



Revision of the species of Psenini in America north of Mexico (Hymenoptera: Schecidae)
by Arthur Richard Gittins

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
DOctor of philosophy in Entomology
Montana State University
© Copyright by Arthur Richard Gittins (1963)

Abstract:

The results of a systematic study on the species of Pemphredoninae within the tribe Psenini which occur in America north of Mexico are presented. In addition to seven new species described, included are re-descriptions of all valid species within the genera *Diodontus*, *Ammopsen*, *Mimumesa* and *Mimesa*, diagnoses of the genera *Psen*, *Pseneo* and *Pluto*, and an annotated list of the species of the latter three genera.

Keys to the various taxa are included along with distribution data and available information on the biologies of each species. A historical review of systematic and nomenclatorial studies on the tribe precedes the present systematic treatment of this group, as do sections dealing with psenine external anatomy and phylogeny.

REVISION OF THE SPECIES OF PSENINI
IN AMERICA NORTH OF MEXICO (HYMENOPTERA: SPHECIDAE)

by

ARTHUR RICHARD GITTINS

A thesis submitted to the Graduate Faculty in partial
fulfillment of the requirements for the degree

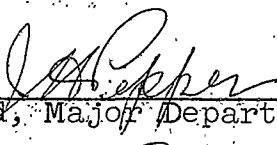
of

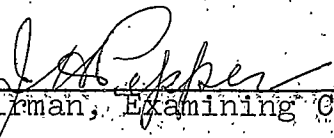
DOCTOR OF PHILOSOPHY


in

Entomology

Approved:


Head, Major Department


Chairman, Examining Committee


Dean, Graduate Division

MONTANA STATE COLLEGE
Bozeman, Montana

June, 1963

ACKNOWLEDGMENTS

I am greatly indebted to Dr. William F. Barr, Professor of Entomology, University of Idaho, for his many valuable suggestions concerning the problem and his critical examination of this manuscript. I also take this opportunity to express my appreciation for the advice and assistance received from Dr. Richard C. Froeschner, former Associate Professor of Zoology and Entomology, Montana State College, and Dr. J. H. Pepper, Head, Department of Zoology and Entomology at that institution. Many thanks are further due Dr. R. M. Bohart, Professor and Head, Department of Entomology, University of California, Davis, California, and Dr. Karl V. Krombein, United States National Museum, Washington, D. C., for their valuable suggestions.

I would like to recognize Dr. Harold Grant, Philadelphia Academy of Sciences, and Dr. Barney D. Burks and Dr. W. H. Anderson, United States National Museum, for their kind assistance during the examination of types and other material at those institutions. Thanks are also due to Miss M. Statham, American Museum of Natural History, and Dr. Rosco Hill, Department of Entomology, University of Nebraska, who sent types located at their institutions for examination.

The generosity of the following persons and institutions for the loan of material examined during this study also is acknowledged: Professor, G. E. Spencer, University of

British Columbia; Dr. Herman A. Scullen, Oregon State University; Dr. P. D. Hurd and Dr. Jerry Powell, University of California, Berkeley; Dr. R. M. Bohart and Mr. Frank Parker, University of California, Davis; Dr. M. T. James, Washington State University; Dr. George E. Knowlton, Utah State University; Department of Entomology, University of Idaho; Department of Zoology and Entomology, Montana State College; Dr. George E. Ball, University of Alberta; Dr. Edwin F. Cook, University of Minnesota; Dr. C. D. Michener, University of Kansas; Dr. J. F. Gates-Clark, United States National Museum; Dr. W. R. Mason, Canadian National Museum; Dr. James A. C. Rehn, Philadelphia Academy of Sciences; Miss Marjorie Stratham, American Museum of Natural History; Dr. Henry Dietrich, Cornell University; Dr. Howard E. Evans, Museum of Comparative Zoology; Mr. Hugh B. Leach, California Academy of Sciences; Dr. Marius Wasbauer, California Department of Agriculture; and Dr. R. R. Dreisbach, Midland, Michigan.

TABLE OF CONTENTS

LIST OF FIGURES.....	vi
ABSTRACT.....	vii
INTRODUCTION.....	1
HISTORICAL REVIEW.....	1
PROCEDURES.....	9
BIOLOGY.....	12
ANATOMICAL FEATURES.....	13
PHYLOGENY.....	18
SYSTEMATICS.....	23
Key To The Genera Of Nearctic Psenini.....	24
Group Diodonti.....	26
Genus <u>Diodontus</u> Curtis.....	26
Genus <u>Pluto</u> Pate.....	49
Group Pseni.....	68
Genus <u>Ammopsen</u> Krombein.....	68
Genus <u>Mimumesa</u> Malloch.....	73
Genus <u>Mimesa</u> Shuckard.....	138
Genus <u>Psen</u> Latreille.....	233
Genus <u>Pseneo</u> Malloch.....	241
Nomina Dubia.....	250
LITERATURE CITED.....	252
APPENDIX.....	258

LIST OF FIGURES

FIGURE 1.....	Head and thoracic features in the Psenini...	260
FIGURE 2.....	Frontal view of head of <u>Diodontus frontalis</u> (Fox).....	262
FIGURE 3.....	Illustration of the propodeum, petiole and first abdominal tergite of <u>Mimumesa mixta</u> (Fox).....	264
FIGURE 4.....	Wing venation in the Psenini.....	266
FIGURE 5.....	Intromittent organs in <u>Mimumesa</u>	268
FIGURE 6.....	Intromittent organs in <u>Mimumesa</u> (continued).	270
FIGURE 7.....	Lateral lobes of the phallic structures in <u>Mimumesa</u>	272
FIGURE 8.....	Lateral lobes of the phallic structures in <u>Mimumesa</u> (continued).....	274
FIGURE 9.....	Phylogenetic relationships of the nearctic genera of Psenini.....	276

ABSTRACT

The results of a systematic study on the species of Pemphredoninae within the tribe Psenini which occur in America north of Mexico are presented. In addition to seven new species described, included are re-descriptions of all valid species within the genera Diodontus, Ammopsen, Mimumesa and Mimesa, diagnoses of the genera Psen, Pseneo and Pluto, and an annotated list of the species of the latter three genera. Keys to the various taxa are included along with distribution data and available information on the biologies of each species. A historical review of systematic and nomenclatorial studies on the tribe precedes the present systematic treatment of this group, as do sections dealing with psenine external anatomy and phylogeny.

INTRODUCTION

This thesis presents the results of studies, largely systematic, on the species of the wasp tribe Psenini present in North America, north of Mexico.

This work was undertaken with the express purpose of establishing the relationships of species and higher categories within this large but poorly known sphecoid tribe belonging to the subfamily Pemphredoninae. The study also was carried out so as to provide a means of identification of the North American forms. It is the earnest hope that presentation of this research may act as a stimulus to further studies on classification and biology of these wasps.

In this revision, seven genera are considered, including a monotypic genus Ammopsen recently described by Krombein (1959) and not previously included in systematic papers dealing with the tribe. A total of 58 species are considered herein, seven of which are new.

HISTORICAL REVIEW

First mention of a species pertaining to the group now under discussion was that of Sphex atra, the female of which was described by Fabricius in 1794 in "Entomologica Systematica." Following this, Latreille (1796) erected the genus Psen in "Precis Caracteres Genera Insecta," giving a brief description of the genus but assigning no species to it.

In 1798, Panzer, in his famous paper "Fauna Insecta Germanica," described a second species of this group, naming it Sphex pallipes. This species, which appears to have been misidentified by earlier workers, is the generotype of Diodontus Curtis (= Psenulus Kohl of European authors). Then in 1801, Panzer published a list of wasp genera that Jurine enlarged upon later. In this second publication, "Intelligenzblath der Literatur-Zeitung," Panzer accepted Latreille's genus Psen and designated Sphex atra Fabricius as the generotype.

Fabricius, in 1804, in "Systema Piezatorum," described a number of psenines but assigned them to genera other than Psen. Four European species which Fabricius described at that time were Pelopeus compressicornis, P. unicolor, Trypoxylon atratum and T. equestre, all of which were later transferred to the genus Psen. It is interesting to note that Pelopeus compressicornis later proved to be the male of Sphex atra and P. unicolor a variant female of the same species. In his paper, Fabricius also described Pepsis lutaria which may be conspecific with the currently recognized Mimesa bicolor Shuckard. However, because of the vague description which accompanied publication of the Fabrician name, European workers have been forced to relegate Pepsis lutaria to the status of a nomen dubium.

The fine discriminating eye of Panzer was again evident

through a "Kritische Revision" published in 1806. While he assigned no additional generic names to the material known to him, he recognized three groups within the genus Psen. He noted that the first group was typified by Psen atra (Fabricius), the second by P. pallipes (Panzer), and the third by P. equestris (Fabricius). Each of these species is now assigned to different genera of the Psenini and are presently named Psen atra (Fabricius), Diodontus pallipes (Panzer), and Mimesa equestris (Fabricius) respectively. Additionally, Panzer did much toward clarifying the classification of the Psenini by placing in synonymy a number of species names, among which were those of Fabricius previously mentioned.

One year later, in 1807, Jurine published his famous "Nouvelle Methods de Classer l'Hymenoptera," relying in great part upon the wing venation for his classification. In this paper, Jurine defined with precision the genus Psen and considered this taxon as composed of two distinct groups or "families." In the first group he placed P. atra (Fabricius) and in the second group P. equestris (Fabricius). Van der Linden, in 1829, agreed with Jurine's division of the Psen into two groups and described P. unicolor as another member of the second group or "family."

Curtis (1834) erected the genus Diodontus for specimens he believed to be P. pallipes (Panzer). Curtis thought, as Panzer had indicated in 1806, that this species was not

congeneric with either P. atra or P. equestris. Most European workers, however, believe Curtis misidentified material and they have not recognized or accepted Diodontus in spite of nomenclatorial rules to the contrary. Three years after the Curtis publication, Shuckard, in his "Essay on Indigenous Fossorial Hymenoptera," proposed the name Mimesa for Jurine's and Van der Linden's second group, with the type being Mimesa equestris (Fabricius). Additionally, he added the species bicolor Jurine to this taxon. Also in 1837 the first two North American species were described by Say who assigned both to the genus Psen. These were leucopus and mellipes, re-described by Fox in 1898 and now both assigned to the genus Mimumesa.

The next work of note was that of Dahlbom who, in 1843, recognized both Psen and Mimesa in his publication, "Hymenoptera Europaea." Of note here is his admitted recognition of two divisions within the genus Mimesa. Although he indicated that a decided gap was evident between two groups of species, he assigned no names to these groupings but simply stated ... "Chez les representats de la premiere, unicolor et borealis, le front presente une carene entre les antennes, tandis que chez ceux de la deuxieme, atra, lutaria, et equestris il est arme d'un tubercule." It is interesting to note that Dahlbom assigned the Psen generotype atra to the genus Mimesa on the basis of wing venation, and placed Psen atratus (Fabricius)

(=pallipes Panzer) in Psen as the generotype. In 1849, Wissman apparently recognized the difficulty arising from Dahlbom's handling of atra (Fabricius) and created the genus Dahlbomia for this species, a name later assigned to synonymy with Psen.

In 1852, Wesmael published on the psenine species of central Europe, calling attention to some synonymy he considered evident. He concurred with Panzer's and Dahlbom's recognition of Psen and Mimesa as the generic representatives of the Psenidae, but he erred in following Dahlbom and assigned atratus (Fabricius) and concolor Dahlbom to Psen and misplaced atra (Fabricius) in Mimesa. He also felt, as Dahlbom had indicated, that Mimesa contained more than one distinct group of species, but differed in considering that there were three groups rather than two within that genus. To each of these groups within Mimesa he assigned the following subgeneric names: Mesopora -- to contain the generotype of Psen, P. atra; Mimesa -- to contain a group including M. unicolor; and Aporia -- to contain the group including the generotype M. equestris. While this created some nomenclatorial difficulties, Wesmael contributed much to the taxonomy of the group in recognizing that subgeneric levels did exist through discontinuity between species groups within the genus Mimesa.

In 1856, Smith described the third North American species from a male specimen collected in the Hudson's Bay area of

Canada giving it the name Mimesa borealis. Pate, in 1944, recognized a case of primary homonymy between Smith's Mimesa borealis and Dahlbom's Mimesa borealis and renamed Smith's species M. psychrus. Cresson, in 1865, published descriptions of three new species apparently indigenous to the North American continent. He, like Smith before him, followed the generic concepts of Shuckard and assigned his new species to the genus Mimesa. Packard (1867) was the first worker to attempt a comprehensive treatment of the species occurring in North America. He also followed the classification of Shuckard and assigned all previously described species of Say, Smith and Cresson, along with seven new species, to Psen and Mimesa.

The next major revision of North American forms was published by Fox in 1898. While describing a number of new species and establishing some new synonymy he supported the older contention that the tribe was composed of a series of species belonging only to a single genus Psen. It is interesting to note, however, that several years previously Fox (1893) had named a new species Mimesa maculipes. By this time, however, European workers had come to agree that both Psen and Mimesa constituted valid genera.

Following Fox's paper a number of North American workers published short notes on psenine wasps. Largely, these papers dealt with descriptions, often incomplete, of new species.

While most of these persons recognized Mimesa as a separate genus, a few, such as Rohwer and Cameron, considered Mimesa as a subgenus of Psen. During this period one American worker, Viereck (1901), supported the opinion of Shuckard but also recognized Psenulus Kohl as a distinct genus. Kohl (1896), in a paper dealing with European psenines, stated that he was erecting the genus Psenulus for a group of species closely related to Psen fuscipennis Dahlbom, a species designated as the generotype of Psenulus by Ashmead three years later. On the untenuous basis of wing venation, later shown to be variable, Viereck decided, however, that the North American forms showed sufficient divergence from their palearctic Psenulus (= Diodontus) allies to deserve separate generic recognition. As Malloch later indicated, Viereck was unaware of the existence of the previously used name Diodontus Curtis and hence Viereck erroneously proposed the name Neofoxia for the American species of Diodontus (= Psenulus). At that time, Viereck recognized four genera in the group he referred to as the subfamily Pseninae: Psen Latreille, Mimesa Shuckard, Psenulus Kohl, and Neofoxia Viereck.

The next major work relating especially to changes in concepts with regard to higher taxa was a near-contemporary paper published by Malloch in 1933. This author, dealing exclusively with the North American forms, recognized three genera, Psen Latreille, Diodontus Curtis, and a new genus

Psenia Malloch peculiar to the new world fauna. Additionally, Malloch considered that there were four distinct groups of species within Psen that deserved subgeneric names. He treated the subgenera in the following manner: Psen (Psen) Latreille, with atra (Fabricius) as the type; Psen (Mimesa) Shuckard, with equestris (Fabricius) as the type; Psen (Pseneo) Malloch, with Kohlii Fox as the type; Psen (Mimomesa) Malloch, with niger (Packard) as the type. In addition to the new concepts relating to higher taxa, Malloch's paper presented a summary of the species of our fauna and described a number of new species. M. deBeaumont (1937) stated Malloch's work is to be considered one of the really major contributions to Psenini taxonomy.

A historic sketch of works pertaining to the psenine wasps would be far from complete if two important, modern, European contributions were not mentioned. While neither contributes any new concepts relating to changes from Malloch's classification, other than recognizing Psenus Kohl and discarding Diodontus Curtis, both add greatly to our knowledge of the biologies and taxonomy of the Palearctic species of this tribe of sphecoid wasps. This in itself leads to considerations of our own species in light of their evidences. In 1937 deBeaumont presented a revision of the palearctic species. His efforts are congruent with Malloch's and his paper is deserving of glory equal to that he affords the

American author. A British worker, Spooner, in 1948 published an outstanding paper on the British Isles species of psenine wasps. The greatest import of this paper lies with the voluminous data on the biologies of the British Isles species which substantiated the currently accepted classification of higher categories based entirely on structural attributes.

A further contemporary North American work, as it pertains to generic classification, was presented by Krombein in 1951. He considered the North American Psenini as composed of four genera, two of which were further divided into two subgenera. His groupings were as follows: Diodontus Curtis; Psen (Psen) Latreille, and Psen (Pseneo) Malloch; Mimesa (Mimesa) Shuckard, Mimesa (Mimumesa) Malloch; Pluto Pate. The last generic name had been proposed by Pate in 1937 as a new name for Malloch's genus Psenia which was found to be preoccupied. The most recent addition to psenine classification was again proposed by Krombein in 1959 when he employed the generic name of Ammopsen for a new form discovered in the southwestern United States.

PROCEDURE

The taxonomic portion of this study is based on an examination of approximately 5,000 specimens and all but five holotypes of the nearctic species under critical review. Species of Pluto, Psen and Pseneo are considered only in

annotated style for previous treatments (Malloch 1933; Krombein 1959) of those three taxa appear adequate and little new information on them is available.

Redescriptions of species have been standardized. Holotypes (and allotypes), paratypes or topotypes in descending order of availability were selected for redescription with statements on variation within the species incorporated into the redescription or appended in a diagnosis following descriptions of new species. Whenever possible both sexes were described.

Additionally, it was felt that in order to obtain parallel descriptions of genera which could be directly compared with one another, it was necessary to briefly redescribe all North American Psenini genera. This I have done with the genus Ammopsen, however, I have presented a more detailed description since this genus has not been included previously in any treatment of the tribe.

All measurements were made with the aid of a micrometer disc and all figures given are average values from a series unless otherwise indicated. Ratios expressed in descriptions are also based on micrometer measurements but are not meant to express definitive values.

Illustrations, used to supplement text discussion or keys, were prepared through use of an ocular grid. Only in the case of genitalial illustrations were drawings prepared to a

consistent scale. Before examining genitalia of most species and illustrating those of the Mimumesa species, reproductive structures were removed from specimens, cleared in creosote and mounted in Canada balsam.

Specific distributional information based on present and previous studies has been gathered and is included in the form of statements delimiting the range of each species under study. Additionally, type locality and type location are recorded for each species in which types are known to exist.

Regrettably, biological information on North American Psenini is at best fragmentary. Therefore, all available biological data for each species is recorded, having been obtained from ecological notes attached to preserved material or from literature records even while cognizant of the questionable determination of species referred to in earlier publications.

Finally I have included in species treatments two terminating sections entitled "Diagnosis" and "Discussion" -- the former concerned with statements relative to distinctive features of the taxon and variations I have found to exist within the species, and the latter dealing with synonymical and nomenclatorial considerations of the species and other taxonomic evaluations deemed pertinent.

BIOLOGY

As previously stated, there is only meager information available concerning the biologies of psenine wasps of North America. Sphecoid specialists still await publication of the first detailed biological study on an American species within the tribe. Not only is this gap in our knowledge regrettable for its own sake, but this void constitutes an unfortunate situation whereby biological characters are unavailable for use in the classification of North American Psenini. While admittedly selection of behavioral patterns toward reproductive isolation does not follow a predetermined mathematical time-model, in general relationships of behavioral patterns between taxa can materially contribute in interpreting or tracing phylogenetic relationships.

Spooner (1948), published the results of an excellent study on the British Isles species and presented valuable biological data which substantiates the presently recognized super-specific groupings based largely on structural characters. As Krombein (1951) states in reference to Spooner's work, "Thus, in Europe, Psen (Psen) uses larger Auchenorrhyncha (Cercopidae, Membracidae and Cicadellidae) and nests in ready-made cavities in wood or sandstone: Mimesa excavates burrows in the soil, and stores smaller Auchenorrhyncha (Cicadellidae), which are carried ventrally with the middle

legs; Mimumesa also uses smaller Auchenorrhyncha (Delphacidae, Cicadellidae), but carries the prey in the mandibles to nests in cavities in wood and stems; and Psenulus (recte Diodontus) preys on Sternorrhyncha (Aphidae, Psyllidae), which are carried ventrally by the middle legs to ready-made cavities in wood or plant stems." Fragmentary biological information on nearctic species indicate a similar correlation which is discussed in the body of the text under each appropriate taxon.

ANATOMICAL FEATURES

The anatomical nomenclature used in this paper is basically that previously employed by Malloch (1933), Krombein (1950) and others, but includes some terms newly introduced by the present writer.

Size and body form are of limited use since most nearctic species groups maintain a relatively constant appearance. Thus, while members of Ammopsen are much smaller than those of other genera, while Pluto spp. tend to be generally more elongate than most except for some Mimesa and Diodontus, and while Mimumesa and Psen are more robust, these characteristics are seldom clear-cut.

Head. Terminology employed for various areas of the head is included in the illustration (Fig. 1D). For the frontal region between the fronto-clypeal suture and the antennal

orbs, the term lower frons is used. The upper frons is designated as that area lying between the antennal orbs and the median ocellus and bounded laterally by the ocular sulci. The area contained by the ocellar triangle is termed the ocellar area. The "temple" a term used by some authors, is vague and has been discarded for the more appropriate "upper gena" -- an area bounded dorsally by the vertex, anteriorly by the ocular sulcus and posteriorly by the occipital carina. The portion of this same sclerite below the mid-lateral line is termed the lower gena. A careful examination of the punctation on these areas is essential since punctation frequently varies on these same areas between members of different species.

Facial ornamentation is a feature which has considerable value at the generic and specific levels of classification. The presence and gross appearance of a median longitudinal facial carina, which achieves its greatest development in Diodontus (Fig. 2), is a reliable character used by this and earlier workers. This carina is also present but not highly elevated in species of Psen, Pseneo, Mimumesa and Pluto, but is reduced to a simple tubercle between the antennal orbs in Mimesa and Ammopsen. The presence and shape of transverse facial carinae (Fig. 2) are also useful in a more restricted sense in distinguishing species within some genera.

The clypeus is a head structure which frequently deserves

special attention. Some species, particularly in Mimesa, have the clypeus armed with a subapical tumidity which assumes many different shapes. The structure of the apical margin of the clypeus is one additional feature which can be used to advantage in determining several species and genera. An extreme condition is attained in Pseneo where the distinctly thickened and denticulate apex distinguishes this taxon from all other Psenini genera. At the species level, in several genera, truncate vs. dentate conditions of the clypeal apices are frequently useful diagnostic features.

The postero-ventral surface of the head yields characters which are also of diagnostic value, especially in the relation of the occipital carina to the hypostomal carina (Fig. 1 A,B). This character is of a more profound nature than heretofore realized. Thus in Pluto the occipital carina is widely separated from the hypostomal carina; in Mimesa, Mimumesa, Pseneo and Psen the occipital carina meets or nearly meets the hypostomal carina some distance before the median ventral line; and in Ammopsen the occipital carina is restricted to the dorsal regions and becomes evanescent laterally. Additionally, whether coalescence of the occipital carina with the hypostomal carina or the obsolescence of the occipital carina a short distance before juncture with the hypostomal carina occurs is a feature frequently distinct between species within Mimesa and Mimumesa (Fig. 1 B,C).

The antennae have valuable diagnostic usage in relation to sensory structures which are evident medially on the ventro-lateral areas of the flagellar segments in the males of most species. The position, shape and numbers of these sensory areas which are known as antennal tyloides, frequently differ between species.

Thorax. The classical terms are generally used in this paper in reference to the thorax (Fig. 1E,F). Thus, I differ from Van Lith (1959) and continue use of the term postscutellum in preference to metanotum. As seen in Fig. 1F, I follow Snodgrass (1935) in terminology of sulci on the mesoscutum. The terms prepectus and prepectal carinae are used in contrast to Van Lith who considers these as the epicnemial and epicnemial carinae respectively. While that author believes the shape of the prepectus to be of considerable diagnostic value at the species level with the Indo-Australian Psenini and deBeaumont (1937) makes some use of this character in discussing the European material, I have not found it to be of significant value in nearctic forms. However, the form of both the acetabular carina (of Richards, 1956) and the prepectal carina have value at the generic level of classification in the nearctic psenines.

Most authorities agree on the importance of the structure and ornamentation of the propodeum as useful taxonomic characters. This paper departs from earlier studies in

respect to the naming of various propodeal areas (Fig. 3). Thus, the term enclosure used herein is restricted to the impressed medial area, while the area anterior to this enclosure is termed the dorsal area and the lateral concentric areas are called the lateral spheres. The ornamentation of the dorsal area and lateral spheres are frequently important at the species level.

Abdomen. Morphologically, the propodeum should be considered as the first abdominal segment. However, I have followed the usage of most Hymenopterists and accepted the petiole as representing the first abdominal sternite with the first abdominal tergite forming a posterior, cap-like structure, distinct from the petiole per se (Fig. 3). The remainder of the abdomen needs little clarification except for the pygidium and terminalia. In *Psenini* females, there commonly occurs a conspicuous pygidium delimited by a carina along the posterior and lateral margins. This structure is seldom evident in the males. The ornamentation of the female pygidium, particularly with reference to the size, density and distribution of punctations and the character of pubescence, is frequently of taxonomic value. Additionally, the ratio of pygidial width to length is of importance especially for species of the genus *Mimesa*. The genitalia of the males (Figs. 5-8) have been evaluated during the present study. Some early authors confused the sexes and erroneously c

considered the spur-like projection of the eighth abdominal sternite of the male to represent occasionally the female "stinger" or more commonly the male aedeagus. Actually, the male aedeagus is a paired structure, the form of which has limited use in species discrimination. In the genus Mimumesa, however, the paired parameres (lateral lobes) exhibit variations of a distinctive nature.

Wings. Wing venation and cells have been named according to a modified Comstock-Needham system (Fig. 4). While early workers assigned considerable taxonomic importance to wing venational patterns at both generic and species levels, these patterns today are generally considered to be of little value. One exception to this involves the hind wing where the origin of the cubital vein with respect to the transverse cubito-anal vein (Fig. 4) allows separation of the Diodonti and Pseni groups. Distinctive difference in wing venation of this nature assumes considerable phylogenetic importance when one assumes these differences to be basic and not adaptive.

PHYLOGENY

The taxon considered here is the Psenini which, along with the related tribe Pemphredonini, comprises the subfamily Pemphredoninae of the family Sphecidae. The author accepts but does not dogmatically hold to the taxonomic level at which these groups should be considered. Differences of opinion

exist, not with the relationships, but to whether Psenini and Pemphredoninae are deserving of tribal, subfamily or family rank. Such differences of opinion are inseparably linked to the level at which the sphecoid wasps are considered -- here treated as a super family.

While problems involving phylogenetic relationships remain, there is little doubt that the Psenini are more closely related to the Pemphredonini than to any other group of Sphecoid wasps. Many workers have indicated or pointed to the similarity of external features between adults of these two tribes (Latreille 1796, Ashmead 1899, Rohwer 1910, Malloch 1933, and deBeaumont 1937). Recently, Evans (1959) has found important similarities in structure of the larval forms of the two groups. It is additionally recognized that the known biologies of members of Pemphredonini and Psenini are markedly similar.

The tribe Psenini is represented in the nearctic region by seven genera, Diodontus Curtis, Psen Latreille, Pseneo Malloch, Mimesa Shuckard, Mimumesa Malloch, Pluto Pate and Ammopsen Krombein. It is with these genera alone that I confine my discussion on phylogenetic relationships, since representatives of the Hawaiian genera, Caenopsen Cameron, Deinomimesa Perkins, and Nesomimesa Perkins were not available for study.

In the absence of paleontological records and because of

a paucity of ecological evidence, comparative anatomy remains the most important basis for an interpretation of psenine phylogeny. The author's interpretation of the phylogenetic relationships of the nearctic genera are shown in Fig. 9.

It is apparent that fundamental differences in wing venation and facial carina in the adults and in the appearance of the integument, apical form of the spinnerets and shape of head and mandibles of the larvae set the genus Diodontus apart from other genera. That Diodontus is, in fact, phylogenetically distinct from Psen is further supported through comparisons of European and Asian material.

Pluto, whose origin is probably nearctic and whose known distribution is restricted to the western hemisphere, appears to occupy a position intermediate between Diodontus and Psen s.l. Thus, while Pluto shares with Diodontus fundamental wing venational features such as the second and third submarginal cells of the forewing each receiving a recurrent vein and cubitus of hind wing arising distad of the cubito-anal cross vein, adult features, such as the ornamentation of the facial area, and various larval characteristics place it nearer Psen. Additionally, however, the complete occipital carina, shortness of the third submarginal cell, dentate condition of the labrum, dorso-ventrally flattened hypopygidial spine in the male and bristles on the mid and hind coxae in the females are features unique to this genus. These latter features readily

attest to the early separation of Pluto from Diodontus on a monophyletic line. Hence, while I believe both genera have a common ancestry apart from other genera of the tribe and collectively belong to the Diodonti group, these two genera have become widely separated.

It has been previously proposed (Malloch 1933, deBeaumont 1937, Spooner 1948, Van Lith 1959 and others) that there are close ties between Mimesa and Mimumesa which are reflected in the historical placement of these two taxa in the same genus. It should be pointed out, however, that Spooner appears to do so with some reservation. He states, "Some well-marked differences exist between this group (Mimumesa) and the foregoing Mimesa" Van Lith carries this further in stating, "The differences between Mimesa and Mimumesa are more striking than those between Mimumesa and Psen s. str." I agree with Spooner and Van Lith to the greater extent that Mimesa and Mimumesa should no longer be considered as two aggregates of the same genus. To continue to recognize these as being so closely related reflects a phylogenetic relationship not supported by anatomical, biological or geographic evidence. The possession of a complete longitudinal facial carina and the well-developed episternauli are of sufficient import to place Mimumesa phylogenetically closer to Psen and Pseneo than to Mimesa. The lack of the aforementioned characters in members of Mimesa attest to an early divergence of this taxon from the

Pseneo phyletic line. Mimemesa therefore, is considered to have separated from the Pseneo-Pseneo line at a later date than Mimesa.

Both Pseneo and Pseneo have much in common anatomically. Features such as the evenly rounded petiole, which lacks a longitudinal row of dorso-lateral hairs, longitudinal frontal carina on the frons, transverse facial carinae and many other features attest to the close relationship of these two genera. So many features are common and exclusive to these two taxa as to leave little doubt that Pseneo and Pseneo share a closer relationship to one another than to any other psenine genus. Additionally, this relationship validates the contention that Pseneo and Pseneo have a more recent common ancestral line than do any other North American genera within the tribe.

Finally, the origin of Ammopseneo is still obscure. Tribally unique features indicate that this taxon's origin was paleolytic. Zoogeographic considerations stand in contradiction to this opinion in that distribution and speciation within Ammopseneo support the theory of recent evolution. Further studies are needed before an understanding of the phylogeny of this genus can be gained. Presently, anatomical features such as the shortened form of the petiole, the presence of a simple tubercle between the antennal bases, lack of a longitudinal median carina on the upper frons, lack of transverse facial carinae and the incomplete character of the

mesoepisternal suture combine to place Ammopsen closer phylogenetically to Mimesa than any other genus.

SYSTEMATICS

The Psenini are slender forms with a distinctly petiolate abdomen. They differ from the Pemphredonini in having three submarginal cells in the forewing, the petiole formed by the anterior portion of the first abdominal sternite and with the male eighth sternite narrowed, curved and produced caudally to a sharp point.

Within the tribe Psenini there are two supergeneric groups, Diodonti and Pseni. The Diodonti group, containing the genera Diodontus and Pluto, is characterized by the cubitus in the metathoracic wing arising distad of the cubito-anal cross vein (Fig. 4C). The Pseni group, containing the genera Psen, Pseneo, Mimesa, Mimumesa and Ammopsen, is characterized by the cubitus in the metathoracic wing arising proximad of the cubito-anal cross vein (Fig. 4B).

KEY TO THE GENERA OF NEARCTIC PSENINI

1. Metathoracic wing with cubitus arising distad of the cubito-anal cross vein (Fig. 4C). Diodonti group..... 2
- Metathoracic wing with cubitus arising proximad of the cubito-anal cross vein (Fig. 4B). Pseni group..... 3
2. Occipital carina meeting hypostomal carina; frons with a highly elevated, median, longitudinal carina often expanded between the antennal bases; pronotum black, lateral lobes never whitish in color..... Diodontus Curtis
- Occipital carina seldom meeting hypostomal carina, usually considerably distant from it on the mid-ventral line; frons with a thin, feebly elevated, median, longitudinal carina; pronotum with lateral lobes usually whitish in color..... Pluto Pate
3. Median dorsal faces of propodeum with at least some evidence of striations or rugose-reticulations; pronotum with a subapical, transverse carina..... 4
- Median dorsal faces of propodeum granular, never striate or rugose-reticulate; pronotum lacking a subapical, transverse carina..... Ammopsen Krombein
4. Meso-anepisternum distinctly sculptured and generally dull, striate or striato-punctate..... 5
- Meso-anepisternum generally smooth and shining, never striate or striato-punctate, at most with only a few

scattered punctures..... 6

5. Clypeus thickened apically and bearing three thickened teeth..... Pseneo Malloch

-- Clypeus not thickened apically, rounded, emarginate, or notched but lacking distinctly thickened teeth.....
..... Mimesa Shuckard

6. Petiole sulcate and carinate above, with a series of piliferous punctures near the latero-dorsal edges, hairs quite conspicuous..... Mimumesa Malloch

-- Petiole neither carinate nor sulcate above, although a weak carina may be evident at the latero-dorsal edges, never with a series of piliferous punctures along the latero-dorsal edges..... Psen Latreille

Group Diodonti

Genus *Diodontus* Curtis

- Diodontus* Curtis 1834:496; Malloch 1933:3
Psenulus Kohl 1896:293; deBeaumont 1937:76; Pate 1937:23
(synonymy)
Neofoxia Viereck 1901:338; Malloch 1933:3 (synonymy)
Diodontus (*Diodontus*), Krombein 1950:35; 1951:958

Head. Front with a well-developed longitudinal median carina, highly elevated between bases of antennae, sulcate except in *alienus*, frequently with transverse facial carinae extending laterally from base of longitudinal median carina; clypeus with apex not noticeably thickened, bearing two blunt teeth near middle, separated by a shallow emargination; occipital carina complete dorsally and laterally, meeting hypostomal carina on venter; antennae of female clavate, nearly filiform in male.

Thorax. Pronotum with well-developed, subapical, transverse carina becoming more cristate laterally, lateral lobes dark; prepectus triangular, well-defined; episternal suture of mesopleuron incomplete, effecting only a partial separation of the mesoepisternum; mesoepisternum with upper portion similar in sculpture to lower portion; propodeum variably ornamented, striate to rugose-reticulate, lightly striate in some extra-limital forms of *frontalis*; forewing with first recurrent vein joining second submarginal cell, second recurrent

vein received by the third submarginal cell or interstitial with the second transverse cubital vein, second submarginal cell greatly narrowed above; hind wing with juncture of M and Cu veins distad of cu-a cross vein; hind femur with inner surface sparsely covered with fine hairs, distinctly shorter than those on other surfaces.

Abdomen. Petiole variable, with or without a complete dorsal sulcus or dorso-lateral carinae, without a well-developed series of hairs laterally, and usually not greater in length than hind femur; pygidium of female present or absent, when present, narrow, delimited posteriorly and laterally by a carina.

DISCUSSION. Diodontus belongs in the Diodonti group along with the genus Pluto. The genus Diodontus, however, is readily distinguished from Pluto by the possession on the frons of a highly elevated longitudinal median carina, and by the coalescence of the occipital and hypostomal carinae on the venter of the head. Superficially, Diodontus can be separated from Pluto by the more robust form, blacker and shinier color, and the uniform darkness of the lateral lobes of the pronotum.

The synonymy as indicated has already been discussed in detail in the historical section of the work. The North American species considered here are all referable to the

subgenus Diodontus. Apparently the other subgenus, Eopsenulus Gussakovskij, is confined to Asia (Gussakovskij, 1933).

GENEROTYPES. Diodontus -- Psen pallipes Panzer (orig. des.).
Psenulus -- Psen fuscipennis Dahlbom. Neofoxia -- Psen atrata Panzer (orig. des.).

DISTRIBUTION. Members of the genus appear to be southern in nearctic distribution. Northern-most collection records are from New Hampshire and Washington. The genus is not known from Canada. Four species are currently recognized from the continental United States.

BIOLOGY. All members of the genus appear to nest in hollow-stemmed or pithy-stemmed plants or in previously formed burrows in wood. None is known to nest in the ground. In the west, pithy-stemmed plants, such as Sambucus and Sumac appear to be the more highly favored nesting sites. Little is known of the prey of American forms but conjecture, based on Spooner's study of English species, leads me to believe that the prey is typically, perhaps entirely, Aphididae.

