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Pipunculidae Research by Elmo Hardy: Another Founding Event on the Hawaiian Islands

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Abstract

For 50 years, D. Elmo Hardy studied the dipteran family Pipunculidae. During that period he produced numerous articles, covering all taxonomic groups within the family and nearly all zoogeographical regions. His contribution to the knowledge of the group has been tremendous and pivotal for all future work. This article gives an overview of the taxonomic knowledge prior to Hardy's work, his contribution from 1939 until 1989, and the impact of his study on the contemporary research of the last decades.

Introduction

Pipunculidae or big-headed flies are distinctive, but inconspicuous, relatives of the Syrphidae (hover flies or flower flies). Over 1,300 species have been described worldwide and it is estimated that well over 2,000 species exist. They can be differentiated from syrphids by the large compound eyes that occupy most of their hemispherical head, the distinctive wing venation (no *vena spuria*, cell r4+5), the chitinized postspiracular plate found in the larvae, and their unique life history. During their larval stage they are known as endoparasitoids of several families of Auchenorrhyncha (Homoptera). It is because of this parasitoid lifestyle that Elmo Hardy started studying the representatives of this family. His first endeavors focused on Nearctic fauna but later covered material from all zoogeographical regions. For 50 years (1939 to 1989) Hardy studied the group, although he published most of his articles on this family between 1939 and 1972. Later, his interests turned completely towards other dipteran groups although he did produce some occasional papers after 1972. His main contribution was on descriptive taxonomy (alpha taxonomy), and cataloging particular faunas.

Early Work on Pipunculidae

The first pipunculid species were described at the turn of the eighteenth century (Bosc, 1792; Latreille, 1802; Meigen, 1803). Throughout the early nineteenth century, descriptions of new species were sparse and occasional (Fig. 1) and were mainly based on Palaearctic material. Descriptions of "exotic" (i.e., non European) Pipunculidae were rare (e.g., Wiedemann, 1830) and usually formed part of general works dealing with several dipteran families. By the end of 1897 only 85 species were described, with 74% originating from Europe. Only one paper focusing solely on this family was published before 1897 (Walker, 1834).

At the turn of the 19th Century, some more detailed studies appeared, in particular by Theodor Becker, a German entomologist. In his two major papers (Becker, 1897, 1900) he described 38 partly non-European species and produced the first major classification, splitting the genus *Pipunculus* into different species groups. In the Nearctic region, E.T. Cresson published a review of the North American species, describing several new species (Cresson, 1911). His monograph was the result of a two-year study and included notes and comments made by Nathan Banks. Material from other geo-

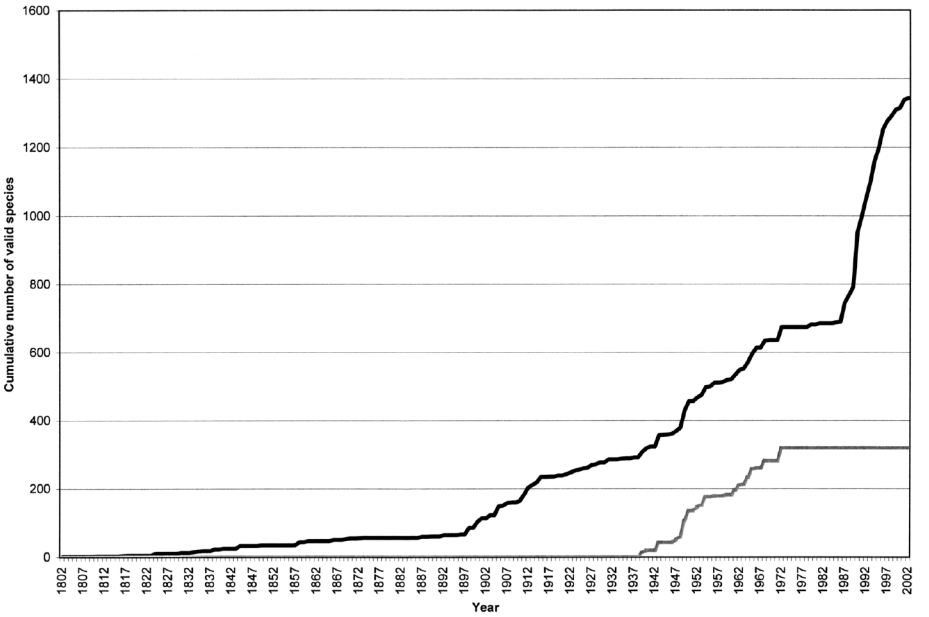

Figure 1. Cumulative curve of Pipunculidae species described over time (top black line: all authors; bottom gray line: species described by D.E. Hardy).

graphical regions, like Asia, soon became available to researchers and resulted in publications of the pipunculid faunas of those areas. Noteworthy in this respect is Kertész's work (1903, 1907, 1912).

During the 1920s and early 1930s a lull appeared in descriptive work on Pipunculidae (Fig. 1). The major researchers active in that period were J. Collin (England) and C.H. Curran (North America). Collin produced revisions of the British representatives of taxonomic entities within the family, in particular the genus *Pipunculus*, like the *sylvatica* group (now the genus *Tomosvaryella*) (Collin, 1920) and the *rufipes* group (now the genus *Dorylomorpha*) (Collin, 1937). Curran described several American and non-American species (Curran, 1927, 1928a, 1928b, 1929, 1934a, 1934b, Curran *et al*., 1936). Nevertheless, the number of described species remained low. By 1938, 292 pipunculid species were described worldwide (Table 1). Palaearctic and Nearctic species comprised 125 (43%) of these. Of the genera recognized today, most representatives were from the genera *Eudorylas* and *Tomosvaryella* (Table 2).

Contribution by D. Elmo Hardy

Hardy started working on Pipunculidae in the late 1930s. His interest in this group started as a research fellow at the Utah Agricultural Experiment Station in Logan, Utah where he worked under George Franklin Knowlton. One of his interests was the sugar-beet leafhopper [*Eutettix tenellus* (Baker)]. Parasitoids of this pest species were studied in order to find a biological control agent that could regulate the populations (Hardy & Knowlton, 1939a). Pipunculid species were found to be of considerable importance in this respect (Knowlton, 1937). During their investigations, Hardy and Knowlton realized that several species, especially in the western states of the USA were unknown to science. The first articles on Pipunculidae by Hardy dealt with these parasitoids and two were written with Knowlton as co-author (Hardy, 1939; Hardy & Knowlton, 1939a, b). Hardy's further exploration of Nearctic Pipunculidae promoted the importance of male genitalic characters for an unam-

Table 1. Comparison of faunal knowledge over time by region (number of valid species)

Region	1938	1972	2002	Hardy only	% by Hardy
Exclusively Nearctic	36	85	120	46	38.3
Exclusively Neotropical	33	103	239	70	29.3
New World	9	11	14	1	7.1
Exclusively Palaearctic	88	142	495	4	0.8
Holarctic	4	8	9	2	22.2
New World/Holarctic	2	3	3	1	33.3
Palaearctic/Oriental/Australasian/ Oceanian	4	6	6	1	16.7
Palaearctic/Oriental	17	22	22	3	13.6
Exclusively Afrotropical	17	125	149	105	70.5
Exclusively Oriental	34	81	148	47	31.8
Oriental/Australasian/Oceanian	5	9	9	4	44.4
Exclusively Australasian/Oceanian	35	71	119	36	30.3
Cosmopolitan	1	1	1	0	0
Holarctic/Oriental	3	3	3	0	0
Palaearctic/Afrotropical	1	1	2	0	0
Palaearctic/Australasian/Oceanian	0	0	1	0	0
Palaearctic/Afrotropical/Oriental	1	1	1	0	0
Palaearctic/ Afrotropical/Oriental/ Australasian/Oceanian	1	1	1	0	0
Note: No data available in database for region: (nomen dubium: *Tomosvaryella unguiculatus* Loew 1860).	1	1	1	0	0
Totals:	**292**	**674**	**1343**	**320**	**23.8**

biguous identification of pipunculid species. This was probably partly due to his contact with the Hungarian entomologist Martin Aczél who, at that time, was one of the main European researchers working on this family (Hardy, 1940). Although Aczél did some descriptive work, his main interests were on the phylogeny of the group and reviewing previous research (on elements such as host-parasitoid records, higher classification, fossil record, and phylogenetic reconstruction). Aczél left Hungary for Argentina after the World War II for political reasons. His subsequent work on Pipunculidae became limited and stopped after 1948. Hardy was in contact with Aczél, but apparently did not collaborate or produce joint papers with him.

Elmo Hardy had by the late 1930s moved to the Department of Entomology at the University of Kansas and had embarked on a monographic study of the Nearctic representatives of the Pipunculidae. This revision formed part of his thesis in partial fulfillment of the requirements of a Ph.D. degree and was published in the *University of Kansas Science Bulletin* (Hardy, 1943). The monograph is 231 pages, and provides an introduction to the group with elements on their taxonomy, morphology, biology, and collecting methodology. It continues with a brief description of all world genera, and a taxonomic revision of all Nearctic species, comprising 117 species, subspecies and varieties (including 27 new ones). A large part of the study was based upon recently collected material, with a strong emphasis on the western U.S.; partly by the Beamer expeditions (Hungerford, 1958) and partly by Hardy himself. Together, Beamer and Hardy had the most productive collecting of southwestern pipunculids ever documented during their 1940 trip to Arizona. For example, they collected dozens of pipunculids including over 60 specimens of 7 species of *Pipunculus* on 4 July 1940 in the Chiricahua Mountains (Skevington & Marshall, 1998). Although Hardy mentioned the paucity of information on host relationships, he apparently never reared pipunculids; however, he did

Table 2. Comparison of faunal knowledge over time by genus (number of valid species)

Genus	1938	1972	2002	Hardy only	% by Hardy
Allomethus	0	3	5	2	40.0
Amazunculus	0	1	3	1	33.3
Basileunculus	2	2	3	0	0.0
Cephalops	35	112	179	72	40.2
Cephalosphaera	10	25	52	14	26.9
Charalus	7	13	41	1	2.4
Claraeola	5	11	20	6	30.0
Claraeosphaera	0	0	1	0	0.0
Clistoabdominalis	10	11	34	1	2.9
Collinias	3	4	5	1	20.0
Dasydorylas	7	15	16	7	43.8
Dorylomorpha	18	30	83	9	10.8
Elmohardyia	5	17	51	12	23.5
Eudorylas	99	237	416	121	29.1
Jassidophaga	7	10	24	1	4.2
Microcephalops	6	23	31	16	51.6
Nephrocerus	5	5	14	0	0.0
Pipunculus	16	23	71	4	5.6
Protonephrocerus	1	1	1	0	0.0
Tomosvaryella	47	110	270	51	18.9
Verrallia	2	4	6	0	0.0
Incertae Sedis	7	17	17	1	5.9
Totals	**292**	**674**	**1343**	**320**	**23.8**

make numerous references to possible associations of leafhoppers found in the vicinity of the collecting sites.

After his period at the University of Kansas and as an officer and medical entomologist during World War II, he was appointed Assistant State Entomologist at Ames, Iowa and, by the end of the 1940s, moved to the University of Hawaii where he would stay until retirement. His dipterological interests would widen but throughout the following 3 decades (until 1972) Hardy would continue publishing on Pipunculidae. The first papers after the 1943 monograph dealt with nomenclatorial notes (Hardy, 1946) and further additions or elaborations on his findings regarding Nearctic Pipunculidae (Hardy, 1947, 1948a). He started dealing with the faunas of other zoogeographical regions as well. First, he studied exotic material in the Museum of Comparative Zoology, the American Museum of Natural History, the U.S. National Museum, Ohio State University, and the California Academy of Sciences (Hardy, 1948b, 1948c, 1949a). Much of this material was from the Neotropics and it seems to have been Hardy's plan to produce a monograph of the Neotropical Pipunculidae, probably comparable to his Nearctic work (Hardy, 1948c: 1; see also Hardy 1953a: 299). Although no such monograph was ever published, he did produce several articles on the Neotropical Pipunculidae over the next 17 years (Hardy, 1950b, 1954a,b, 1962a, 1963, 1965a,b). These articles dealt with collections that were put at Hardy's disposal, often of particular countries. Included was Aczél's collection made in Argentina, which could not be studied by Aczél himself due to his untimely death (Hardy, 1965a).

In 1949, he also produced a monograph on the Afrotropical pipunculid fauna (Hardy, 1949c), including the south Mediterranean region. However, the work was rendered obsolete soon after publication because of much new additional material that could only be studied after completion of the monograph. The new material was largely from the Democratic Republic of Congo. Several general expeditions were organized by Belgian researchers to the different National Parks that were newly

erected in the then Belgian Congo and material of these expeditions was sorted and sent to specialists worldwide. Hardy published a number of papers, often dealing with both Pipunculidae and Bibionidae of the several different parks (Hardy, 1949b, 1950a, 1952a, 1959b, 1961) as well as other material from the former Belgian colonies present in the Royal Museum for Central Africa, Tervuren and the Royal Belgian Institute for Natural Sciences (Belgium) (Hardy, 1952b, 1952c, 1955). In addition, he studied collections made in South Africa (Hardy, 1959a, 1962a), Madagascar (Hardy, 1962b), Mauritius (Hardy, 1956a), and Tanzania (Hardy, 1960). All of these resulted in a thorough contribution to the knowledge of the pipunculid fauna of the African continent.

His move to Hawai'i also initiated the study of the Hawaiian fauna. As with many other elements of the Hawaiian fauna, the pipunculid diversity is the result of a single founder event with successive dispersal throughout the archipelago and high speciation rate (De Meyer, 1996). Some knowledge was available on the Hawaiian Pipunculidae prior to Hardy's study. Most of this was gathered by R.C.L. Perkins (1905, 1906), who worked for the Experiment Station of the Hawaiian Sugar Planters' Association, in connection with work on the parasites of homopteran pests. The first addition to Perkins' Hawaiian work was published by Hardy (1953b). Later, he revised his work on Hawaiian pipunculids (Hardy, 1964b) as part of the ongoing *Insects of Hawaii* series. Most of the new species described by him were based on material that he collected personally on the different islands of the archipelago. Probably in conjunction with this work, Hardy also studied some other collections housed in the Bishop Museum, Honolulu and published some papers on the fauna of the Micronesian islands (Hardy, 1956b) and Australian type material described by Perkins (Hardy, 1964a).

Studies of the Oriental fauna started somewhat later than for other regions. Again, parts of this research was based on collections put at the disposal of Hardy, like the material of the Danish Noona Dan Expedition to the southern Philippines and Bismarck Islands (Hardy, 1968), the Swedish Expedition to Burma (Hardy, 1972a), and the British Museum expedition to East Nepal (Hardy, 1966b). However, part of this research also based on material collected by Hardy himself in the Philippines. A paper reviewing data on pipunculids parasitic on rice leafhoppers in the Orient (Hardy, 1971) summarized the impact of big-headed flies on this economically important group of pests. A review of the Oriental fauna published in 1972 (Hardy, 1972b) largely marked the end of Hardy's active pipunculid research, although he did publish some occasional papers on the family like the chapter in the *Manual of Nearctic Diptera* (Hardy, 1987).

In addition to his taxonomic papers, Hardy also produced catalogs for all zoogeographical regions, except the Palaearctic region (Hardy, 1965c, 1966a, 1975, 1980, 1989).

Hardy was involved in 2 different nomenclatural disputes that were submitted to the International Commission on Zoological Nomenclature (Hardy, 1951a,b, 1958). The first dispute revolved around the use of Meigen 1800 names that had been out of circulation for over 100 years before being discovered and pressed into service. This dispute involved many genera in several fly families and created a pronounced polarity within the pipunculid community at the time. Hardy, Aczél, and Stone all advocated using the Meigen name *Dorilas* and indicated to the Commission that they and most other contemporary pipunculid workers such as Becker, Enderlein, Kertész, and Sack had been using this system for about 40 years (Aczél, 1951; Hardy, 1951a,b; Stone, 1951). However, there were several letters to the Commission and other published statements supporting the suppression of *Dorilas* Meigen, 1800 and validation of the name *Pipunculus* Latreille, 1802 (Collin, 1945; Oldroyd, 1951; Rapp, 1951; Smart, 1951). Despite the fact that the most productive pipunculid workers of the time supported the use of the name *Dorilas* over *Pipunculus*, the Commission made the decision based on usage in several families and ruled to suppress Meigen's 1800 publication (International Commission on Zoological Nomenclature, 1963).

The only other nomenclatural ruling that Hardy was involved in was a successful appeal to suppress the names *Prothechus* and *Alloneura* by Rondani and to place the names *Verrallia*, *Cephalosphaera* and *Tomosvaryella* on the Official List of Generic Names in Zoology (Hardy, 1958; International Commission on Zoological Nomenclature, 1961).

Hardy has had 1 subtribe, 1 genus, and 4 species of big-headed flies named in his honor [*Elmohardyina* Kuznetsov, *Elmohardyia* Rafael, *Cephalops hardyi* De Meyer, *Dorylomorpha hardyi* Albrecht, *Eudorylas hardyi* (Yang & Xu), and *Pipunculus hardyi* Rafael].

Hardy's Impact on Pipunculidae Taxonomy

In total, Elmo Hardy published 51 articles dealing with Pipunculidae between 1939 and 1989. Fig. 1 shows the accumulative species description curve for Pipunculidae in general and by Hardy. From this, it is clear that Hardy's impact was substantial from 1939 onwards. By 1972 he had doubled the number of described (and currently valid) species: from 292 known in 1938, he described an additional 320 (347 including synonyms ands subspecies).

Table 1 summarizes the number of species described prior to Hardy's work and his contribution, divided along zoogeographical regions. Table 2 presents the same data according to taxonomic genera recognized today (valid species only in both tables).

When taken per zoogeographical region (Table 1), his largest impact was on the Afrotropical region. From 17 valid species previously described from that region, he added 105. For the Neotropical fauna he tripled the number of known species during his active period, and for the Nearctic and Oriental faunas he doubled the number. Even when compared with the currently known valid species, Hardy described 70.5% of the Afrotropical fauna, while he accounts for 38.3, 31.8 and 29.3% respectively of the Nearctic, Oriental, and Neotropical faunas. From the Australasian/Oceanian fauna, Hardy described 30.2%, mostly from the Hawaiian Islands. His contribution is thus substantial for most zoogeographical regions, the only exceptions being the Palaearctic fauna with only 0.8% and the Australasian fauna. For the latter he never embarked on a program of study of the Australian fauna, which is poorly understood and apparently very species rich (Skevington, 1999, 2001, 2002). Additionally, articles by Hardy focusing solely on the Palaearctic fauna are few (see for example Hardy, 1967).

When examined along generic lines (currently accepted genera), a large difference in impact is noticed between the genera (Table 2). For the larger genera, his most significant impact is on *Cephalops* and *Eudorylas* with 40.2% and 29.1% respectively of the currently valid species. A lesser contribution was made to *Tomosvaryella* with 18.9%. For the smaller genera, Hardy described approximately half of the known valid species of the genera *Allomethus*, *Dasydorylas,* and *Microcephalops*. On the contrary, he had much less impact for *Dorylomorpha* (10.8%) and *Pipunculus* (5.6%). Also descriptions of *Chalarus*, *Jassidophaga*, and *Nephrocerus* are negligible. These genera have limited diversity outside the Holarctic; hence, he did not have such specimens in the extensive collections of Afrotropical, Neotropical, and Oriental faunas that he studied. In addition, a proportionally large part of the Holarctic species were described from the Palaearctic, leaving only a few new species for Hardy to describe from the Nearctic. The species complexity of some of these genera, such as *Chalarus*, was also only recently realized (Jervis, 1992).

However, his work was largely limited to the collections or geographical areas as discussed above. He never embarked on a systematic revision of any of the generic or suprageneric divisions recognized within the family. Also, type material of older described material was not always consulted or verified, especially for collections that were not readily available. For example, neither Becker's nor Loew's types were consulted during the revision of the Afrotropical fauna (Hardy, 1949c). Nevertheless, the number of species described by Hardy that are now synonymized is relatively low compared to the total number he described. Only 17 out of the 126 synonyms currently recognized are species described by Hardy.

Regarding higher classification, he mainly followed Aczél. Aczél (1940, 1948) published a framework for the family by erecting two main subfamilies: Chalarinae and Pipunculinae. The latter was divided into 2, and at a later stage 3 tribes: Nephrocerini, Protonephrocerini, and Pipunculini. Aczél also indicated which genera belonged to each of these taxa based on a phylogenetic tree he composed partly on *ad hoc* assumptions and partly on the study of the fossil record (Aczél, 1948).

Aczél also erected or discovered supporting evidence for the generic status of the several groups within the genus *Pipunculus*. These groups were first recognized by workers like Becker and accepted by subsequent researchers. Only in the 1940s were most of these groups given generic status by Aczél (1940), Enderlein (1936), and Collin (1945). Hardy followed this principle initially; however, in his later work (Hardy, 1953a) he considered some of these genera to be based on superfluous or too few characters and considered them merely as subgenera or entirely synonymous with *Pipunculus sensu stricto*. This was certainly a problem for Hardy as he again changed the status of some at a later stage. He had similar concerns for the status of *Jassidophaga*.

The evolution of his thoughts about higher classification can be followed through his catalogs of different zoogeographical regions that were published between 1965 and 1989. In his first catalog, covering the Nearctic region (Hardy, 1965c), he treated *Cephalops* as a synonym of *Pipunculus* s.s., *Eudorylas* and *Cephalosphaera* as subgenera of *Pipunculus*, and *Verrallia* and *Jassidophaga* as full genera. All genera of the Pipunculinae were treated within a single tribe, Pipunculini. A year later, in his Neotropical catalog (Hardy, 1966a), Tomosvaryellini was treated as a separate tribe from Pipunculini with *Tomosvaryella*, *Dorylomorpha* and *Allomethus* included in the former. In the Oriental (Hardy, 1975) and subsequent catalogs (Hardy, 1980, 1989), *Cephalops* was treated as a separate subgenus within *Pipunculus* and *Jassidophaga* was treated as a subgenus of *Verrallia*.

Contemporary Research

During Hardy's active period, only a few other researchers took up the study of Pipunculidae. The British workers J.E. Collin (e.g., 1920, 1937) and R.L. Coe (e.g., 1966a, b) worked on the Palaearctic fauna and K. Koizumi (1959, 1960) worked on species occurring in Asian paddy fields. For many years after 1972 this trend continued and there was little interest in taxonomic work on the group.

Taxonomic research accelerated again in the 1980s. Several researchers in different geographical regions initiated either regional faunistic studies or taxonomic revisions of particular groups. Regional revisions for the fauna of India (Kapoor *et al.*, 1987) and Japan (Morakote & Hirashima, 1990a–d; Morakote *et al.*, 1990a, 1990b) were produced. Kuznetzov described many Palaearctic species, predominantly from the former Soviet Republic States (e.g., Kuznetzov, 1990, 1991, 1994), while Rafael and co-workers revised the Neotropical fauna (e.g., Rafael, 1986a, 1986b, 1987a, 1987b, 1988; Ale Rocha & Rafael, 1995). Systematic revisions of several genera such as *Dorylomorpha* (Albrecht, 1990) *Chalarus* (Jervis, 1992), and *Cephalops* (De Meyer, 1989a, 1989b, 1990, 1992a, 1992b) were also produced in that period. Currently, the research continues with Skevington on the genus *Pipunculus* (Skevington & Marshall, 1998) and on the Australian fauna (Skevington, 1999, 2001, 2002), Földvári on Afrotropical Eudorylini, and a number of German workers (von der Dunk, Dempewolf, Kehlmaier). This surge has resulted in a dramatic increase in the number of described species (from 674 in 1972 to 1,343 in 2002; see Fig. 1).

Many of these revisions benefited from Hardy's pioneering work on these groups. His contributions often formed the basis for the work, despite his lack of comprehensive revisions. Early in his research, Hardy recognized the importance of male genitalic structures in the identification of Pipunculidae. He started including illustrations of these structures in his publications from 1943 onwards, although not always in a consistent way (for example, "*in situ*" views or the shape of syntergosternite 8 only). In many cases his descriptions and drawings are sufficient for recognition. Hardy also pointed out the importance of obtaining host records for pipunculid parasitoid species (Hardy, 1943). However, he did not engage in rearing himself but often noted homopteran species that were found in association with pipunculids as an indication of potential hosts. Even now, rearing records are scant and their presence would form an important asset in the study of this group. There is some indication that Pipunculidae tend towards oligophagy, attacking more than one species of host but showing a preference for a particular set of host species (Skevington, 2001). Part of this preference might be along generic lines.

Some of the issues raised by Hardy still form a topic of discussion among current pipunculid

researchers. For example, the validity of species groups given generic rank based on the presence or absence of wing vein M_2 is still a source of discussion. In general, the work of D. Elmo Hardy on the dipteran family Pipunculidae can be considered fundamental and is the primary reference source for researchers today and in the future.

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