster Co.*: Lincoln. *Lincoln Co.*: North Platte. *McPherson Co.*: Sandhills Ag. lab. nr. Tryon. *Merrick Co.*: No data. *Morrill Co.*: 10 mi. SW Alliance. *Nance Co.*: No data. *Otoe Co.*: No data. *Platte Co.*: Duncan. *Rock Co.*: Newport. *Sarpy Co.*: Bellevue, Gretna. *Scotts Bluff Co.*: Scottsbluff. *Thomas Co.*: Halsey, Halsey Forest Reserve, 2.5 mi. W. Halsey, Thedford. *Valley Co.*: Arcadia.

NEVADA: *Clark Co.*: No data.

NEW MEXICO: *Bernalillo Co.*: Albuquerque (University NM campus). *Catron Co.*: 9.5 mi. NE Glenwood at 6900 ft. *Dona Ana Co.*: Las Cruces, Mesilla Park (SE of Franklin), State College. *Eddy Co.*: Artesia, Carlsbad, Carlsbad Caverns. *Grant Co.*: No data. *Hidalgo Co.*: Cienega Lake, 13 mi. N. Rodeo, 1 mi. E. Rodeo. *Lea Co.*: No data. *Luna Co.*: Deming. *McKinley Co.*: Thoreau. *Otero Co.*: Alamogordo at 4300 ft. *Rio Arriba Co.*: Espanola. *Sandoval Co.*: 7 mi. S. Jemez Springs at 5800 ft., 5 mi. N. Jemez at 6300 ft., Jemez Springs at 6400 ft. *San Juan Co.*: Chaco Canyon National Monument. *San Miguel Co.*: Las Vegas. *Santa Fe Co.*: Santa Cruz, 10 mi. NE Santa Fe at 9500 ft., Santa Fe, 2 mi. E. Tesuque Pueblo at 7000 ft. *Socorro Co.*: Magdalena, San Marcial, Socorro. *Valencia Co.*: Los Lunas.

NORTH DAKOTA: *Billings Co.*: Medora. *Burleigh Co.*: No data. *Cass Co.*: No data. *McHenry Co.*: T156N-R78W-Sec. 36, 11 mi. N. Towner. *McKenzie Co.*: Theodore Roosevelt National Memorial Park (N. Unit). *Ransom Co.*: McLeod. *Richland Co.*: Walcott Dunes, Mirror Pool.

OKLAHOMA: *Beaver Co.*: Beaver. *Beckham Co.*: Sayre. *Canadian Co.*: El Reno. *Choctaw Co.*: No data. *Cimarron Co.*: Black Mesa. *Garvin Co.*: No data. *Jackson Co.*: Elmer. *Jefferson Co.*: Waurika. *Lincoln Co.*: SW Section. *Marshall Co.*: Lake Texoma nr. Willis, Lebanon. *Noble Co.*: Arkansas River. *Okfuskee Co.*: Okemah. *Oklahoma Co.*: Oklahoma City. *Ottawa Co.*: Afton. *Pawnee Co.*: No data. *Roger Mills Co.*: Cheyenne. *Woods Co.*: 3 mi. W. Waynoka. *Woodward Co.*: Woodward.

SOUTH DAKOTA: *Brule Co.*: Chamberlain. *Clay Co.*: Vermillion. *Union Co.*: Elk Point. *Yankton Co.*: Yankton.

TEXAS: *Brewster Co.*: Big Bend, Castolon. *Cameron Co.*: Brownsville. *Comal Co.*: New Braunfels. *El*

*Paso Co.*: El Paso, nr. El Paso. *Gillespie Co.*: No data. *Hemphill Co.*: Canadian. *Hidalgo and Hudspeth Cos.*: No data. *Kleberg Co.*: Kingsville. *Matagorda Co.*: Bay City. *Maverick Co.*: Eagle Pass. *McLennan Co.*: nr. Waco. *Potter Co.*: Amarillo. *Presidio Co.*: Presidio. *Reeves Co.*: Pecos. *Travis Co.*: Austin. *Val Verde Co.*: Del Rio. *Webb Co.*: Laredo International Bridge. *Wichita Co.*: Burkburnett. *Wilbarger Co.*: Red Road.

UTAH: *Emery Co.*: Green River. *Grand Co.*: Moab at 4000 ft. *Kane Co.*: Mt. Carmel. *San Juan Co.*: Bluff, 5 mi. W. Monticello (Dalton Springs Camp at 8500 ft.). *Washington Co.*: Leeds, Leeds Canyon (Oak Grove Camp), Santa Clara, St. George, Zion National Park (Grotto Camp). *County Unknown*: Pine Valley.

WYOMING: *Goshen Co.*: Torrington. *County Unknown*: Landon.

MAY (25), JUNE (85), JULY (648), AUGUST (965), SEPTEMBER (74), OCTOBER (11), NOVEMBER (7), DECEMBER (4). All the Oct.-Dec. records are from Mexico with the exception of two males collected in southern Arizona in October.

**Biology.**—Hayes and McColloch (1928) collected 18,781 scarabaeid larvae over an eight year period in Kansas. One was *P. hammondi*; they stated that larvae of this species live in fallen logs and stumps. I believe this to be incorrect. Baker (1972) wrote that *P. hammondi* deposits its eggs in rotten wood; again, I doubt this is correct. Stein and Kennedy (1972) listed adult *P. hammondi* as solitary defoliators of shelterbelts with white willow as the food plant, though they did not personally collect *P. hammondi* from that plant species. They also published photographs of the undescribed pupa. Lago (1979) found no host plants during 1974 and 1975. He did a gut content analysis on 40 specimens of both sexes collected at various North Dakota localities, at various dates. No plant material was found in these adults; Lago's implication is that they may not feed, at least in North Dakota.

Lago also observed mating behavior in North Dakota during 1974 and 1975. Males emerged from their tunnels at dusk and took flight. The females emerged after dark and rested near their emergence holes. After copulation the females burrow into the sand where it is presumed they lay their eggs. Lago never observed flying females and he could not induce them to fly. He suggests that they probably do not or can not fly. My observations, and those of others in parts of Arizona, New Mexico, and Utah, support this view.

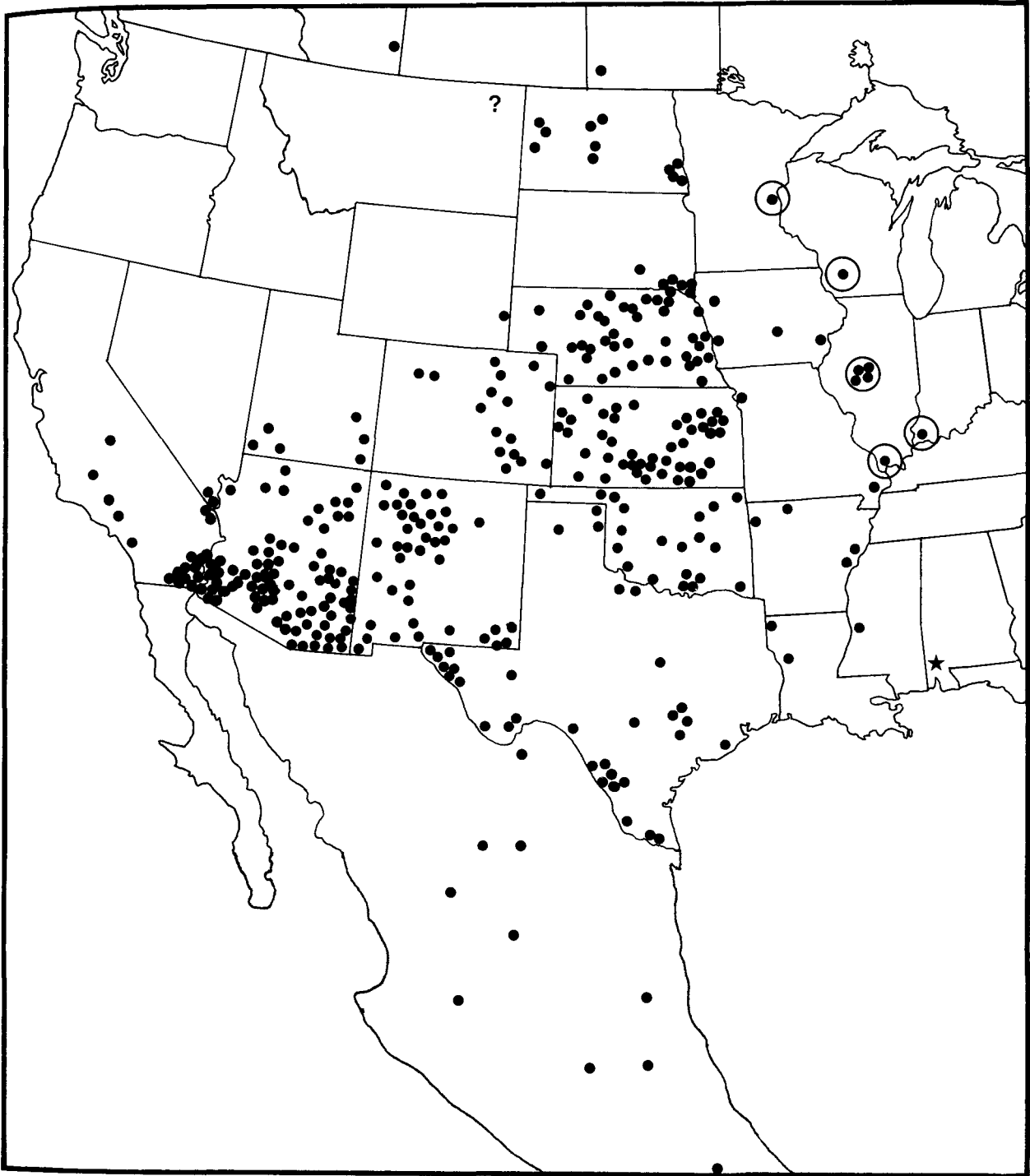


Fig. 30.—Distributions of *P. brownae* (★) and *P. hammondi* (●).

I have never taken a female *P. hammondi* at light nor have I ever seen one fly (see further field data below).

*P. hammondi* adults are subject to various parasites and predators. In a sample of 25 living adults collected at McLeod, North Dakota by R.D. Gordon, July 16, 1966, every one was heavily infested internally with a species of *Sarcophaga*. The abdominal cavity of each male *P. hammondi* contained 1–5 mature dipterous larvae, a condition which inevitably caused host death. These same beetles were also infested with an undetermined mite species on the dorsal abdomen. A pinned male from Beaver, Oklahoma is on hand which is labelled "prey of *Proctacanthus rodecki* James." It is assumed this refers to the dipterous asilid genus *Proctacanthus*, with the one letter difference simply being a labelling error (see also biology of *P. arguta*, *P. comes*, and *P. crinita* re. Diptera predacious on adult *Polyphylla*).

Field data from 1967 are summarized below and in Table 4.

A single avittate male was collected at ultraviolet light July 6, near Bristow, Oklahoma. The site was at ca. 900 ft. elevation, near a small lake, and covered with an oak-savannah vegetation type growing in red laterite soil.

On July 14, a single vittate male was taken at the mouth of Madera Canyon, Arizona, at 4500 ft. This is primarily a mesquite grassland bajada (Martin 1963). This *P. hammondi* was taken to the exclusion of all other species, though within the canyon at 5400 ft., *P. diffracta* was collected. The *P. diffracta* evidently did not extend into the lower area inhabited by vittate *P. hammondi*. The reverse, however, was true, as a single avittate *P. hammondi* was taken syntopically with *P. diffracta* at 5400 ft. on July 24. This avittate male at the higher elevation, taken only 900 ft. above a vittate deme, emphasizes the apparent effect of environment on coloration and vittation. Specimens from the higher, cooler, more mesic areas are, in color characters, most similar to more northern demes, such as that sampled in Oklahoma. Overall size, however, increases as one samples southwards.

On July 30 a single, large, vittate male was taken at the AMNH Southwestern Research Station, Arizona. This 5400 ft. site is within a pinon pine (*Pinus edulis* Engelman)-Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) zone, but with deciduous species such as Arizona white oak (*Quercus arizonica* Sarg.) also represented. This is the highest record

personally collected for vittate *P. hammondi*. Taken syntopically with it was *P. decemlineata*.

Specimens were collected within the desert grassland formation, also on July 30. The site was Hidalgo Co., New Mexico, 13 miles N. of Rodeo, at ca. 4000 ft. These specimens were typically large and heavily vittate, a color pattern predicted to occur in this relatively low, xeric area by the hypothesis here presented.

On July 31, a 4300 ft. dry stream bed dominated by mature Fremont cottonwood (*Populus fremontii* S. Wats.) was sampled. The site was 1.3 miles in from the mouth of Guadalupe Canyon, 32 miles E. of Douglas, Arizona. Other common species in this community included coyote willow (*Salix exigua* Nutt.), Arizona sycamore (*Platanus wrightii* S. Wats.), velvet ash (*Fraxinus velutina* Torr.), velvet mesquite (*Prosopis juliflora* var. *velutina* [Woot.] Sarg.), and one-seed juniper (*J. monosperma* [Engelman] Sarg.). Flight of *P. hammondi* males started at 8:30 PM and continued until 10:16 PM. On the same date specimens were collected at ca. 4200 ft., near the mouth of the Canyon, in an area vegetated primarily with large Arizona sycamore and mesquite. Flight duration of males at these two localities was 186 and 285 minutes, respectively, far longer than that recorded in any other species. On August 1, this 4200 ft. locale, 0.4 miles NE of the mouth of the Canyon, again yielded a large sample. Primary male flight ran from 8:30–10:30 PM, with occasional males taken until 2:30 AM. On August 14 a third sample was collected at this site. Just at dusk ca. 15 males started their searching flight. They flew primarily over a stand of dense grass growing in sand. The grass was ca. nine inches tall and interspersed with low tree seedlings. This male searching flight was again recorded at Canyon de Chelly, Arizona and I believe it to be very typical for *Polyphylla*. Females seem to fly only rarely, if ever. They are obviously sedentary animals which remain on the ground near their emergence tunnels while the males aggressively search for them to initiate mating.

A total of 89 males was collected at these two locales within Guadalupe Canyon. These demes, well above the true desert floor and most xeric-adapted vegetation, were typically avittate, bearing only traces of minute yellow elytral scales on a brown to deep black background. Only two specimens could be considered clearly vittate. This correlates well with the hypothesis that the vittate color phase occurs primarily in the true, hot, dry desert and the avittate color

**Table 4.** *P. hammondi* flight activity at selected sites, July and August, 1967

Date	Elevation	Biotic Zone	First	Last	Flight Duration
<i>Bristow, Oklahoma</i>					
July 16	900	oak parkland	9:10	9:10	—
<i>Madera Canyon, Arizona</i>					
July 14	4500	mesquite grassland	10:10	10:10	—
July 24	5400	oak-juniper	no flight		
<i>Cave Creek Canyon, Arizona</i>					
July 30	5400	oak-pinon-juniper	no flight		
<i>nr. Rodeo, New Mexico</i>					
July 30					
August 4	4000	desert grassland	no specific data, collected by other individuals		
August 5					
<i>Sierra Vista, Arizona</i>					
August 7	4000	desert grassland	same as above		
<i>Guadalupe Canyon, Arizona</i>					
July 31	4300	cottonwood	8:30	10:16	186
July 31	4200	sycamore	8:30	11:15	285
August 1	4200	sycamore	8:30	2:30	360
<i>Canyon de Chelly, Arizona</i>					
July 22	5400	cottonwood grove	8:15	9:00	45
August 11	5400	cottonwood grove	8:30	9:59	129 (plus daytime flight)
August 13	5400	cottonwood grove	8:10	9:45	135
MEAN FLIGHT DURATION					190

phase in the more mesic north or the more mesic higher altitudes of southern latitudes.

On August 4, 5, and 7, the desert grassland was again sampled, at the New Mexico locality discussed above, and ten miles east of Sierra Vista, Arizona. The New Mexico specimens were heavily vittate as before, and as expected. The Sierra Vista specimens, however, collected at 4000 ft., were avittate. This is the lowest record for avittate specimens in this southern latitude; it does not correlate well with my hypothesis and is the primary exception seen in this field season.

On July 22, D.E. Rich collected 76 male *P. hammondi* within ca. 45 minutes at the Canyon de Chelly campground (Apache Co., Arizona), just below the Ranger Station. Flight typically began at dusk with the major burst of activity between 8:15–9:00 PM. Rich observed (personal communication) the male searching flight discussed above. Two males flew in and landed near a burrow which contained a female, which remained motionless with only her head pro-

truding above ground level. She was not stridulating. One male flew away while the other crawled down the burrow head first, over the back of the female. After physically pushing her out of the hole with his metathoracic legs, the male emerged after her and the pair copulated on the surface. No females were taken at lights during this evening, though they were obviously in the area.

On August 11 and 13 I collected at this locale. The campground is in a cottonwood grove, with a river nearby. It is essentially an ecological island like the southern Arizona mountains, with rocky, sandy desert on all sides. It is an oasis, in a sense, which provides all the requisites of life for all life cycle stages of *Polyphylla*. On the first day two males were collected at 5:15 PM, while actively flying through the grove. The males are very strong fliers, making rapid forward progress with abrupt ups and downs; a distinctive pattern somewhat reminiscent of hummingbird flight. That same evening a third male was collected within the grove at 8:15 PM as he circled very

rapidly over the grass, about 8 inches above the ground, searching for females. At ultraviolet light, 28 males were collected between 8:30–9:59 PM. On August 13 diurnal flight began at 8:10 PM, males again searching for females. A caged female had no apparent effect on incoming males. Twenty males were collected from 8:23–9:45 PM, a total duration of 135 minutes, counting the first diurnal flight at 8:10 PM. This locale showed real promise for the excavation of females and perhaps immatures. Many likely looking burrows were examined on the first day, with negative results. On the night of August 12 the campground was hit by a major flash flood, turning it into a sea of mud. All evidence of burrows was obliterated; nonetheless, male flight continued as normal the next evening as discussed above.

All *P. hammondi* taken at Canyon de Chelly were heavy, robust, vittate specimens. They were collected to the exclusion of all other species and were well isolated ecologically from *P. decemlineata* demes sampled on the high cold plateau above the canyon (see biology of *P. decemlineata*). This vittate deme of *P. hammondi*, collected at the lowest elevation in the area except for the canyon floor itself, which is not open to the public, supports my coloration/latitude/elevation hypothesis.

In summary *P. hammondi* is believed to contain two primary color phases (in three clusters, see morphometrics below). The vittate phase (Casey's *P. speciosa* and others) is found primarily in the hot, dry, southern latitudes while the avittate phase of the type series is much more widely distributed. When occurring together in the southwestern states, the avittate phase most commonly occurs at higher, cooler, more mesic sites and the larger vittate phase occupies the hotter, more xeric desert grasslands. As in all things biological this does not hold true in every case but the majority of evidence does support this view. Within these morphological extremes all variations may be found within a single area; I see no evidence to support the nomenclatural fragmentation of these demes.

**Morphometric Analysis.**—Raw data for this analysis consisted of measurements of 15 external morphological characters on each of 165 male *P. hammondi*. Samples were taken from 17 states and Manitoba to represent the entire geographic range of the species. Sample size varied from 6–22/state or province.

The first analysis was a data summarization program with homogeneity tests included, in an effort to obtain an indication of presence or absence of clustering. These results could also be subjected to selected tests for the statistical significance of homogeneity shown. The data were clumped by character and geographic area; the primary result being the calculation of group means. Fig. 31 shows the results, with each histogram representing one character and each bar within the histogram representing the mean value for that character within a geographic area. Three of the 15 characters measured (length of the penultimate and terminal segments of the maxillary palpi, and length of eye canthus) were not plotted as they showed no significant between-group variation.

To test the hypothesis that characters show a broad north to south or east to west clinal increase in size, these mean values were not artificially sorted by size; rather they were plotted in a geographic order. Three primary clusters are formed within the histograms: (1) the far eastern, northern, and midland demes (bars 1–9) cluster into what is termed the grassland avittate phase, (2) the desert avittate phase (bars 10–13) falls midway between extremes and (3) the desert vittate samples (bars 14–18) cluster at the opposite extreme with the largest mean values. In each of the histograms the same broad tendency for large size as one samples east to west or north to south is repeated. Primary exceptions are the eastern-most sample from Illinois (grassland avittate), which varies widely as one might predict in a peripheral area; the South Dakota sample (grassland avittate) which often has smaller values than more northern demes; and the California sample (desert avittate), which always has smaller values than the more eastern Arizona sample. These exceptions are within expected range and do not disprove the overall tendency for clinal increase.

The data were next subjected to a program for community ordination. Of the 165 stands (individual beetles) measured, 15 were not included within the data deck because of dimension limitations. To form the ordination constellation, each stand was compared with every other stand, thereby yielding a matrix of similarities/dissimilarities for all possible comparisons. In order to position stands along the X-axis the similarity and dissimilarity values for each stand were summed. That stand having the greatest dissimilarity sum with all other stands became the low

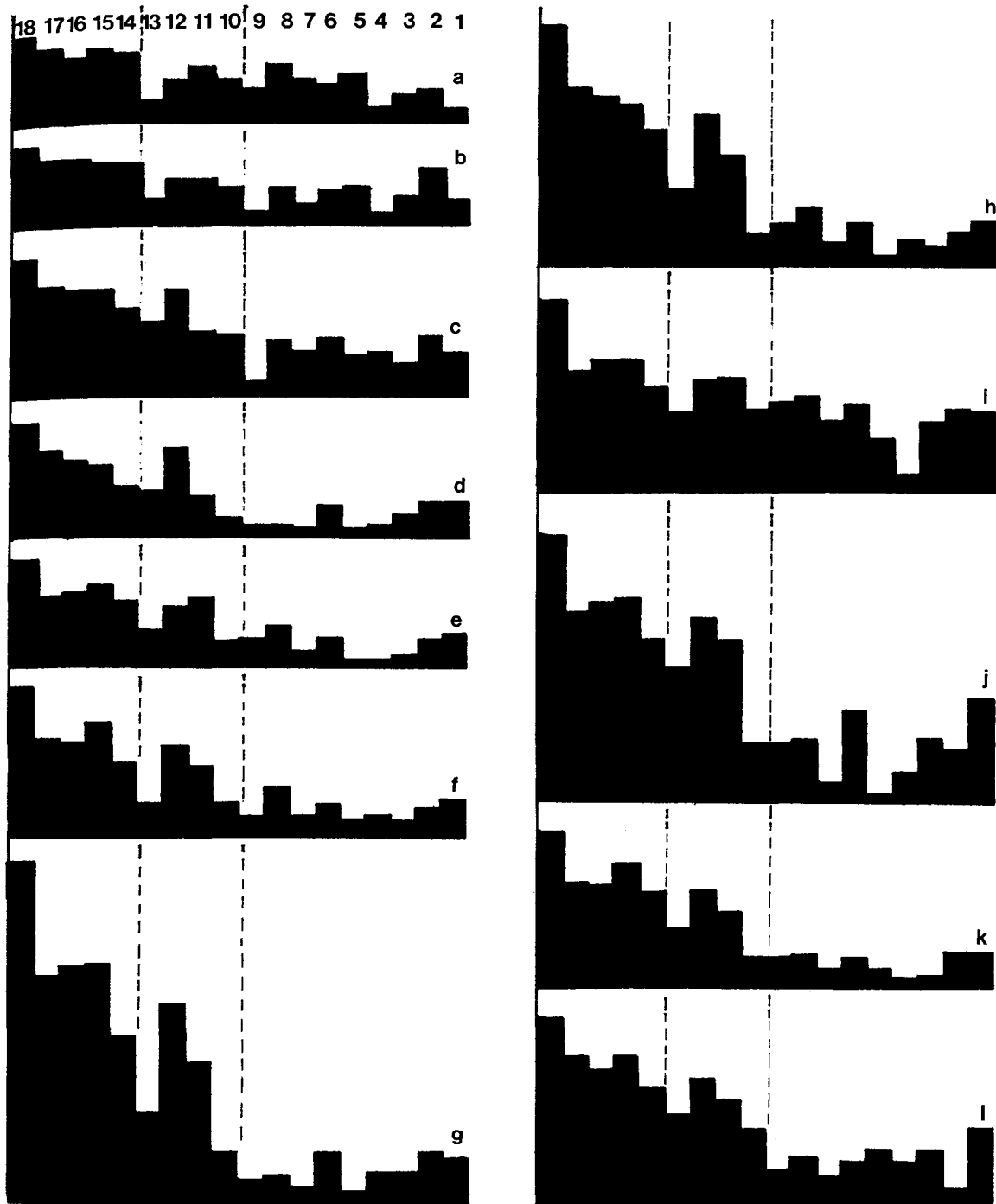


Fig. 31.—Clinal variation in characters of *P. hammondi* (see text for discussion). Bars 1–18 are samples from (1).—Illinois. (2).—Manitoba. (3).—North Dakota. (4).—South Dakota. (5).—Nebraska. (6).—Kansas. (7).—Oklahoma. (8).—Texas avittate. (9).—Colorado avittate. (10).—West Texas avittate. (11).—New Mexico avittate. (12).—Arizona avittate. (13).—California avittate. (14).—Texas vittate. (15).—New Mexico vittate. (16).—Arizona vittate. (17).—Colorado vittate. (18).—Utah vittate. Clusters 1–9 represent grassland avittate demes, 10–13 desert avittate demes, and 14–18 desert vittate demes. Characters illustrated are: (a).—length of male antennal club. (b).—clypeal length. (c).—clypeal apex width. (d).—clypeal basal width. (e).—pronotal length. (f).—pronotal width. (g).—elytral length. (h).—elytral width. (i).—metatarsal length excluding pretarsus. (j).—metatibial length. (k).—pygidial length. (l).—pygidial width.

reference point on the X-axis, and the stand having the greatest dissimilarity to the first became the high reference point. The dissimilarity value between these two reference stands became the length of the X-axis. The 150 stands were then plotted along the X-axis but such a one-dimensional constellation is misleading, as highly dissimilar stands cluster. To separate these the Y-axis was constructed, resulting in a two-dimensional scattering of stands (Fig. 32).

The degree of correlation between these data established by this ordination is exceptionally high. For the X-axis the low reference stand is 122 (Utah vittate), and the high reference stand is 9 (North Dakota avittate). These two are therefore assigned values of 0 and 100 respectively, and all other points plotted between them on a relative scale. On the Y-axis reordination, stand 122 has the greatest positive value while stand 9 has the greatest negative value. Within the 0 to 100 framework, the low stand is 6 (Manitoba avittate) and the high stand is 126 (Utah avittate) matching almost precisely the geographical extremes sampled.

Fig. 32 shows the X to Y ordination constellation. The three primary clusters of grassland avittate, desert avittate, and desert vittate are represented by dissimilar symbols. The far northern and eastern grassland avittate specimens cluster on the lower right of the constellation. As one samples to the south and west, size increases gradually, with the desert avittate demes centrally scattered and the desert vittate stands showing the largest sizes of all. This constellation also shows the intergradation of all geographic areas, with no single deme or color phase totally disassociated from all others. The arrows show the range of values within each geographic sample. Not only does size increase clinally from east to west and north to south, but degree of variation also. The grassland avittate demes show the least variation (the Illinois deme again being the exception), while the desert avittate show considerably more. The desert vittate demes express the greatest range of morphological variation, with values represented over the entire breadth and length of the constellation.

In summary, this analysis shows clinal variation in size of morphological structures and color phases in males of *P. hammondi*. Size varies with latitude and longitude, with each deme gradually phasing into the next. There are no disjunctions which might translate into named taxa. Faced with specimens from the extremes of this cline, the taxonomist would surely place

them as separate species, as have all past workers. When samples from the entire range of the species are available, however, the gradual nature of the variation is readily apparent. This variation seems most logically correlated with the climatic regime of the habitat. The small avittate phase occurs most commonly at cool, mesic northern or high (cool), mesic southern sites, while the large vittate demes are collected within the hot, xeric desert grassland or desert floor vegetation. On these bases all included variable demes are considered conspecific and representative of the polymorphic *P. hammondi*.

**Remarks.**—Avittate *P. hammondi* may be distinguished from the eastern *P. brownae* by the presence of body scales and absence of elytral hairs; from *P. erratica* by the absence of clumped elytral scales; from *P. anteronivea* by the same character and the pronotum lacking a solid covering of white scales; from *P. squamiventris* by overall length exceeding 23 mm and the lack of a sutural vitta; and from *P. cavifrons* by its unicolorous brown or black appearance, or the bicolorous appearance caused by yellow scales on black. Avittate *P. hammondi* never have the pruinose appearance of *P. cavifrons*.

Vittate *P. hammondi* may be distinguished from the eastern *P. brownae* by the presence of body scales; from *P. erratica* by the presence of hard-edged vittae; from *P. anteronivea* by the absence of a solid covering of white scales on the pronotum; from *P. squamiventris* by length being greater than 23 mm, and the presence of elytral vittae but never the sutural one alone; and from *P. cavifrons* by the presence of elytral vittae. From all other species, both color phases of *P. hammondi* may be distinguished by their overall large, robust size, and the deeply reddish-brown to black elytral color.

In avittate specimens, elytral length varies from 15.6–24.1 mm; elytral width from 9.8–16.05 mm. In southern vittate specimens elytral length varies from 17.85–28.1 mm and elytral width 11.05–18.3 mm. It is this latter color phase, commonly collected throughout the American southwest, which includes the largest North American specimens. Males from Arizona, Colorado, and especially southern Utah, reach lengths up to 42 mm.

**Synonyms.**—Ten Casey specific names, one LeConte name, and one Hatch name were first synonymized under *P. hammondi* by Fall (1928). The

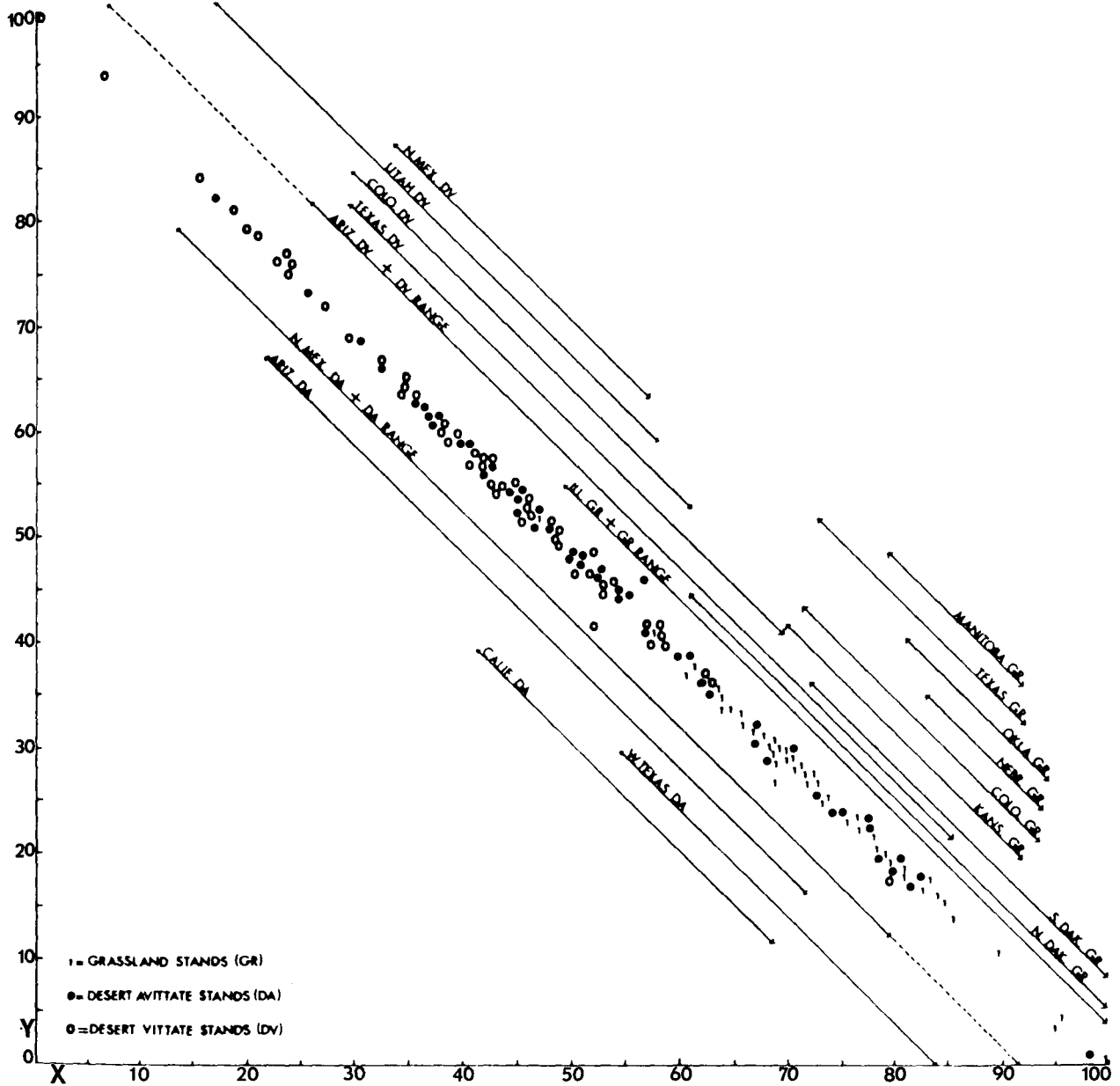


Fig. 32.—Community ordination of 150 males of *P. hammondi*, X- to Y-axis. See text for discussion.

examined all the Casey types at two different times, separated by some three years. My conclusions are identical to those of Fall, and inevitably so, for these names are based on such minute variations that in many cases one is at a loss to discover them.

Three additional Casey names and one Tanner name are here placed as new synonyms of *P. hammondi*. *P. latifrons* was erected by Casey on the bas-

es of a single male showing large overall size, the elytra less shining and more rugose than normally seen, pronotal shape, and details of elytral scale density. The name-bearing type is a typical New Mexico vittate *P. hammondi*. In 1889 Casey erected the name *P. speciosa*. He had two exceptionally large, heavily vittate specimens, from Colorado and New Mexico before him. This is a perfect example of being faced



with one extreme of what is here perceived as a clinal species. Casey also considered as significant the short humeral vittae continuing posteriorly in broken clumps of scales, a common character seen in many different species. *P. speciosa* and *P. speciosa acomana* are large, desert vittate *P. hammondi*. The same may be said for *P. rufescenta*, placed as a synonym of *P. speciosa* by Hardy and Andrews (1978).

***Polyphylla squamiventris* Cazier**  
(Figs. 8g, 29, 76)

*Polyphylla squamiventris* Cazier 1939: 199; Cazier 1940: 137; Blackwelder and Blackwelder 1948: 33; Young 1967: 285; Blackwelder and Arnett 1974: R30.68; Hardy and Andrews 1978: 4. (Holotype male AMNH 24. Type locality: TEXAS: Presidio, Rio Grande).

**Holotype Male.**—Narrow, parallel-sided, diminutive. Length 21 mm, width 9.7 mm. Clypeus and head black, to reddish-black on disc; elytra dark reddish-brown. Clypeus nearly parallel-sided, all margins strongly reflexed, outer angles prominent and sharp; with nearly confluent punctures on disc bearing small, ovoid, white scales; scales much more concentrated along anterior and lateral margins. Head impunctate on vertex, shining, between eyes clothed with white squamae and dense, erect, yellow setae, eyes bordered with dense, white squamae, canthi covered with scales and yellow setae. Antennal club minute, the smallest seen in any western species, funicular segments plus scape ca. three-fourths length of club; essentially no recurve in club. Pronotum widest at middle, without hairs except along anterior margin which bears a row of long, yellowish setae; ovoid, white squamae forming normal three vittae, interstitial areas with scattered minute white scales. Elytra without hairs; ovoid, white scales forming a thin vitta along suture and an indication of a dense vitta just mesad to humeral umbone; interstitial areas with scattered, minute, white scales. Pygidium as long as wide, with individually scattered small, white scales, midline naked. Protibiae deeply, broadly tridentate.

**Female.**—Unknown.

**Distribution.**—Specimens examined: 18 males including the holotype. A poorly known species rarely

represented in collections. Of the few specimens seen, nearly all are from the state of Chihuahua in northern Mexico. Cazier's holotype seems to represent a northern-most record for what may be primarily a Mexican species (Fig. 29).

MEXICO: CHIHUAHUA: Camargo, 10 mi. S. Las Delicias.

UNITED STATES: TEXAS: *Presidio Co.*: Presidio. JUNE (5), JULY (13).

**Biology.**—Unknown. Collected at light.

**Remarks.**—*P. squamiventris* is, by far, the smallest species in the *hammondi* complex and it is easily identified by this character. Very occasional specimens of *P. cavifrons* approach this diminutive size but the "dusted" or pruinose appearance of this species distinguishes it from *P. squamiventris*. Aedeagi of *P. squamiventris* are typically narrow, parallel-sided, and distally truncate, characters shared by members of the *hammondi* complex (Fig. 8g). On external characters alone, however, it is possible to confuse *P. squamiventris* with mostly avittate specimens of *P. diffracta* from the American southwest. In these cases *P. squamiventris* is best identified (in addition to the aedeagal characters) by its lack of pronotal hairs, which are usually long and dense in *P. diffracta*.

In overall appearance the males of *P. squamiventris* on hand vary from a deep reddish-brown to unicolorous brown (avittate) to mostly vittate, especially along the suture and the second line laterad to the suture.

**DISTRIBUTION AND ISOLATING MECHANISMS**

*Polyphylla* is known from all conterminous states except Connecticut, Michigan, Ohio, and West Virginia. In Canada the genus is recorded from the southern portions of Alberta, British Columbia, Manitoba, Ontario, Quebec, and Saskatchewan. The northern-most record for the genus in the New World is 53 degrees latitude at Quesnel, British Columbia (Fig. 1). For the broadly distributed *P. hammondi* (Fig. 30), geographically disjunct demes restricted to sandy environmental refugia are recorded from Illinois, Indiana, Minnesota, and Wisconsin (Young, 1972). Of the 28 species in America north of Mexico here recognized, 13 are recorded from entirely or mostly restricted localities. Future collectors should resist the compulsion to collect long series of these species,

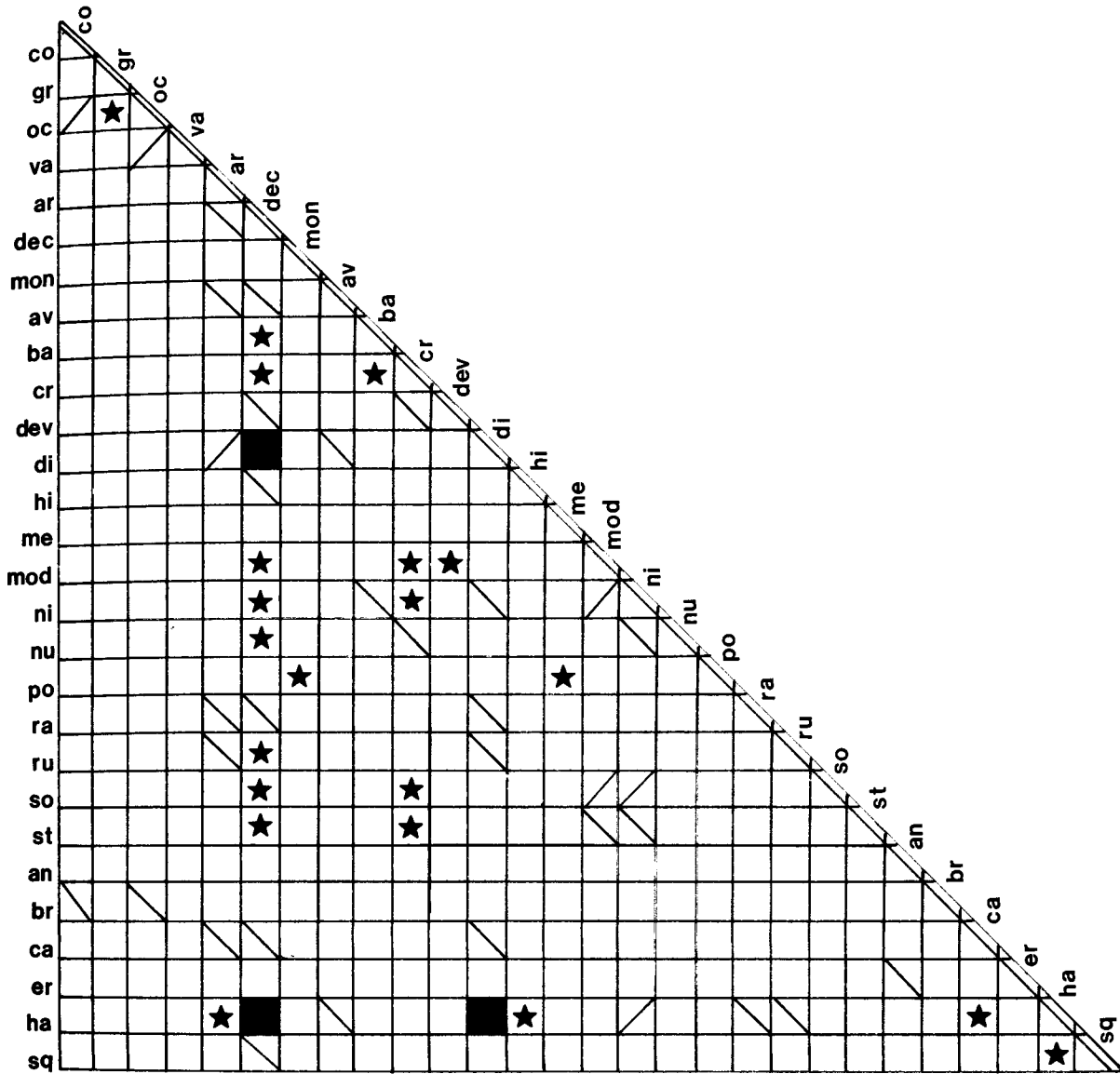


Fig. 33.—Known isolating mechanisms in *Polyphylla*. Symbols show allopatry (□), allopatry with sympatry in peripheral areas (▤), proven sympatry (▣), record of allotopic when sympatric (■), and potential sympatry, additional field data needed (▣).

rather our primary concern should be to conserve them. These 13 species are: *P. anteronivea*, *avittata*, *barbata*, *brownae*, *devestiva*, *erratica*, *hirsuta*, *mescalerensis*, *monahansensis*, *nubila*, *pottsorum*, *ratcliffei*, and *stellata*.

Fig. 33 summarizes what is known about the geographic and ecological isolation of North American *Polyphylla*. Comparing each species with every other species results in 379 possible species pairs. Of this

number, 319 comparisons or 84.16% show complete allopatry. Seven comparisons (1.85%) show allopatry with some sympatry in peripheral areas. Twenty-two comparisons (5.8%) show the compared species to be primarily sympatric with no additional data available to suggest how (or in some cases, if) the populations maintain reproductive integrity. Twenty-eight species pairs (7.4%) are recorded as potentially sympatric but without field data to prove or disprove

the hypotheses. In sum, of the 60 species pair comparisons showing marginal, complete, or hypothetical sympatry, field data are available on only three. These three pairs are known to be in at least one instance subject to effective ecological isolation through the occurrence of adult breeding demes at dissimilar elevations. These 3 comparisons are: *P. decemlineata*—*P. diffracta* (Zion Natl. Park, Utah), *P. hammondi*—*P. diffracta* (Madera Canyon, Arizona), and *P. decemlineata*—*P. hammondi* (Canyon de Chelly, Arizona). In each case these species have been recorded in the field as being isolated allopatrically though shown on standard distribution maps as sympatric (see discussion of biology of these species). Unlike the data from Canyon de Chelly, B.C. Ratcliffe reports (personal communication) that *P. decemlineata* and *P. hammondi* are commonly taken together at light in western Nebraska. Lago (1979) reports that these two species occur together in western North Dakota.

### PHEROMONES

Lilly and Shorthouse (1971) first demonstrated the presence of pheromones in *Polyphylla* (see details under the biology of *P. decemlineata*). Certainly we have intuitively suspected pheromones were present in these insects before the data of Lilly and Shorthouse; by postulating their emission by the females the enormously developed antennal lamellae of the males, and their development in only the males, makes evolutionary sense. It seems reasonable to postulate that all female *Polyphylla* emit pheromones and that each biological species, whatever that may prove to be in the future, has its unique pheromone "signature." Hopefully this primarily taxonomic monograph will encourage future workers to concentrate on the biological species of *Polyphylla*.

Fowler and Whitford (1981) published a note on the mating behavior of *P. diffracta* near Las Cruces, New Mexico (see discussion under that species). Their observations, though very seriously flawed, along with those of Lilly and Shorthouse, support a perception of female *Polyphylla* as basically fossorial animals which emerge, and fly, only during a very narrow diel window to accomplish a single mating. A three year life cycle is 26,280 hours long; of that perhaps 60 days or 5.48% is spent as a sexually mature (?) adult. Allowing two hours per day for dusk and early evening flight, *Polyphylla* species have only

0.46% of their life cycle to locate, identify, and copulate with a mate. Even these generalized numbers suggest that it must be a fairly precise process or the odds are, it wouldn't happen. Species unique pheromones in the females and the coevolution of the remarkable receptor antennae in males is the most likely mechanism enabling reproductive success, against the odds.

### PHYLOGENETIC ANALYSIS

The methodologies of Hennig (1965, 1966) form the foundation for cladistic analyses. Much of the current literature dwells on the minutiae of computer techniques and is not useful to the practicing taxonomist. The works of Estabrook (1972), Ross (1974), Cracraft (1979), Eldredge (1979), Watrous and Wheeler (1981), Wiley (1981), Brooks, et. al. (1984), Ball (1985) and Noonan (1985) have been consulted extensively during the course of these analyses. My purpose here is not to join into the arguments on method and theory. Rather, it is to pragmatically apply these computer-assisted techniques to *Polyphylla*, knowing that the results will remain preliminary and incomplete until the world fauna is considered. Even then, I have reservations concerning their reflection of natural, historic reality. These techniques are "internally" testable (within or between taxa or between investigators) but in the absence of a fossil record I see no definitive way to reach "external" testability. Biogeography, perhaps the most theoretical (least data based) of disciplines used by systematists, is suggested as an external test of hypothetical cladograms. In some ways this seems to move even further away from testable data. What is actually known about *Polyphylla* is external and aedeagal morphology, where they occur, and a few hints concerning biology and ecology. It would be equally foolish to refuse to move beyond those data or to drift off into computer gamesmanship. I have tried to strike a balance between those extremes.

*Phyllophaga* was selected as the outgroup for this analysis. As used by Eldredge (1979) and Watrous and Wheeler (1981) among many others, commonality of character states between *Polyphylla* and this outgroup are deemed to be plesiomorphic and unique states are deemed to be apomorphic, that is, derived from a pre-existing homologue. Table 5 lists the 23 characters used.

Plesiomorphic character states are scored 0, and

**Table 5.** Plesiomorphic and apomorphic character states in *Polyphylla*

No.	Character	Plesiomorphic	Apomorphic
1.	frontal clypeal emargination	present	reduced, absent
2.	clypeal concavity	moderate	extreme
3.	clypeal lateral margins	widening	narrowing
4.	clypeal angles	not produced	produced, toothlike
5.	setae on clypeal disc	absent	present
6.	frontoclypeal suture	entire	reduced
7.	terminal segment of maxillary palp	smooth, rounded	flattened, excavated
8.	setae on antennal club	present	absent
9.	setae on pronotum	absent	present
10.	pronotal punctures	fine	coarse
11.	protibial dentition	tridentate	bidentate
12.	setae on elytra	absent	present
13.	setae on pygidium	absent	present
14.	separation of parameres	deep	shallow
15.	pronotal scales	absent	present
16.	elytral vittae	absent	present
17.	pygidial punctures	fine	coarse
18.	abdominal scales	absent	present
19.	midline of pygidium	not defined	defined
20.	lateral edges of aedeagus	parallel	narrowing
21.	recurve of antennal club	absent	present
22.	tip of aedeagus	edges parallel	edges not parallel (narrowing or widening)
23.	aedeagal shape	broad, robust	thin, elongate

1, 2 indicates increasingly derived states. Characters 1, 2, 4, 6–8, 10, 17–19, and 23 are binary. Characters 3, 5, 9, 11–16, and 20–22 are multistate, each one forming a logical transformation series. Character 3 for example, the lateral margins of the clypeus, has been polarized as widening (0), subparallel (1), and narrowing (2). Character 9 (pronotal setae) was polarized absent (0), moderate (1), and dense, long (2). For the outgroup comparison character 16, elytral vittae, was scored absent (0), broken (1), and complete (2). Within *Polyphylla*, I believe degeneration and eventual loss of these vittae to be secondary, that is apomorphic. Character 22 (tip of aedeagus) is a multistate character but with the outgroup having the lateral edges parallel, the range of states in *Polyphylla* varying from narrowing to widening does not form a logical transformation series. The parallel state in the outgroup has been scored 1. Combined with an in-group comparison the final polarization was parallel (1), narrowing (0), and widening (2). Table 6 gives the complete polarizations of character states.

These data were analyzed using Swofford's 1984

PAUP (Phylogenetic Analysis Using Parsimony) program, Version 2.3. This program infers phylogenies under the principle of maximum parsimony. Of the many numerical methods for inferring phylogenies (see Felsenstein, 1982 for a recent review), this seems to be the most straightforward parsimony model. The preferred tree is the one of minimal length, with no *a priori* restrictions on the nature of permissible character state changes. Minimizing tree length is equal to minimizing the number of transformations from one character state to another. Inherent in this technique is a concomitant maximum possible reduction of homoplasy events (parallelisms, convergences, and reversals). This factor is especially important in trying to construct a phylogeny of *Polyphylla* where, in my opinion, homoplasy in all its forms is rampant.

*Polyphylla* species endemic to a given sand dune complex or primary sandy habitat (*P. anteronivea*, *avittata*, *brownae*, *devestiva*, *erratica*, *mescalensis*, *monahansensis*, *nubila*, *pottorum*, *rattcliffei*) tend strongly to show loss and acquisition of the same

**Table 6.** Polarization of character states in *Polyphylla*  
0 = plesiomorphic; 1, 2 = increasingly apomorphic

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
anteronivea	1	1	1	1	0	0	0	0	0	1	0	0	1	1	2	1	1	1	0	1	2	1	1
arguta	1	1	1	1	0	0	0	1	0	1	1	0	0	1	2	1	0	1	0	2	2	0	1
avittata	1	0	2	0	1	1	1	0	2	1	0	1	1	1	2	1	0	1	0	1	1	2	1
barbata	1	0	2	0	2	0	1	0	2	1	1	2	2	1	1	1	0	1	0	1	2	2	1
brownæ	1	0	1	0	2	0	0	0	2	1	1	2	2	1	0	0	0	0	0	1	1	1	1
cavifrons	1	1	2	1	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1
comes	1	0	2	0	1	0	0	0	0	0	1	0	1	2	1	1	0	0	0	0	2	1	0
crinita	1	0	2	0	2	0	0	0	2	1	1	0	1	1	2	2	0	1	0	1	2	2	1
decemlineata	1	0	1	0	0	0	1	0	0	1	1	0	0	1	2	2	0	1	1	2	2	0	1
devestiva	1	0	2	1	1	0	1	0	1	1	0	1	1	1	1	0	0	1	0	1	2	2	1
diffracta	1	0	1	0	1	0	0	0	2	1	0	0	1	1	2	1	0	1	0	1	1	2	1
erratica	1	1	1	1	0	0	0	0	0	1	0	0	1	1	2	1	1	1	0	1	2	1	1
gracilis	0	0	1	0	0	1	1	0	0	0	2	0	0	2	1	1	0	1	0	0	1	1	0
hammondi	1	1	2	0	2	0	0	0	0	1	0	0	1	1	2	2	1	1	0	1	2	1	1
hirsuta	1	0	1	0	2	0	0	0	2	1	1	2	2	1	0	0	0	0	0	1	1	2	1
mescalerensis	1	1	2	0	0	0	0	0	2	1	0	1	0	1	1	1	0	1	0	1	2	2	1
modulata	1	0	1	0	2	0	0	0	2	1	1	0	1	1	2	2	1	1	0	1	1	2	1
monahansensis	1	0	1	0	0	0	1	0	2	1	0	0	0	1	2	2	0	1	1	2	2	0	1
nigra	1	0	2	0	2	0	0	0	2	1	1	0	1	1	2	1	0	1	0	1	2	2	1
nubila	1	0	2	0	2	0	1	0	2	1	1	2	2	1	2	0	0	1	1	1	1	2	1
occidentalis	1	1	1	0	1	0	0	0	1	1	1	1	2	2	1	2	0	1	0	0	2	2	0
pottorum	1	1	2	0	1	0	1	0	1	1	0	0	1	1	2	0	0	1	1	1	2	2	1
ratcliffei	1	0	2	0	1	1	1	0	2	1	0	1	1	1	2	1	0	1	0	1	1	2	1
rugosipennis	1	0	1	0	2	0	0	0	2	1	1	2	1	1	1	1	0	1	1	1	1	2	1
sobrina	1	0	1	0	0	0	0	0	1	1	1	0	0	1	2	2	0	1	0	1	2	2	1
squamiventris	1	1	1	0	1	0	0	0	0	1	0	0	0	1	2	0	1	1	1	1	1	1	1
stellata	1	0	1	0	0	0	0	0	1	1	0	0	0	1	2	0	0	1	0	1	1	2	1
variolosa	1	0	2	0	1	0	0	0	0	0	1	0	1	2	1	1	0	0	0	0	2	1	0

character states repeatedly. Nearly without exception the tendencies are towards 1) decreased overall size, 2) loss of scales and vittae, and 3) acquisition of increasingly long, dense pronotal and elytral setae.

The phenotypes of individuals are constrained by genetic, developmental, and environmental factors (Brooks and Wiley, 1986). In these sand habitats, I believe the relative paucity of organic nutrients below ground to be the controlling environmental constraint on adult size. Compared to more moist habitats with greater vegetative biomass, sandy areas restrict the growth and development of *Polyphylla* larvae. The phenotypic expression of this constraint is a marked reduction in adult size, and selection for that attribute in each generation. Loss of vittae and ultimately, all

scales, has the appearance of protective camouflage. Especially in species like *P. anteronivea*, *erratica*, and *pottorum*, it is striking how closely the animals resemble the color of their sandy substrate. *Polyphylla* are primarily fossorial animals. The repeated acquisition of long, dense body hairs by otherwise dissimilar species is, perhaps, an adaptation to movement through sand. They may play a role in keeping abrasive sand grains away from critical body joints, especially on the venter of the animal.

Phenetic convergence is also common in response to high altitude or high latitude, best shown by *P. crinita*, *P. decemlineata*, and *P. modulata* in the Pacific northwest, where all three species show deep coloration and clear, hard-edged vittae on the elytra. *P. barbata* (California) and *P. hirsuta* (Arizona), both

restricted to a single mountain are convergent in the aforementioned decreased size, loss of vittae, and increased setae. Most remarkable is the close convergence in color and overall appearance between *P. sobrina* from primarily Yosemite Natl. Park and *P. monahansensis* from Monahans Sandhills State Park in Texas. These two areas seem grossly dissimilar yet their respective *Polyphylla* species are externally so similar that in many cases only aedeagal characters and locality data will separate them.

Because the genus is widely distributed there is perhaps an unconscious assumption that the species are highly adaptable, having broad genetic plasticity. The opposite is true. *Polyphylla* are first and foremost animals restricted to xeric sand/grass associations (over a broad range of latitudes) and coniferous forests. Historically the humid deciduous forests east of the Mississippi River have been and are a major barrier, never fully overcome. As demes are isolated in sandy refugia as relicts or newly invade such habitats, they show a limited, restricted phenetic response. The same morphological expressions arise repeatedly in a pattern so regular that given the location one can now predict what yet undiscovered species will look like.

This repetitive loss and acquisition of character states does not lend itself easily to parsimonious cladistic analysis. The species complexes first discussed by Fall (1928) and used by many authors since, including myself, form phenetic clusters of within group similarity "surrounded" by significant dissimilarities; in short an excellent example of "gap" taxonomy. Recognition of these species complexes constitutes an *a priori* hypothesis and discovery of new species is a way to test it. Hardy and Andrews (1978) and Young (1966, 1986, and this monograph) have each discovered five new species in America north of Mexico. Using primarily aedeagal characters and secondarily characters of size, color, and vestiture, these ten new taxa "fit" easily and logically into one or another of the species complexes. Nine of these ten species can be associated with its species complex at a glance; the exception is the aforementioned convergent *P. monahansensis*.

Fig. 34 shows the most parsimonious cladogram generated. All characters of size and color were eventually eliminated. This is a test of the phenetic hypothesis; it is interesting to note that the four species complexes do emerge from the cladogram, but imperfectly so. The small *decemlineata* complex

forms a clade, as does the *hammondi* complex excluding *P. brownae* from Alabama. This species is so strongly convergent with *P. hirsuta* of the *diffRACTA* complex (total replacement of scales with setae) that even aedeagal characters shared with the *hammondi* complex will not override that convergence, as shown in the PAUP runs. Resolution within this complex is quite good with *P. anteronivea* and *P. erratica* being sister species, as are *P. cavifrons* and *P. squamiventris*. Clinal, variable *P. hammondi* stands alone, though logically *P. brownae* is its sister species, an obvious eastern isolate of the *hammondi* lineage. The *diffRACTA* complex forms an imperfect clade which does not include *P. sobrina* and *P. stellata*. *P. sobrina* emerges as one would predict, in a position of convergence with *P. monahansensis*. The position of *P. stellata* remains unresolved, though it is clearly a member of this species complex.

Of the four species complexes the eastern *occIDENTALIS* group shows both the most dissimilarity from the rest of the genus and the greatest range of interspecific variation. Phenetically and geographically it is very much a unique entity. It does not form a discrete clade (as expected), which just may be a reflection of historical reality. *P. variolosa* and *P. comes* are close sister species representing respectively the northern coastal lowlands and Appalachian highlands. On the other hand, *P. occidentalis* and *P. gracilis* are very different from this sister pair and each other; they probably represent more ancient products of Pliocene/Pleistocene climatic oscillations (see discussion under biogeography).

This cladogram fits reasonably well with my preconceived thoughts on the evolution and speciation of *Polyphylla* in North America. Discovery of additional new species and more importantly, a consideration of the world fauna, will form important future tests of this first phylogenetic analysis.

## BIOGEOGRAPHY

The model of vicariance biogeography presented by Croizat, Nelson and Rosen (1974) and expanded and refined by Rosen (1975, 1978) and Platnick and Nelson (1978) among others, is partially applicable when considering the distribution of a portion of a worldwide fauna. Parts of this model are applied here to a speculative reconstruction of the evolutionary history of *Polyphylla*, but necessarily the focus is not on the world fauna. Furthermore, I disagree with Cro-

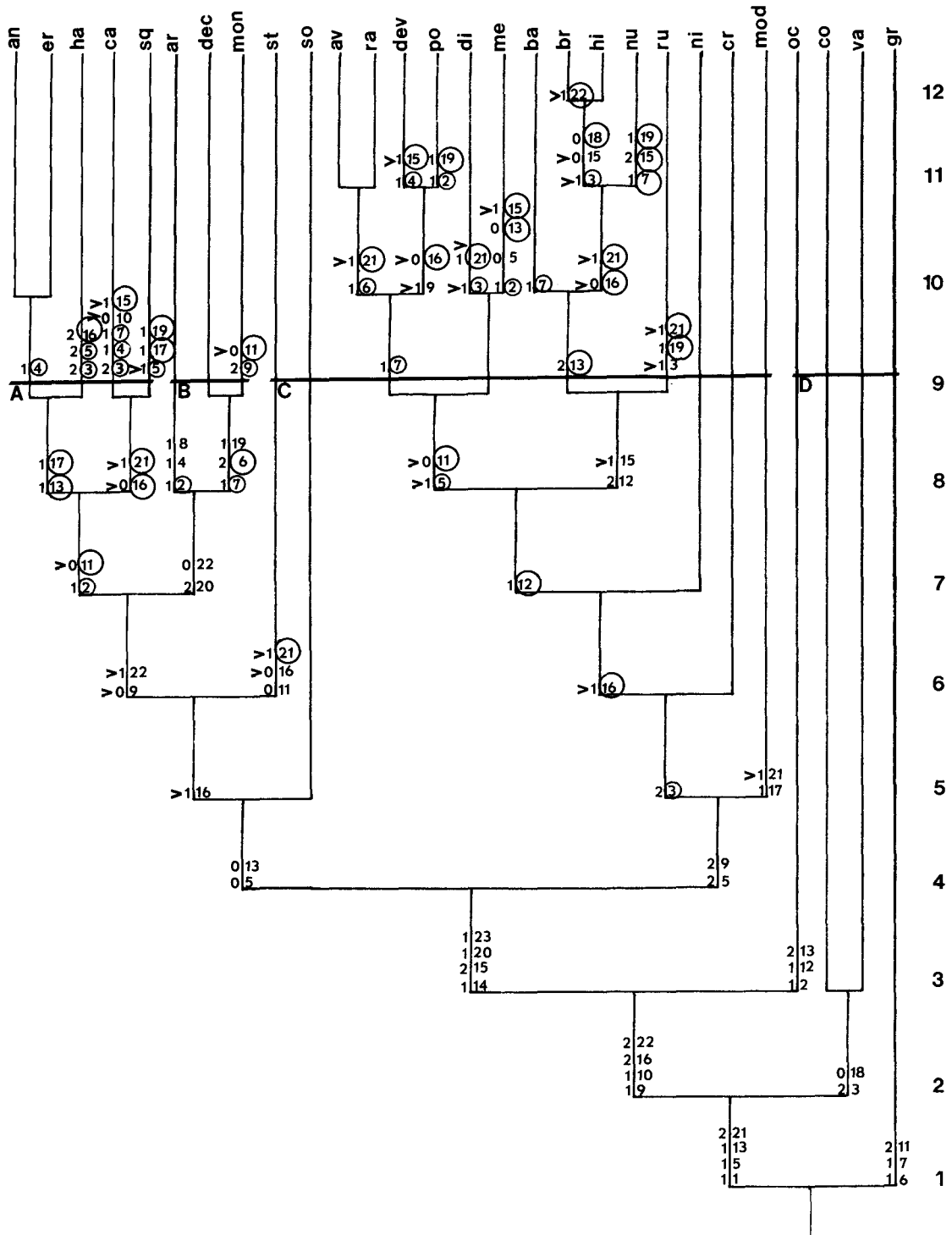


Fig. 34.—Cladistic hypothesis for *Polyphylla* in America north of Mexico. Numbers on the right of lines are characters, on the left are scorings of character states. Circled characters represent a homoplasy of that character state. Arrowhead by character state represents a reversal. A = the *hammondi* complex, B = the *decemlineata* complex, C = the *diffracta* complex, D = the *occidentalis* complex.

izat, Nelson and Rosen (1974) who state "we reject the Darwinian concept of center of origin and its corollary, dispersal of species, as a conceptual model of general applicability..." This center of origin model is primarily applicable when considering the North American *Polyphylla* fauna. Surely both models represent a portion of natural reality; to consider them mutually exclusive is to reject potentially important interpretive techniques. The papers by Ball (1985) and Noonan (1985, 1986) represent excellent examples of synthesis, using both techniques to reach the most complete approximation of past events.

Erwin (1979) wrote that "taxon changes that result from rapid (in geologic time scale) climatic shifts and sudden radiation of major predatory or competitive lineages will be a quick pulse and happen in unstable habitats. Taxon changes that result from long term accumulated genetic differences are usually vicariance-based and will be slow pulses in stable habitats." The dramatic and relatively sudden events of the Cenozoic are the factors that have molded and formed our extant *Polyphylla* fauna. It is, most of all, a highly fragmented fauna characterized by a high percentage of endemics known from only one or two localities. It is postulated here that the repeated and complex fragmentations of the environments of the last 35 million years were the driving vicariance events which produced this fauna.

Based on the combined criteria and methodologies of Cain (1944), Smith (1956), Darlington (1957), Howden (1963, 1966, 1969), Croizat, Nelson and Rosen (1974), and Rosen (1975), the American southwest is postulated as the most likely center of origin of *Polyphylla*. Cain's (1944) criteria of greatest polymorphism, greatest densities, location of closely related forms, convergence of lines of dispersal (a precursor to Croizat's "tracks"; see below), and least dependence upon a restricted habitat all support this hypothesis. Eurasia is considered an area of secondary, though early, success, supporting ca. 19 species (Dalla Torre, 1912 and DeWailly, 1948) compared to 28 in America north of Mexico and ca. 32 in the New World.

Based on the same premise that taxa originate in the most favorable available environments and that those optimal conditions will allow the greatest differentiation of the ancestral lineage, Howden (1966) proposed that our extant *Phyllophaga* fauna is derived from two Pleistocene refugia, one in the southeastern United States and one in Mexico. Fig. 35

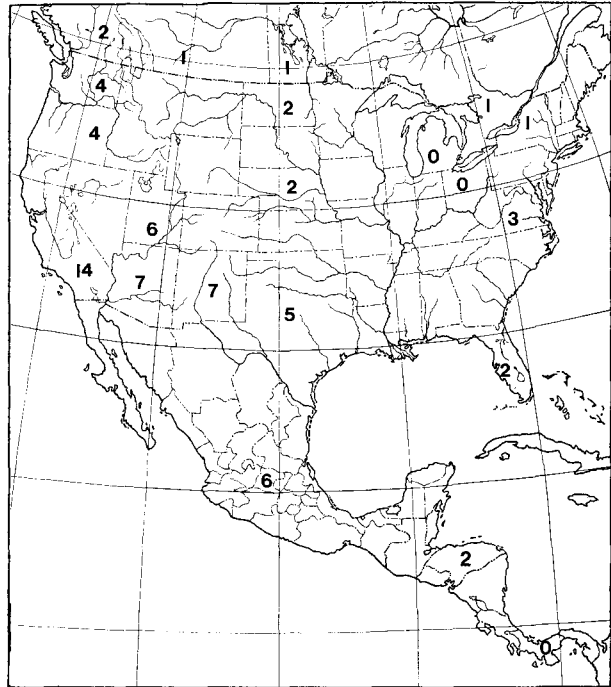


Fig. 35.—The number of *Polyphylla* species recorded from selected states, provinces, and countries showing decreases east, north, and south of the American southwest, a postulated center of origin.

adapts this technique to *Polyphylla*; several conclusions are immediately apparent:

1. Number of species decrease from west to east, e.g., California (14), Arizona (7), Texas (5), and Florida (2). In a more northern tier of states: Washington (4), North Dakota (2), Minnesota and New York (1 each).

2. Number of species decrease from south to north, e.g., Texas (5), Nebraska (2), North Dakota (2), and Saskatchewan (1).

3. The most diverse fauna occurs in a band across the American southwest. Number of species are California (14), Arizona (7), New Mexico (7), Utah (6), and Texas (5).

4. The number of endemic species is greatest in the far southwest and decreases to the east, e.g., California (4), Utah (2), and Arizona, New Mexico, Alabama, and Florida (1 each).

5. The eastern and southeastern *occidentalis* complex is a unique fauna. No species are shared with the fauna west of the Mississippi Basin.

These conclusions support the premise that the American southwest is the center of origin of *Polyphylla*, closely approximating Howden's Pleistocene



refugium in Mexico for *Phyllophaga*. In general the number of *Polyphylla* species decrease as one moves south from this nuclear area with central Mexico having 6 or 7 described species, Honduras 2, and Panama none.

The track technique of Croizat (1958, 1964) and Croizat, Nelson, and Rosen (1974) may be applied here, though on a limited scale. A track is simply a line on a map connecting (as applied here) the endemic species of a monophyletic group. If commonality of distribution patterns occurs, the individual tracks will coincide to form a pathway of mutual tracks. As Rosen (1975) wrote, "these clusters of distributions may be inferred to be fragments of the distribution of the parent biota." This technique is a logical modernization of Cain's use of convergence of lines of dispersal in his 1944 paper. Fig. 36 plots the distributions and tracks of those ten *Polyphylla* species known from only a single location. Clearly the massed tracks form an approximate rectangle across the American southwest, including the southern portions of California, Nevada, and Utah, Arizona, New Mexico, and extreme west Texas. These ten species represent ca. 36% of the fauna in America north of Mexico. The massed tracks in Fig. 36 represent the center of origin and dispersal of a more ancient, widely dispersed fauna. Howden (1966) concluded that our scarab taxa associated with coniferous forests (among others) have "speciated in and dispersed from 3 major regions, 1 in the southeastern United States, a second centered in southern and central California, and a third that includes most of the high mountain regions of Mexico." This track technique

supports the deserts of southern California and Arizona as a center of origin of *Polyphylla*.

*Polyphylla* most probably originated no earlier than the Oligocene, 35 million years before present (mybp). The hot, dry Madro-Tertiary flora (Axelrod, 1958) dominated this period of relatively uniform climatic conditions (Ross, 1962). *Polyphylla* probably originated no later than the early Miocene 25 mybp, a period marked by the origin of our arid and prairie adapted insect fauna (Howden, 1969). With no fossil record such a conclusion is conjectural at best. The following discussion, beginning with the Permian 230 mybp, details the evidences on which these conclusions rest.

The Permian is generally cited as the time of origin for both the Coleoptera and the conifers upon which adult *Polyphylla* could feed (Dodson, 1960). However, the first monocotyledons did not appear until the Cretaceous (Northern, 1958 and Wolfe, 1978, 1985), so it would seem that *Polyphylla* and many related genera of melolonthine scarabs could not have been successful before then due to lack of larval food. Northern (1958) also notes that the true grasses rose from the lily (Liliaceae) family of monocots, which again must move the origin of this coleopterous fauna much closer to the present. Dodson (1960) dates the rise of the higher monocotyledons and flowering plants at the Oligocene. This would seem to be the earliest point at which *Polyphylla* could have arisen, assuming that historical requisites of life were approximately the same as today.

What was the climatic regime of the American southwest during this period? The extensive work of

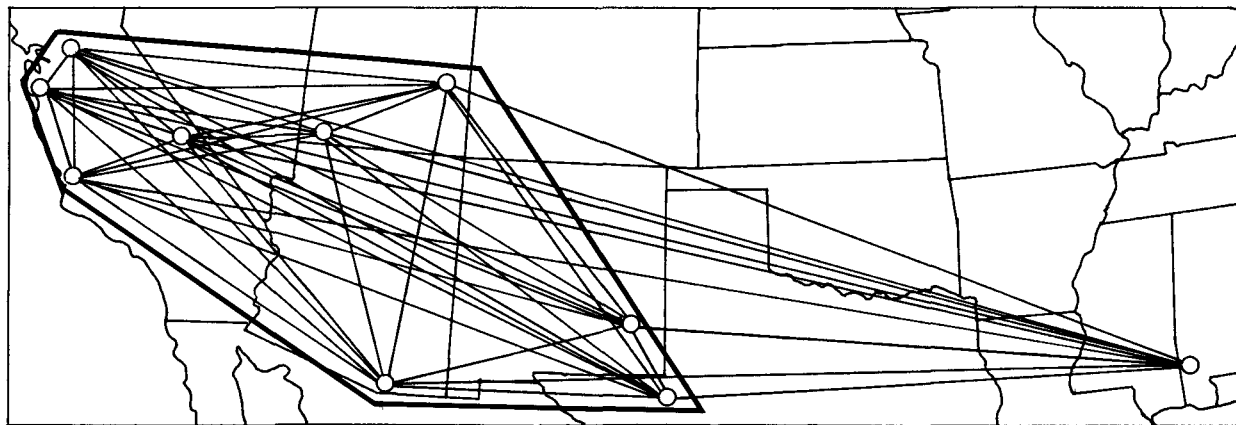


Fig. 36.—Distributional tracks for ten species of *Polyphylla*. Each species is known from only one locality. Limiting polygon marks the postulated center of origin.

Axelrod (1958) established that during the Oligocene, southwestern North America was supporting the Madro-Tertiary flora. Fossil remains of Madro-Tertiary plant genera such as *Pinus* and *Platanus* have been recovered from the Green River and Florissant floras of the central Rocky Mountain region. These middle Eocene plant remains are the earliest record of Madro-Tertiary species, which would offer food for *Polyphylla* adults. By the next epoch (Oligocene) the grasses were present, as has been mentioned above. This source of larval food completes the requirements for survival, at least in the sense of having something to eat.

Discovery of these fossil floras has shown that the southwest was becoming a uniquely hot dry area during the early Tertiary. Reconstruction of this climatic regime is by now based on an impressive array of facts, some of which are outlined in the following discussion.

Madro-Tertiary species are known from the genera *Pinus*, *Juniperus*, *Yucca*, *Populus*, and *Quercus*, to name a few. Fossil floras generally show dry subtropical to warm temperate alliances, with closely related species now found in the American southwest. This hot dry zone between the Arcto- and Neotropical Tertiary zones probably occupied the southwestern states and northern Mexico by the close of the Oligocene. In response to the expansion of dry climate, the Madro-Tertiary flora spread radially during the Miocene, with further expansion during the semiarid Pliocene.

Gross morphology of fossil leaves also offers information on the environment (Bailey and Sinnott 1915, 1916). In modern floras large thick leaves with entire margins are common in the humid tropics, while small-leaved species are found chiefly in semiarid areas. Many of the microphyllous Madro-Tertiary fossil floras reflect an adaptation to low yearly rainfall, high summer temperatures, and long periods of sunshine. Furthermore, fossil species of *Fremontia*, *Ceanothus*, and *Quercus*, among others, were drought resistant sclerophylls. In the broadest sense the Madro-Tertiary vegetation was composed of semiarid live oak-conifer woodland (the *Quercus*—*Juniperus* zones sampled during this work in Arizona, New Mexico, and Utah), chaparral, arid subtropical scrub, plains grasslands, and subdesert to desert vegetation. It seems highly probable that the parent lineage of *Polyphylla* arose within this hot dry Madro-Tertiary complex which offered not only the climate

but the plant species needed for larval and adult survival.

From this nuclear area dispersal was most logically in a somewhat radial pattern in response to the spread of dry climate. Miocene uplift of the Sierra Nevada—Cascade and Peninsular ranges of southern California furnished a new barrier to incoming moisture. By the end of the Miocene, southwestern desert biochores were fully established (Axelrod, 1958). The rain shadow effect produced by this orogeny (King, 1958), along with the general uplift of the interior plains, caused the drier environment which resulted in a major decline of forests and the eastward spread of the grasslands recorded in the Pliocene, 12 mybp (Dodson, 1960). This middle Pliocene grassland steppe is postulated as the most likely pathway by which elements of *Polyphylla* spread to the east.

## DISPERSAL AND DIFFERENTIATION OF SPECIES

(Figs. 34 and 37)

### THE OCCIDENTALIS COMPLEX

Fig. 37 is an idealized synthetic phylogenetic tree. It represents the computer generated model shown in Fig. 34 modified by inputting phenetic, paleoclimatological, and distributional data. Most interesting are the differences between these two hypotheses. My intent is that future data will test these differences and ideally, bring the two models together.

Evidence indicates that many scarab taxa were established in eastern North America long before the Pleistocene (Howden, 1963, 1966, 1969). *Polyphylla* first spread eastwards via the dry Pliocene steppe just discussed. The deep Miocene sands of the Alachua formation with its covering of pine and turkey-oak (Hubbell, 1954) provided an ideal larval and adult habitat. Subsequently this Pliocene pathway was fragmented and destroyed in a series of classic vicariance events by the Pleistocene environment of glaciers (Flint, 1957), pluvial conditions, oceanic oscillations (Cooke, 1945; MacNeill, 1951; Hubbell, 1954; Cronin, et. al., 1981), and periglacial climates (conditions adjacent to glaciers). These events were the driving force for the original cladogenesis of *Polyphylla* (Fig. 37) and isolated the proto-*occidentalis* lineage, which has since evolved in complete isolation from the rest of the genus. It served not only to

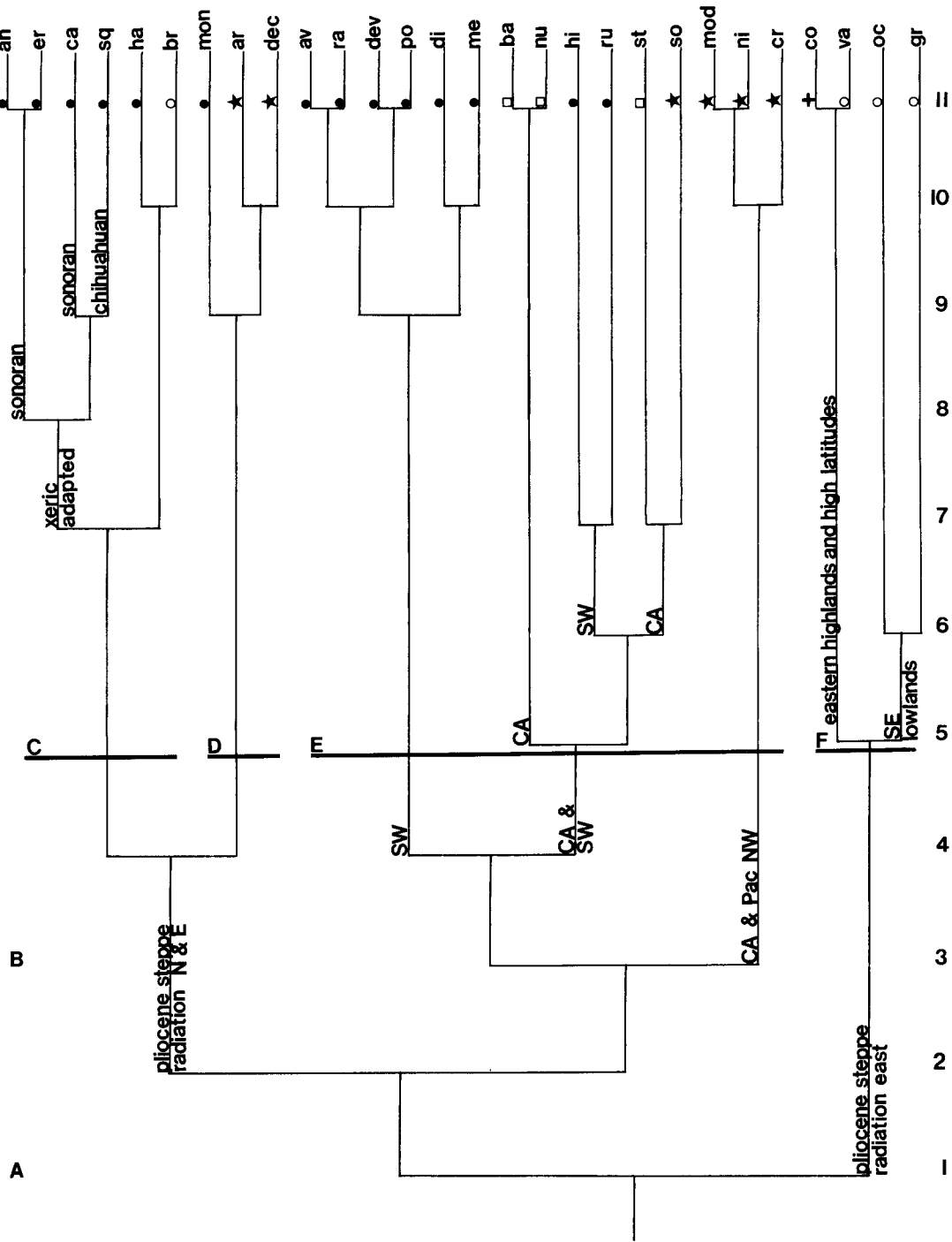


Fig. 37.—Alternate phylogenetic hypothesis for *Polyphylla* in America north of Mexico, modifying Fig. 34 by combining cladistic, phenetic, distributional, and paleoclimatological data. A = midcontinental uplift and development of the grassland steppe, early Pliocene, 12 mybp. B = late Pliocene, 8 mybp. C = the *hammondi* complex, D = the *decemlineata* complex, E = the *diffRACTA* complex, F = the *occidentalis* complex. Symbols mark species which are primarily adapted to: true desert to dry sand/grass associations (●), western montane coniferous forest (★), eastern lowland maritime environments (○), western coastal maritime environments (□) and, eastern highlands (+).

isolate the eastern lineage from the western parent stock, but also probably caused the cladogenesis of that lineage into the two primary sister-pairs shown in Fig. 37. The four extant species of this complex support this interpretation as they are highly dissimilar from each other and entirely dissimilar from their western congeners. No species are shared between the eastern and western clades. The humid deciduous forest biome of eastern North America was and is an insurmountable barrier to *Polyphylla*.

Throughout the Cenozoic, the southeast was subjected to a series of marine inundations. Paleogeography of Florida and adjacent areas enabled Cooke (1945) to reconstruct a sequence of ancient shorelines. Fig. 38 shows for reference the Miocene shorelines and Fig. 39 the subsequent Pliocene limits of inundation. This represents the maximum area then available for colonization by *Polyphylla*. Most of this area was repeatedly inundated during the seven or eight Pleistocene ice retreats, with a fairly uniform sand-hill habitat forming and gradually becoming dissected by rivers, streams and swamps (Cooke, 1945; Howden, 1963). These ingressing seas probably caused widespread extirpation of *Polyphylla* larval populations. Remnant demes closer to the Piedmont were surely pressured not only by subsequent inundations but periglacial climates as well. This constant complex of changes precluded distributional or genetic stasis; rather it caused repeated and constant mixing through time. In turn this precluded reproductive isolation of demes until environmental stasis was realized.

Of the two sister pairs shown in Fig. 37, *P. occidentalis*—*P. gracilis* are much more dissimilar than the often cryptic pair of *P. comes*—*P. variolosa*. The wider dissimilarity of the former pair is interpreted to be a function of greater relative age. Cooke (1945), MacNeill (1951), and others have shown that the maximum level of the Pleistocene seas in Florida was 270 feet above present levels. This area is well known for its diverse endemic biota, ranging from ferns through insects to reptiles (Hubbell, 1954). Howden (1985) reported that of an estimated 254 species of scarab beetles known from these Florida sand hills, 54 are endemic. Pleistocene inundation left only a small portion of central Florida as dry land (Fig. 39), strongly suggesting the following sequence for the eastern fauna:

1. Colonization of the east via the Pliocene steppe and vicariance of the invading lineage into highland

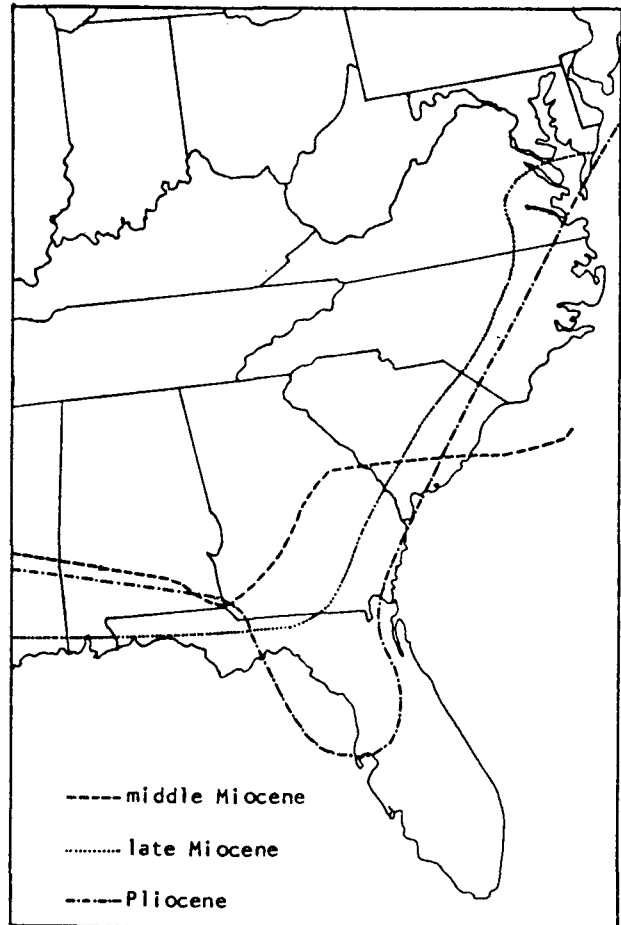


Fig. 38.—Upper Tertiary shorelines over the southeastern United States (adapted from Cooke, 1945 and Howden, 1963.)

Piedmont and lowland coastal elements.

2. Establishment of these two primary lineages throughout the east and southeast.

3. Pleistocene inundations (specifically the Brandywine, see Hubbell, 1954) isolate proto-*gracilis* in central Florida and proto-*occidentalis* inland of the sea but south of the Piedmont.

4. Post Pleistocene stabilization. *P. occidentalis* disperses throughout the southeastern coast, *P. gracilis* radiates from its nuclear refugium throughout Florida. *P. comes* remains primarily restricted to the Appalachian highlands leaving more boreal relicts to the south and *P. variolosa* successfully invades the northern coastal plain.

*P. comes* and *P. variolosa* show a complex of shared apomorphic states and degree of dissimilarity is rel-

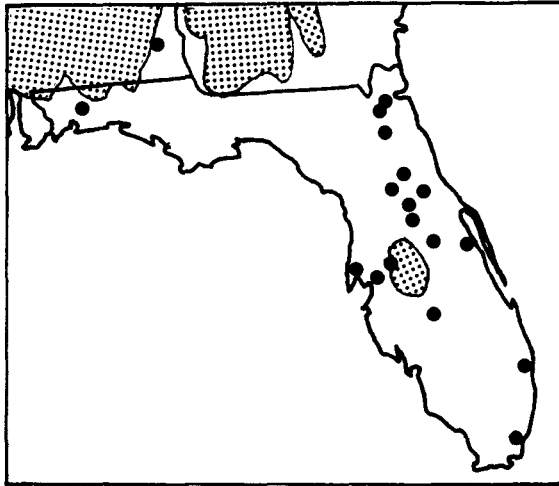


Fig. 39.—Distribution of *P. gracilis* and the maximum inundation of Florida by Pleistocene seas. Stippled areas mark emergent land.

atively low. Most likely they have existed as discrete reproductive entities only since post-Pleistocene climatic stabilization. This fits well with their restriction to higher latitudes (*P. variolosa*, Fig. 18) or higher altitudes (*P. comes*, Fig. 9), areas only recently available for colonization. *P. comes* occurs continuously over the area of Great Smoky Natl. Park. That this species was forced southwards by the Pleistocene is indicated by the occurrence of disjunct demes in Butler and Winston Counties, Alabama and Hinds and Rankin Counties, Mississippi (Fig. 9). Subsequent reinvasion of the deglaciated north must have left these boreal relicts displaced southwards of the primary range of the species. This distributional pattern is strikingly similar to those of four species of reptiles and three of amphibians (Smith, 1957), indicating that southwards retreat of boreal species away from the encroaching periglacial climate was not uncommon.

If all or any of the more boreal species were forced into southern refugia during the Pleistocene, postglacial reinvasion of the north had to take place. Postglacial climatic and floral chronologies offer the environmental matrix for this to have been possible. With the retreat of the ice, pollen records show the concurrent retreat of a belt of tundra parallel to the ice front (Smith, 1957). Other more extensive records of spruce—fir (cool wet), oak—hemlock (warm wet), and oak—hickory (cool dry) zones, indicate a cool—

warm—cool postglacial climatic sequence (Deevey, 1949). By way of this vegetational matrix, which offered both larval and adult food, *P. comes* re-established itself in the Appalachian highlands and *P. variolosa* along the northern coastal plain.

*P. variolosa* (the sister species of *P. comes*) is the northern coastal analog of the southern coastal *P. occidentalis* (Fig. 9). *P. occidentalis* and its sister species, *P. gracilis* (Fig. 17), remain confined to the southern coastal areas and have been unsuccessful in progressing inland since the post-Pleistocene stabilization. In essence, it appears that these four species are the end result of a long isolated primary clade, reflecting their age through levels of dissimilarity unusual in *Polyphylla* and primarily allopatric distributions.

#### THE HAMMONDI COMPLEX

Within the *hammondi* complex the species *P. hammondi* LeConte appears to have undergone the following historical sequence (Young, 1972):

1. Origin within the dry Pliocene steppe.
2. Invasion as far east as Indiana via the Pliocene steppe.
3. Retreat westwards and southwards in response to the Pleistocene.
4. Secondary invasion as far east as Indiana via the postglacial xerothermic prairie peninsula.
5. Secondary retreat westwards in response to destruction of the xerothermic prairie; western relicts left in eastern environmental refugia.

Defense of this sequence rests upon past climatic events (inferring vegetational history as well) and the relict demes of *P. hammondi* now recorded from Minnesota, Illinois, Indiana, and Wisconsin (Fig. 30). These two sources of data are inextricably joined and must be discussed as a single unit.

When conspecific populations are geographically disjunct, it is assumed that either (a) the species is colonizing new areas or (b) the species once had a broader range encompassing the site of the now disjunct deme. As all the disjunct *P. hammondi* demes are found in similar sandy "habitat islands" uniquely suited to their survival, it seems most logical that they do represent geographical relicts rather than new colonies. The probability of such colonies being established in several widely separated but ecologically similar areas is surely very low.

The first two stages in the sequential history listed above have been considered while dealing with the *occidentalis* complex. The Pliocene grassland seems to be the earliest time which offered an environmental pathway to the east for *Polyphylla* species. After this establishment the Pleistocene environmental extremes were the next most significant factor.

Pleistocene glaciers physically covered the Minnesota and Wisconsin localities now hosting *P. hammondi*, while the Indiana and Illinois sites were subject to severe periglacial climates. This factor probably caused a considerable westwards retreat of *P. hammondi* populations (step 3 above). Subsequent post-glacial warming trends, which peaked during that time period termed the Xerothermic, again caused a decrease in wet forest and its replacement by the drier oak-hickory complex and grasslands (Elias, 1942). This phase, now well known as the prairie peninsula, allowed *P. hammondi* to reinvade to the east (step 4 above).

During the final climatic stabilization at the close of the Xerothermic cooler moister conditions returned to much of eastern North America, accompanied by an encroachment of mesic forest onto the more xeric steppe or grasslands. As the great mass of the eastern steppe was destroyed animal species living there were forced to 1) retreat to the west from whence they originally came, 2) adapt, or 3) be subject to extinction. The majority of *P. hammondi* demes were unable to survive, except for those relicts we see today in Minnesota, Illinois, Indiana, and Wisconsin (step 5 above). The relict left in the wetter coastal site in Alabama (*P. brownae*, Fig. 30) has evidently been subjected to more severe selection pressures as it is now a phenetically disjunct unit, strikingly convergent in apomorphic character states with the phylogenetically distant *P. hirsuta* of the *diffracta* complex.

This phenomenon of western relicts displaced east of the species main range is repeated in many species of animals (Schmidt, 1938; Smith, 1957). The pattern shown by *P. hammondi* is nearly the same as that shown by the hog-nosed snake, *Heterodon nasicus*, with a relict deme found in the identical sandy area at Havana, Illinois (Smith, 1957).

In summary, the *hammondi* lineage spread eastwards in response to the same new steppe habitat which allowed the spread of the *occidentalis* lineage. Oscillations of the eastern boundary of the *hammondi* stock have been determined by a series of climatic

and vegetational events, resulting finally in the establishment of relictual demes considerably east of the primary range of its western congeners.

Species relationships within this group are reminiscent of those within the *diffracta* complex, that is, several species are restricted geographically and are phenetically quite similar. Of the six species in the complex four are restricted to small geographic areas (*P. anteronivea*, *P. brownae*, *P. erratica*, and *P. squamiventris*), one is recorded from only the hot deserts of southern Arizona, Nevada, and California and adjoining areas in Mexico (*P. cavifrons*), and only one species (*P. hammondi*) is widely distributed.

Figs. 34 and 37 agree almost entirely within this clade. *P. erratica* and *P. anteronivea* are sister species, forming a tight pair cladistically, phenetically, and distributionally. They are known only from the Saline and Death Valleys of southeastern California and the adjacent Amargosa Desert of Nevada. *P. cavifrons* and *P. squamiventris* are also sister species, representing a more southern and eastern hot-dry adapted lineage. *P. cavifrons* is restricted to the Sonoran Desert around the northern tip of the Gulf of California (southern California and Baja Norte) and Arizona, while *P. squamiventris* is restricted to the Chihuahua Desert of west Texas and Chihuahua, Mexico. In Fig. 37, *P. hammondi* and *P. brownae* are placed as sister species. They are very close phenetically; *P. brownae* represents the terminus of a logical transformation series from vittate, southwestern *P. hammondi* to avittate northern and eastern demes to an avittate setaceous southeastern extreme which is most apomorphic. It is also a geographic terminus of this clade. All evidence indicates that *P. brownae* is another eastern relictual isolate of the *hammondi* lineage, but unlike the isolates in Minnesota, Wisconsin, Illinois, and Indiana, it is distinct from the parent stock. *P. brownae* is another example of the loss of vittae—acquisition of elytral and pronotal hairs sequence seen so often throughout this genus.

#### THE *DIFFRACTA* COMPLEX

The history of the entirely western *diffracta* complex (Fig. 4) is most immediately joined with that of the Madro-Tertiary flora discussed earlier. The northern and westwards spread of this plant matrix from

early Miocene to middle Pliocene most probably offered the environmental pathway for expansion and fragmentation of the complex. If the southwestern origin of *Polyphylla* is accepted, this direction of vegetational expansion correlates closely with what appears to be the primary direction of dispersal of the beetle species themselves.

Western records are not as clear as those from the eastern United States. Such a complex of factors, many of them little known or understood, placed stresses on western and coastal populations during the Tertiary and Quaternary that it is difficult to analyze them sequentially. Orogeny, cordilleran glaciation, periglacial and/or pluvial climates, and floristic migration and evolution, are some of the major factors which must be dealt with during a consideration of the western Pleistocene. The most extensive and readily available source of data has been and is fossil pollen.

Axelrod's work (1958) offers one of the most extensive sources of fossil data on the early Tertiary of the southwest. The Madro-Tertiary flora spread from its southwestern "Mohavia" center as far north as southern Oregon by the early Pliocene, while west-central California hosted the same flora by middle Pliocene. The northern Great Basin was an ecotonal area by early Pliocene, with Madro- and Arcto-Tertiary species mixed. These records show that the Madro-Tertiary plant complex was available for not only establishment, but the northwards and westwards expansion of the *diffRACTA* complex.

Secondly, Hansen (1947) applied palynological techniques to bogs in the Pacific Northwest. Interpretation of these data resulted in proposal of the following postglacial climatic sequence for the area:

1. Cool moist
2. Warm dry
3. Warm dry maximum
4. Cool moist

Deevey (1949) hypothesized that this warm dry maximum *might* have been contemporaneous with the eastern Xerothermic discussed above. Hansen (1947) did record a pollen maximum of grassland species from the Okanogan area of north-central Washington during middle postglacial time (the hypsithermal or altithermal of many authors), which would infer a relatively warm dry interval. These data are from a geographically restricted area, but they do offer much the same postglacial sequence seen in the

east, with a warm dry maximum especially conducive to the re-establishment of the *diffRACTA* complex.

A third set of data has been presented by Martin (1963) and Martin and Mehringer (1965). Martin (1963) offered extensive palynological, vertebrate paleontological, and archeological evidence in support of an updated postpluvial chronology for the American southwest. He lists the following postpluvial history, with 1950 as the "present" base for all BP dates:

- |                 |   |
|-----------------|---|
| Zone V:         | Last pluvial, 11,000 BP; Desert grassland evidence rare, <i>Pinus</i> dominant, Pleistocene megafauna (Bison, camel, ground sloth, mammoth) present; Cool humid.  |
| Zone IV:        | 10,500–8,000 BP; Major rise of the desert grassland, decline of <i>Pinus</i> and Pleistocene megafauna, rise of early man; Warm arid, like present.   |
| Zone III:       | 8000–4000 BP; Major decline in Compositae, slight rise in <i>Pinus</i> , development of the Cochise culture of man; Warm semiarid with greater monsoon rains; This stage corresponds to the classic altithermal of Antevs (1955), which has traditionally been considered a hot dry drought period. |
| Zones I and II: | 4000 BP-present; Rise of desert grassland, levelling off of <i>Pinus</i> , establishment of the modern vertebrate fauna; Warm arid.   |

These data do not support the traditional concept of biologically significant postpluvial droughts in the American southwest. In a broad sense, they seem to conflict with Hansen's warm dry maximum from Washington state. Martin's data cause one to interpret the altithermal as a relatively wet period, rather than hot and dry. If this is indeed the case, as the new data seem to indicate, many of our ideas on western postpluvial time must be reinterpreted. A striking (and controversial) example of this is Martin's comment on the Pleistocene mammal fauna which "disappeared not because they lost their food supply but because they became one."

Endemism offers a fourth possible source of information on past events. Of the 15 species within the *diffRACTA* complex, nine are geographically restricted to a single mountain or other small, presumably ecologically isolated area. Morphologically the species

are not very distinct especially when compared with the other complexes. This relatively high number of endemics would most traditionally be interpreted as indicative of great age. Based on the close phenetic similarity of the species, however, I tend to doubt this concept in this case. Rather, it is proposed that these geographically restricted species represent autochthonous populations only recently isolated which have never covered a larger area.

These various data need to be brought together. First of all, the traditional interpretation of endemism does not seem to apply here. Secondly, neither Hansen's postglacial warm dry maximum for the Pacific northwest nor Martin's wetter alithermal for the southwest are "all or nothing" periods. Pollen records of both show the existence of the forest-grassland complexes needed for the survival and spread of *Polyphylla* populations. Such a vegetational matrix would offer the possibility of reinvasion after the retreats and extinctions which must have taken place during the Pleistocene pluvials. Shifts such as this could have resulted in population fragmentation, isolation, and eventual speciation. The pattern becomes nearly a repetition of the eastern postglacial, yet one must realize it is a conjectural one, especially when considering the Pacific Coast and Northwest.

This complex may be divided into two phenetic clusters, those species not having elytral hairs (the plesiomorphic state) and those species with elytral hairs (the apomorphic state). Because the apomorphic state has arisen repeatedly throughout this complex and the genus as a whole, these clusters do not entirely emerge in Figs. 34 and 37. In the precise sense of sister pairs, only 40% of the idealized tree (Fig. 37) agrees with the cladogram (Fig. 34).

*P. avittata* and *P. ratcliffei* are clear sisters, representing the deserts of western and eastern Utah respectively. *P. devastiva* and *P. pottsorum* form a pair by the synapomorphic pronotal setae and nearly total secondary degeneration of elytral vittae. This pairing is not logical in the distributional sense, as *P. devastiva* is restricted to southwestern Idaho (Fig. 22) and *P. pottsorum* to southeastern New Mexico and west Texas (Fig. 27). *P. diffracta* pairs with its derivative *P. mescalerensis*, as expected, though the analyses run here show no synapomorphies (Fig. 34). This pair is logical distributionally, with *P. diffracta* found throughout the southwest (Fig. 24) and *P. mescalerensis* apparently endemic (and I believe autochthonous) to the Mescalero Dunes of southwestern

New Mexico (Fig. 22). These three sister pairs (six species) constitute the primary southwestern desert element of this complex.

A second element is that found primarily in California and Baja Norte, with secondary success in Arizona, to the exclusion of the Pacific northwest. This faunal element does not emerge well in Fig. 34 because of the inclusion of the convergent *P. brownae* (of the *hammondi* complex) and the exclusion of *P. sobrina* which is convergent with *P. monahansensis* (of the *decemlineata* complex). Fig. 37 shows the proposed phylogenetic relationships when these two homoplasies are resolved by inputting additional phenetic and distributional data. Degeneration of vittae and acquisition of dense, heavy elytral and pronotal hairs are synapomorphies for *P. nubila* and *P. barbata* (coastal California sisters, Fig. 22) and *P. hirsuta* (Arizona, Fig. 22) and *P. rugosipennis* (Arizona and Baja Norte, Fig. 28), sisters. Retaining the plesiomorphic absence of elytral hairs, *P. sobrina* and *P. stellata* form a sister pair which is geographically logical, as they both occur in the more central portions of California (Fig. 25).

*P. crinita*, *P. nigra*, and *P. modulata* constitute the third element within this complex. They occur from California to British Columbia and all are highly convergent with *P. decemlineata* in their deep coloration and heavy vittation. Phenetically and ecologically this element is the high latitude analog of the high altitude *P. decemlineata*. *P. decemlineata* is most often collected at high elevations (4100 ft.—10,500 ft. in this work) to the exclusion of all other species, within the savanna and forest biocoenoses. *P. crinita* is our most northern species, having been collected up to 53 degrees north latitude. The cool-wet matrix of high elevations presents much the same selection pressures as the cool-wet matrix of the Pacific northwest, with the result being the adaptive homoplasies now seen in populations of these species. The widely distributed *P. crinita* shows the most plesiomorphic states. The sister pair *P. nigra*—*P. modulata* is its logical derivative, with *P. nigra* primarily distributed in California (Fig. 26) and *P. modulata* primarily in Oregon and Washington (Fig. 25).

#### THE DECEMLINEATA COMPLEX

Without repeating much of the above discussion, it may be noted that this small group of three species was subjected to the same climatic and vegetational



oscillations as the *diffracta* complex. Synapomorphies for this complex are states of characters 20 (configuration of the lateral edges of the aedeagus) and 22 (configuration of the aedeagal tip). *P. decemlineata* and *P. monahansensis* form a sister pair based on synapomorphies in characters 7, 16, and 19. Phenetically, *P. arguta* and *P. decemlineata* are an obvious sister pair, with the very dissimilar *P. monahansensis* being a much earlier isolate of the lineage (Fig. 37). *P. arguta* is distinguished primarily by its degenerate elytral vittae and occurs primarily in Utah and Nevada (Fig. 19). Though often recorded sympatrically with *P. decemlineata* and recorded up to 8500 ft. elevation, it appears to retain its genetic integrity.

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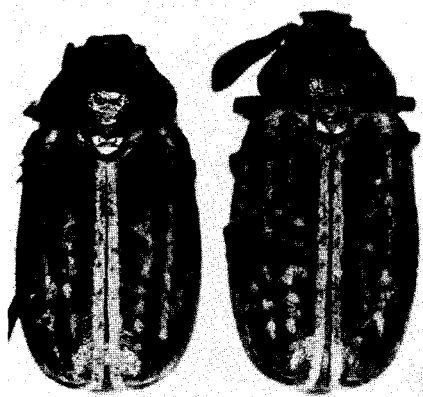
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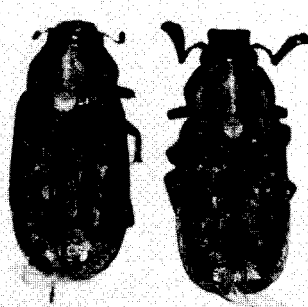
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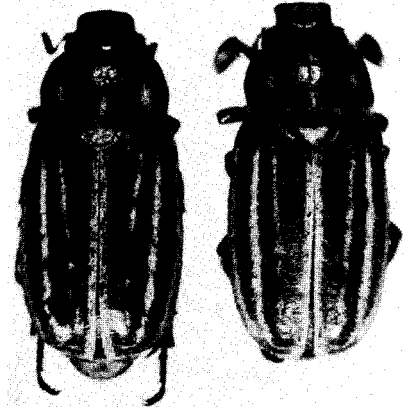
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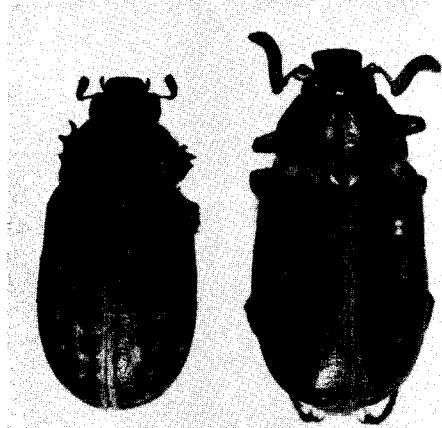
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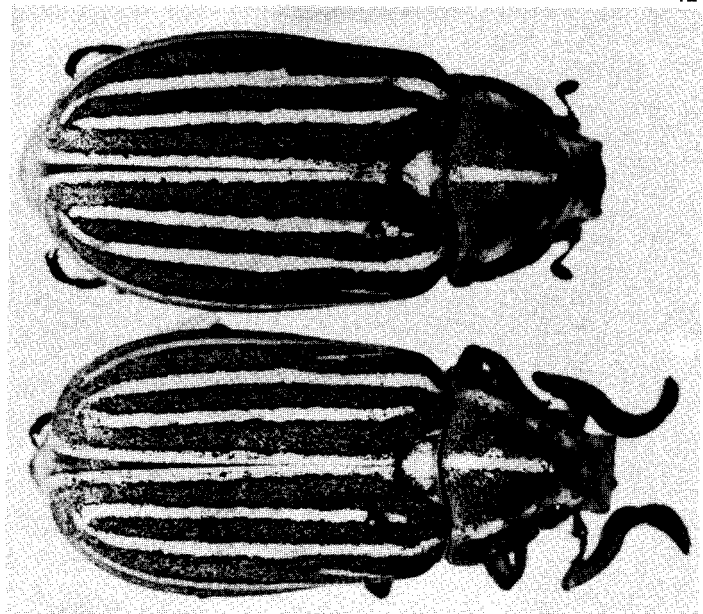
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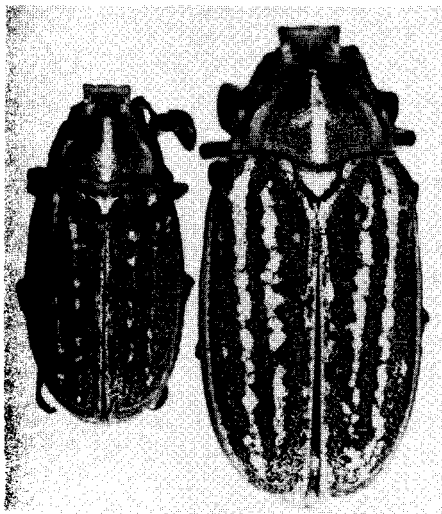
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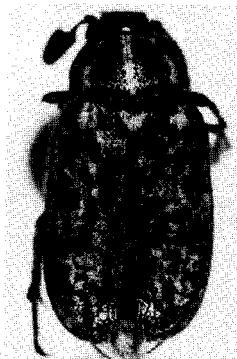
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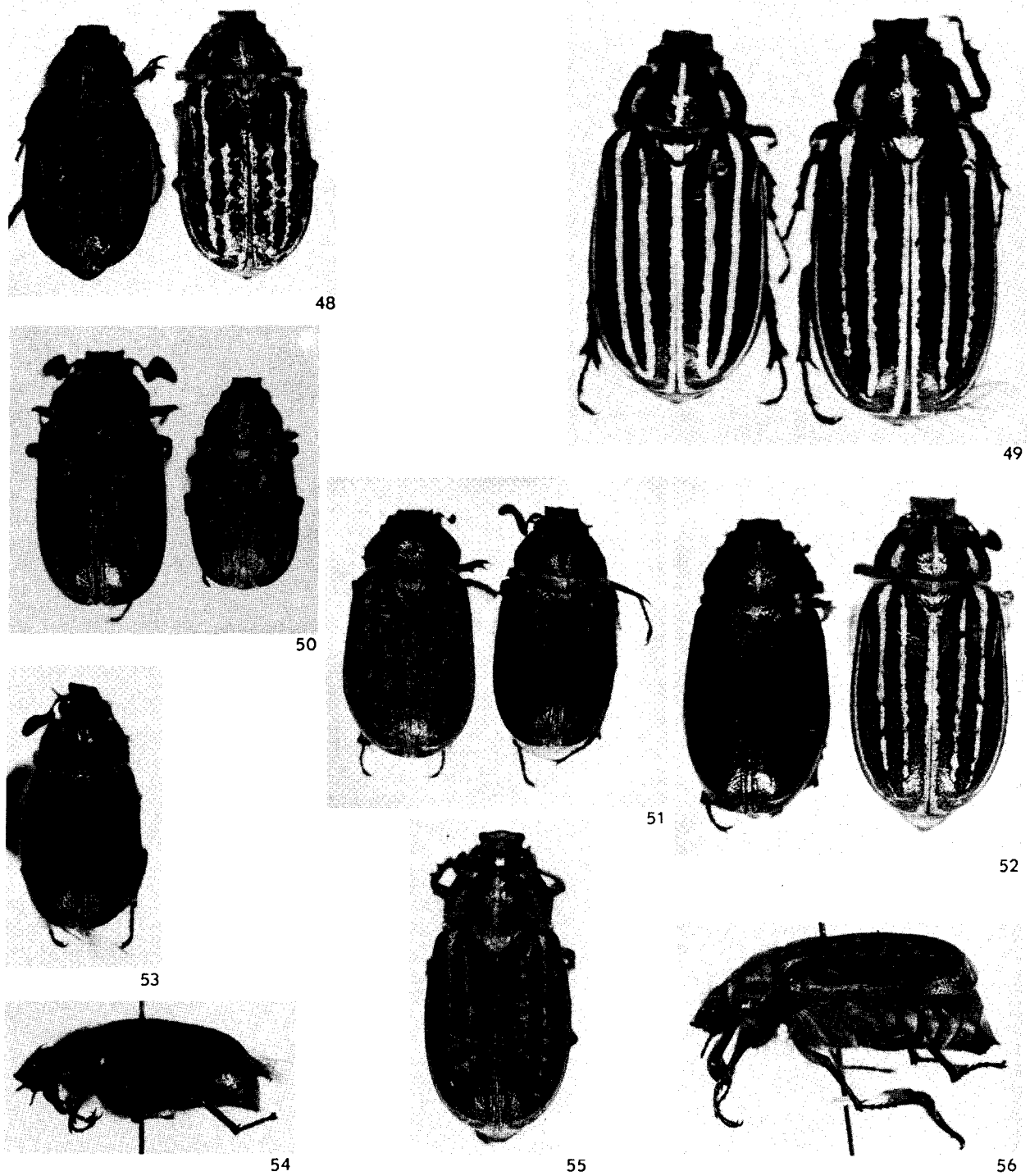


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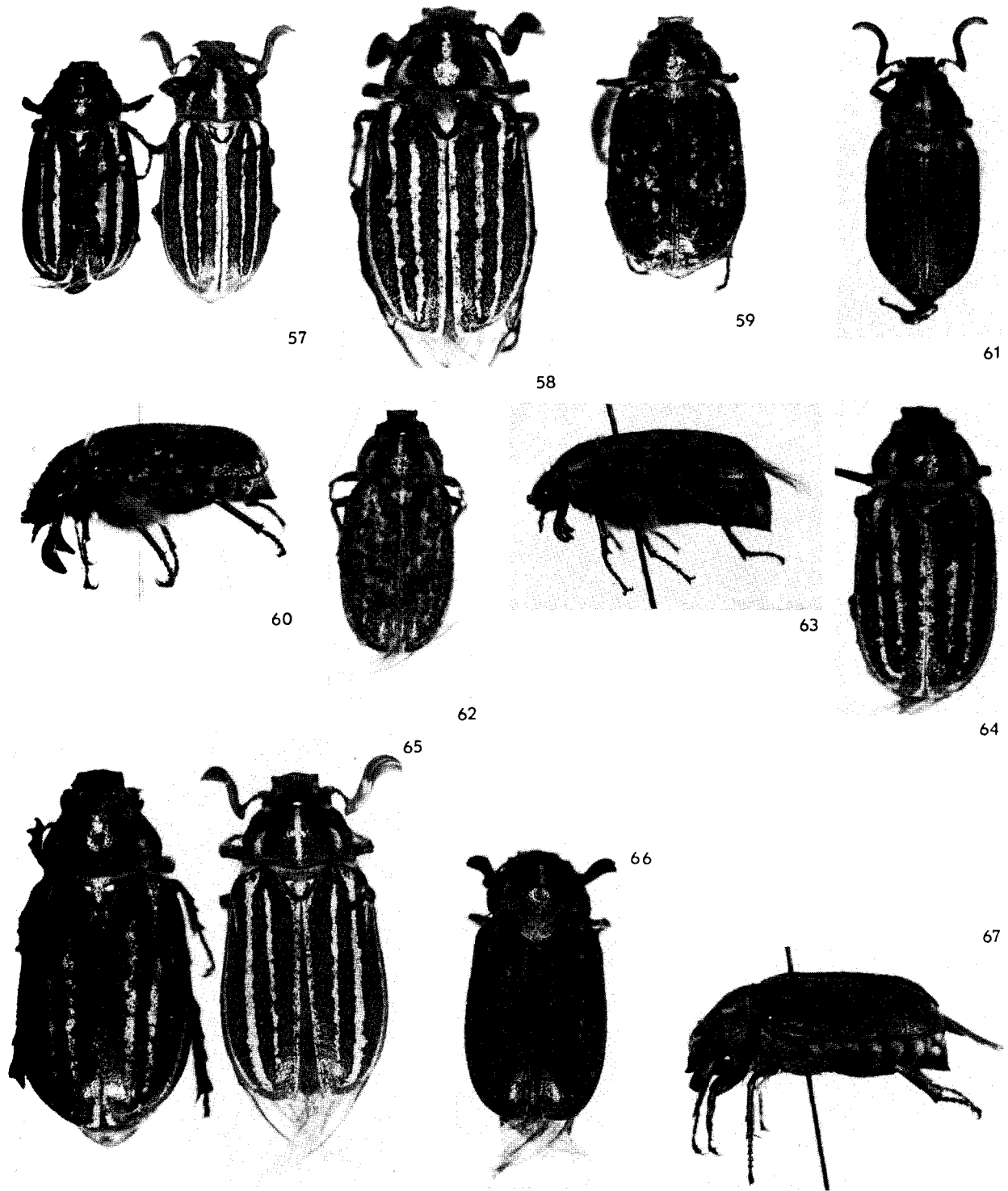


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Figs. 40–47.—*Polyphylla* males (right) and females (left), except as noted, 2X. 40.—*P. comes*. 41.—*P. gracilis*. 42.—*P. occidentalis*. 43.—*P. variolosa*. 44.—*P. arguta*, male size extremes. 45.—*P. decemlineata*. 46.—*P. monahansensis*, paratype male. 47.—*P. avittata*, holotype male.

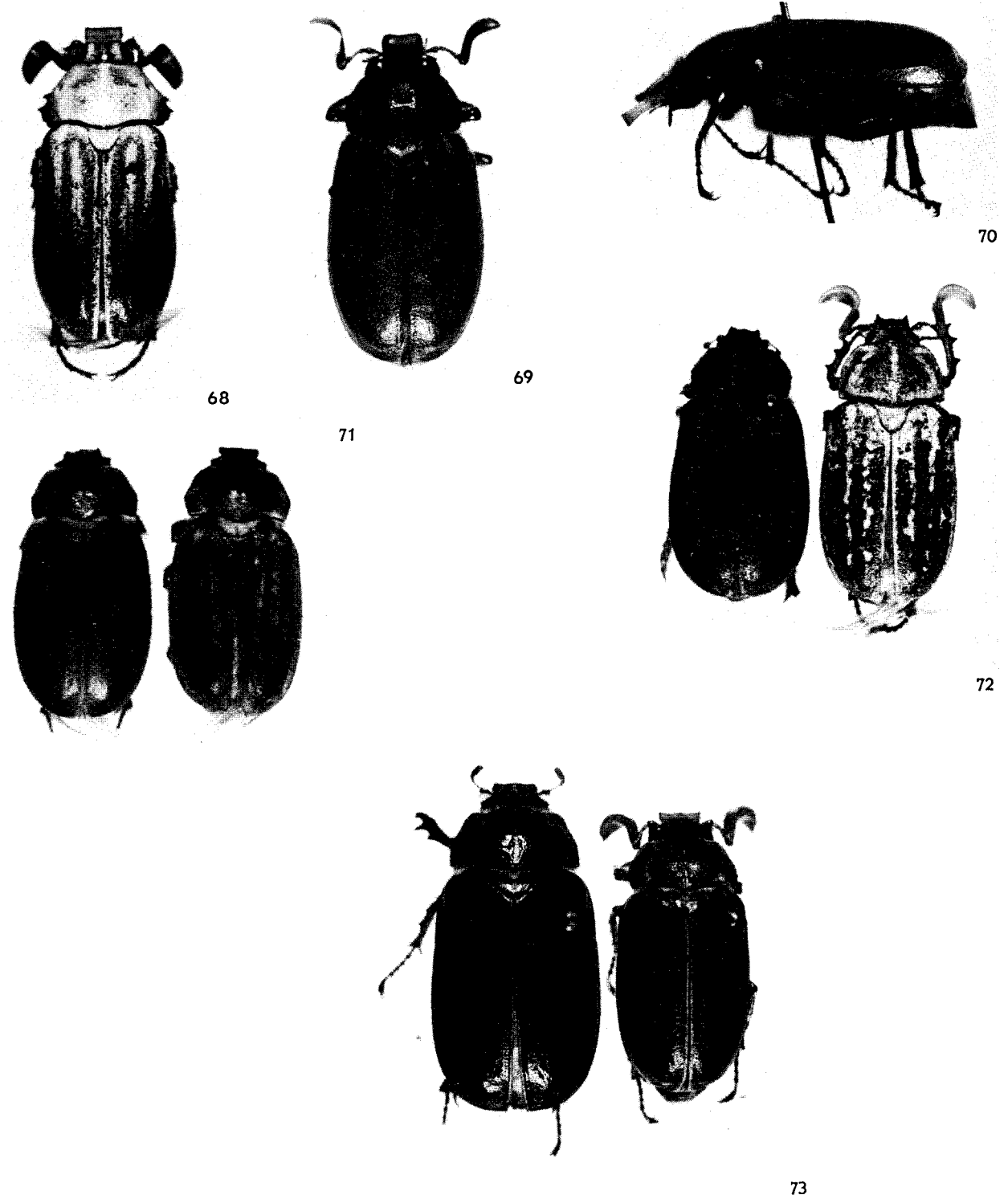


Figs. 48–56.—*Polyphylla* males (right) and females (left), except as noted, 2X. 48.—*P. barbata*, metatypes, including only known female. 49.—*P. crinita*. 50.—*P. devastiva*, male size extremes. 51.—*P. devastiva*, including metatype female. 52.—*P. diffracta*, vittate male and avittate female. 53–54.—*P. hirsuta*, holotype male. 55–56.—*P. mescalensis*, holotype male.

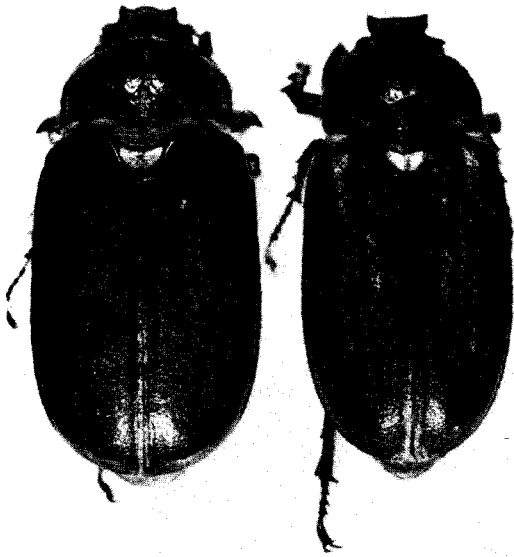


Figs. 57-67.—*Polyphylla* males (right) and females (left), except as noted, 2X. 57.—*P. modulata*. 58.—*P. nigra*, male. 59-60.—*P. nubila*, holotype male. 61.—*P. pottorum*, paratype male. 62-63.—*P. ratcliffei*, holotype male. 64.—*P. rugosipennis*, male. 65.—*P. sobrina*. 66-67.—*P. stellata*, holotype male.

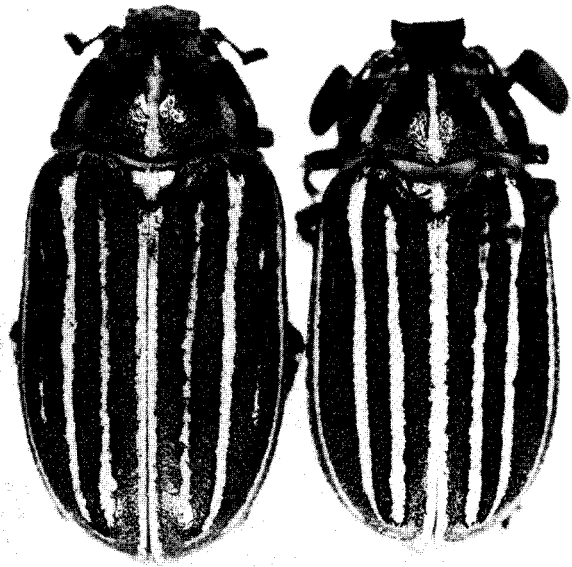




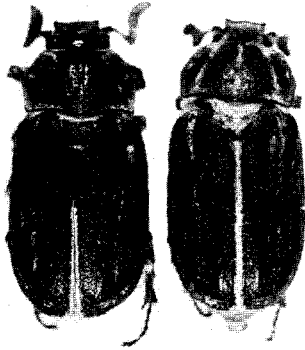
Figs. 68–73.—*Polyphylla* males (right) and females (left), except as noted, 2X. 68.—*P. anteronivea*, holotype male. 69–70.—*P. brownae* holotype male. 71.—*P. cavifrons*. 72.—*P. erratica*, holotype male and first described, metatype female. 73.—*P. hammondi*, northeastern avittate color phase.



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Figs. 74-76.—*Polyphylla* males (right) and females (left), except as noted, 2X. 74.—*P. hammondi*, southwestern avittate color phase. 75.—*P. hammondi*, southwestern vittate color phase. 76.—*P. squamiventris*, males.

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