

Geographical distribution of the spider wasps (Hymenoptera: Pompilidae) of the world

Географическое распространение дорожных ос (Hymenoptera: Pompilidae) мировой фауны

Valery M. Loktionov
В.М. Локтионов

Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch of the Russian Academy of Sciences, Vladivostok, 690022, Russia. E-mail: pompilidaefer@mail.ru
Федеральный научный центр Биоразнообразия наземной биоты Восточной Азии Дальневосточного отделения Российской академии наук, Владивосток, 690022, Россия.

KEY WORDS: spider wasps, distribution, biogeographic regions, extant genera, Ceropalinae, Ctenocerinae, Notocyphinae, Pepsinae, Pompilinae, world fauna.
КЛЮЧЕВЫЕ СЛОВА: дорожные осы, распространение, рецентные роды, Ceropalinae, Ctenocerinae, Notocyphinae, Pepsinae, Pompilinae, мировая фауна.

ABSTRACT. An analysis of the geographical distribution of spider wasp genera (Hymenoptera, Pompilidae) of the world was carried out. The faunas of the Neotropical and Nearctic regions are the closest; the latter is associated with the fauna of the Palaearctic region. The pompilid faunas of the Palaearctic, Afrotropical and Oriental regions form a single complex. The fauna of the Australasian region is the most isolated, having the maximum similarity with that of the Oriental region. The two largest subfamilies, Pepsinae and Pompilinae, with their joint share among other subfamilies being 78 to 95%, constitute the main bulk of the faunas of all biogeographic regions.

РЕЗЮМЕ. Проведен анализ географического распространения родов дорожных ос (Hymenoptera, Pompilidae) в объеме мировой фауны. Наиболее близкими на уровне родов являются фауны Неотропической и Неварктической областей, в свою очередь последняя связана с фауной Палеарктической области. Фауны помпилид Палеарктической, Афротропической и Ориентальной областей образуют единый комплекс. Фауна Австралийской области является наиболее изолированной, имея наибольшее сходство лишь с фауной Ориентальной области. Основу фауны всех зоогеографических областей составляют подсемейства Pepsinae и Pompilinae с долей в составе областей 78–95%.

Introduction

The family Pompilidae (spider wasps) is distributed in six biogeographic regions of the world: Palaearctic,

Afrotropical, Oriental, Nearctic, Neotropical, and Australasian. Representatives of the family inhabit a wide range of natural and climate zones: from deserts to forests, from coastal lands to mountains, from the tropics to the tundra; but the highest species diversity is in the tropical regions. A common biological feature of the family is that these wasps are solitary, predatory insects that exclusively provide their offspring with spiders, although some groups in the family are kleptoparasites [Loktionov, Lelej, 2014, 2017]. Spider wasps constitute a monophyletic family supported by numerous morphological and behavioral traits [Shimizu, 1994]. The extant fauna of the family comprises approximately 5000 species [Aguiar *et al.*, 2013; Loktionov, Lelej, 2017] from 217 genera (an updated number). Waichert *et al.* [2015] reconstructed a molecular phylogeny of Pompilidae from Bayesian and maximum-likelihood analyses of four nuclear molecular markers, resulting in the five currently recognized subfamilies: Ceropalinae, Ctenocerinae, Notocyphinae, Pepsinae, and Pompilinae. According to their Bayesian divergence-time estimation analysis, the family originated 43.3 million years ago (Ma). Most of the extant subfamilies therefore originated from the late Eocene to the Oligocene, and their current distributions are the product of various dispersal events that occurred over the course of approximately 40 million years. However, most recent data based on the phylogenomic study of Mutillidae conducted using ultraconserved elements, suggest that Pompilidae originated 68–71 Ma [Waldren *et al.*, 2023]. Other researchers estimate this time as 44 Ma [Branstetter *et al.*, 2017], 72 Ma [Peters *et al.*, 2017], and 85 Ma [Wilson *et al.*, 2012]. Up to date,

26 extinct species of spider wasps are known, 19 of them from compression fossils, six from amber, and one from an ichnofossil of unclear age from the Ypresian to Messinian (55.5–5.0 million years) [Rodriguez *et al.*, 2017; Waichert *et al.*, 2019; Loktionov *et al.*, 2023].

In this paper, the distribution of extant spider wasp genera of the world is analyzed for the first time, the composition of the faunas of the biogeographic regions is shown, and similarities between these faunas are revealed.

Material and methods

The paper is based on an extensive reference data on the family as well as examined materials from the following Russian and foreign institutions:

- Biologiezentrum des Oberösterreichischen Landesmuseums, Linz, Austria;
- Federal Scientific Center of East Asia Terrestrial Biodiversity, Vladivostok, Russia;
- Hungarian Natural History Museum, Budapest, Hungary;
- Institute of Systematic Zoology, Krakow, Poland;
- Martin-Luther-Universität Halle-Wittenberg, Halle, Germany;
- Museum für Naturkunde, Berlin, Germany;
- South China Agricultural University, Guangzhou, China;
- Zoological Institute, Saint Petersburg, Russia;

– Zoological Museum of Moscow State University, Moscow, Russia.

A table of the distribution of spider wasp genera in the Palaearctic, Afrotropical, Oriental, Nearctic, Neotropical, and Australasian regions was compiled (Suppl. Table 1). The total 217 genera are arranged alphabetically within the five subfamilies which also are given in alphabetical order: Ceropalinae, Ctenocerinae, Notocyphinae, Pepsinae, and Pompilinae. The source of distribution data for each genus is provided. The distribution of subfamilies by the biogeographic region, with indication of the number of genera for each region, as well as the distribution of endemic genera by the biogeographic region, with indication of the total number of endemic genera by region, expressed in numbers and percentages is shown in Table 1.

Analysis of the similarity of the faunas was carried out using PAST — PALaeontological STatistics program (version 4.03) [Hammer *et al.*, 2006]. As a measure of similarity, the Sørensen–Dice coefficient was used [Pesenko, 1972; Legendre, Legendre, 1983], with bootstrap support in 1000 replications. The similarity matrix obtained on the basis of the distribution of 217 genera (Suppl. Table 1) is presented in Table 2. On its basis, Terentyev’s galaxies were created to reflect the connections of the faunas of spider wasps between the biogeographic regions (Fig. 1). The ordinations of faunas are shown on Figs 2, 3, and the dendrogram of the similarity is on Fig. 4. The composition of faunas of spider wasps in the biogeographic regions at the subfamily level is given in the bar chart (Fig. 5).

Table 1. Distribution of five subfamilies of spider wasps by biogeographic regions with numbers of endemic genera.

Таблица 1. Распространение пяти подсемейств дорожных ос по зоогеографическим областям с числом эндемичных родов.

Subfamily	Total number of genera / number of endemic genera						Total sum
	PAL	AFR	OR	NEA	NEO	AUS	
Ctenocerinae	0/0	18/17	2/1	0/0	0/0	6/6	25/24
Ceropalinae	2/0	2/0	2/0	2/0	2/0	2/0	2/0
Notocyphinae	0/0	0/0	0/0	1/0	1/0	0/0	1/0
Pompilinae	46/18	47/22	26/8	26/4	31/13	13/3	107/68
Pepsinae	22/4	17/7	31/10	19/1	32/12	29/13	82/47
Total sum	70/22	84/46	61/19	48/5	66/25	50/22	
Percentage of endemic genera per region	31%	55%	31%	10%	38%	44%	

Abbreviations. Biogeographic regions: PAL — the Palaearctic region, AFR — the Afrotropical region, OR — the Oriental region, NEA — the Nearctic region, NEO — the Neotropical region, and AUS — the Australasian region.

Сокращения. Зоогеографические области: PAL — Палеарктическая, AFR — Афротропическая, OR — Ориентальная, NEA — Неарктическая, NEO — Неотропическая и AUS — Австралийская.

Table 2. Similarity matrix of 217 genera of spider wasps by biogeographic regions.

Таблица 2. Матрица сходства 217 родов дорожных ос по зоогеографическим областям.

	PAL	AFR	OR	NEA	NEO	AUS
PAL	1	0,42	0,47	0,37	0,28	0,32
AFR	0,42	1	0,35	0,26	0,20	0,28
OR	0,47	0,35	1	0,35	0,30	0,36
NEA	0,37	0,26	0,35	1	0,68	0,31
NEO	0,28	0,20	0,30	0,68	1	0,28
AUS	0,32	0,28	0,36	0,31	0,28	1

Abbreviations. Biogeographic regions as in the Table 1.

Сокращения. Зоогеографические области как в таблице 1.

The abbreviation CUG (common unique genus) used in the text means a genus occurring in two or three biogeographic regions, but nowhere else.

Results

The **Palearctic region** comprises 70 genera from three subfamilies: Pompilinae (46 genera, 66%), Pepsinae (22, 31%) and Cerozalinae (2, 3%) (Fig. 5, Table 1).

22 genera (31%) are endemic (Table 1). The fauna of the Palearctic region (Figs 1, 3, 4) is most similar to the faunas of the Oriental (coefficient 0.47, with 10 UCG: *Clistoderes*, *Eopompilus*, *Machaerotherix*, *Macromeris*, *Morochares*, *Mygnimia*, *Nipponodipogon*, *Platydialepis*, *Stigmatodipogon*, and *Telostholus*) and Afrotropical regions (coeff. 0.42, with the six UCG: *Arachnotheutes*, *Ctenagenia*, *Dicyrtomellus*, *Gonaporus*, *Microcurgus*, and *Schistonyx*). *Poecilogenia* is UCG for these

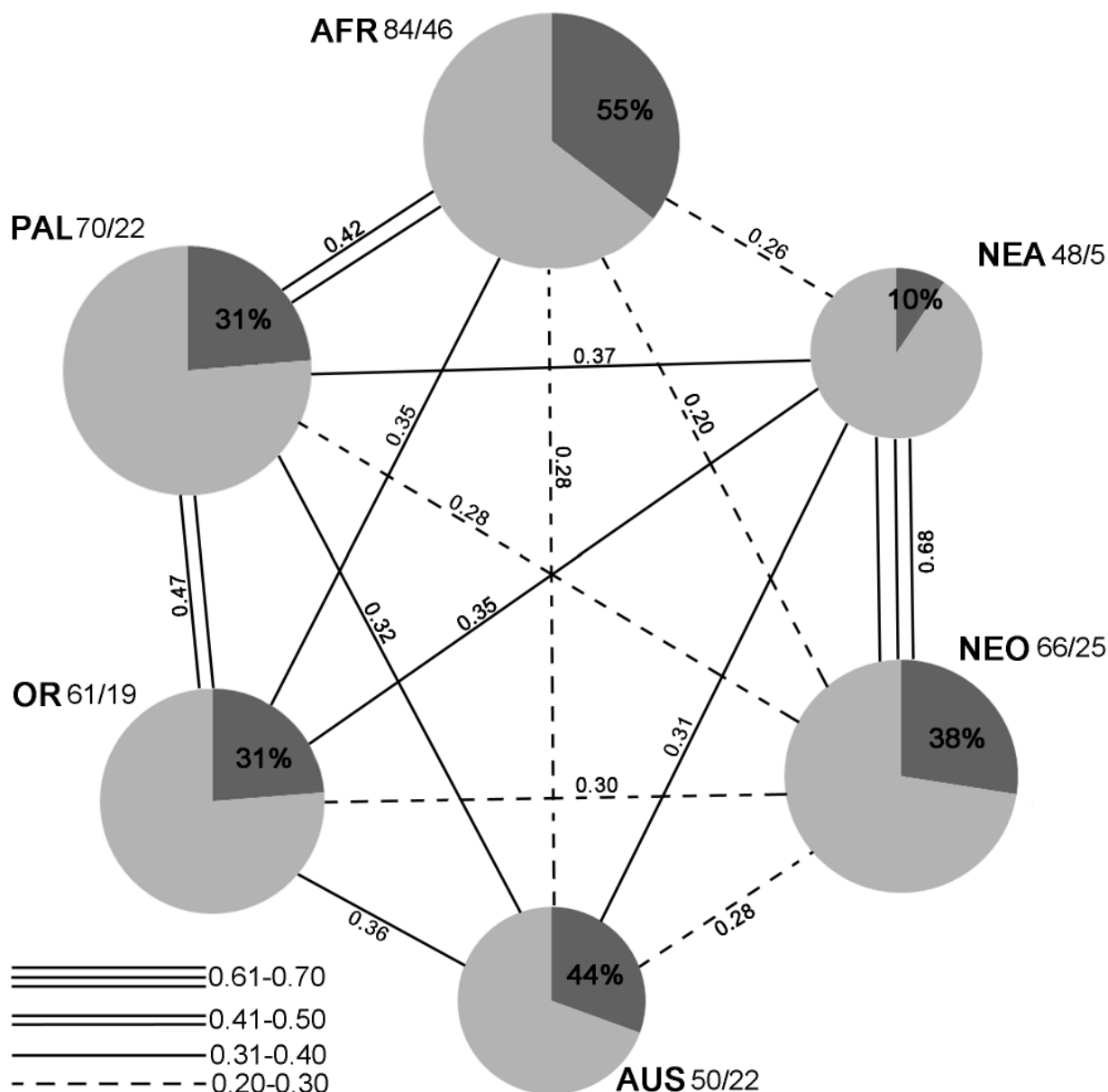


Fig. 1. Relationships between the spider wasp faunas of the biogeographic regions at the genus level, expressed using Terentyev's galaxies based on the Sørensen–Dice coefficient of similarity. Area of the circles is proportional to the number of genera in a biogeographic region. The dark sector denotes the proportion of endemics. Abbreviations: PAL — Palearctic region, AFR — Afrotropical region, OR — Oriental region, NEA — Nearctic region, NEO — Neotropical region, and AUS — Australasian region. After names of the regions, total numbers of genera and numbers of endemic genera (in the numerators and denominators respectively) are given.

Рис. 1. Связи фаун дорожных ос зоогеографических областей мира на родовом уровне, выраженные с помощью плеяд Терентьева на основе меры сходства Чекановского–Сьеренсена. Площадь кругов пропорциональна числу родов. Темный сектор — доля эндемиков. Области: PAL — Палеарктическая, AFR — Афротропическая, OR — Ориентальная, NEA — Неарктическая, NEO — Неотропическая и AUS — Австралийская. После названия области дано число родов (в числителе) и число родов-эндемиков (в знаменателе).

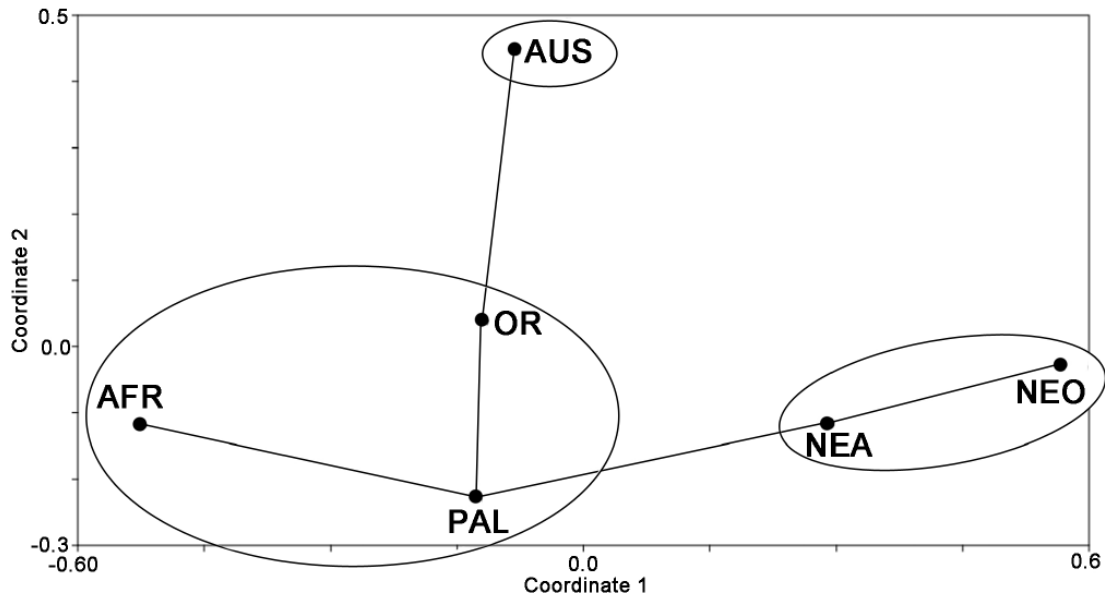


Fig. 2. Non-metric ordination of spider wasp faunas of biogeographic regions at the genus level based on the Sørensen–Dice coefficient of similarity. Abbreviations of biogeographic regions as in Fig. 1.

Рис. 2. Неметрическая ординация фаун дорожных ос зоогеографических областей мира на родовом уровне на основе меры сходства Чекановского–Сьеренсена. Сокращения названий зоогеографических областей как на рис. 1.

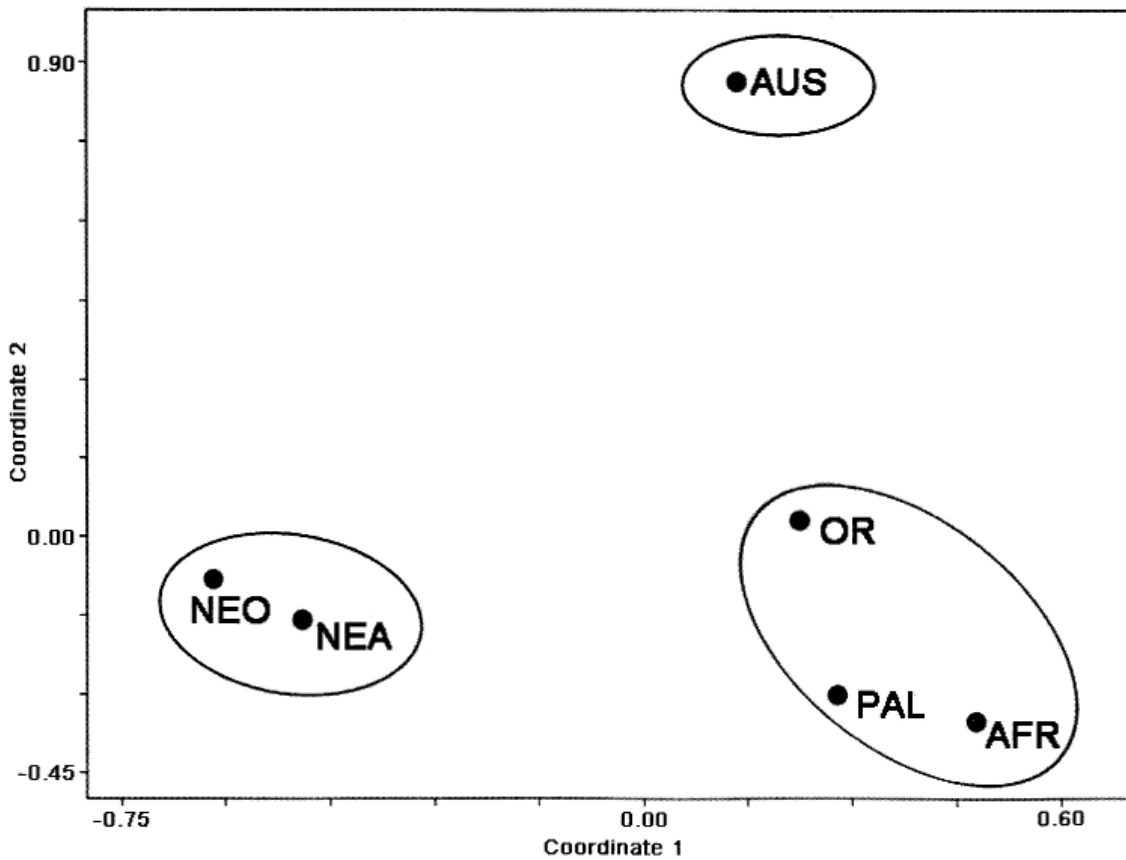


Fig. 3. Ordination of spider wasp faunas (in the space of two coordinates) of biogeographic regions at the genus level based on the Sørensen–Dice coefficient of similarity. Abbreviations of biogeographic regions as in Fig. 1.

Рис. 3. Ординация фаун (в пространстве двух координат) дорожных ос зоогеографических областей мира на родовом уровне на основе меры сходства Чекановского–Сьеренсена. Сокращения названий зоогеографических областей как на рис. 1.

three regions. The similarity with the faunas of other regions decreases in the following order: the Nearctic (coeff. 0.37, with 1 UCG *Lophopompilus*), Australasian (coeff. 0.32, no UCG), and Neotropical regions (coeff. 0.28, no UCG).

The **Afrotropical region** is the richest by the number of pompilid genera, it includes 84 genera from four subfamilies: Pompilinae (47 genera, 56%), Pepsinae (17, 20%), Ctenocerinae (18, 22%), and Ceropalinae (2, 2%) (Fig. 5, Table 1). The level of endemism here is the highest — 46 genera (55%) (Table 1). The fauna is most similar to that of the Palearctic region (coeff. 0.42, with 6 UCG, see above), and the fauna of the Oriental region (coeff. 0.35, with four UCG: *Atopompilus*, *Ctenocerus*, 1845, *Diplonyx*, and *Pygmachus*) (Figs 1–3). The similarity with faunas of other regions is less significant (coeff. 0.20–0.28). There is the only UCG (*Spuridiophorus*) with the fauna of the Australasian region.

The **Oriental region** comprises 61 genera from four subfamilies: Pepsinae (31 genera, 51%), Pompilinae (26, 43%), Ceropalinae (2, 2%), and Ctenocerinae (2, 2%) (Figs 5, Table 1). Of them, 19 genera (31%) are endemic (Table 1). The fauna is most similar to that of the Palearctic region (coeff. 0.47, with 10 UCG, see above) and less similar to that of the Australasian region (coeff. 0.36, with two UCG: *Chrysagenia* and *Heterodontonyx*), the Afrotropical region (coeff. 0.35, with four unique common genera, see above) and the Nearctic region (coeff. 0.35, no UCG) (Fig. 1–3). The minimum similarity is to the fauna of the Neotropical region (coeff. 0.30, no UCG).

The **Nearctic region** comprises the smallest number of genera — 48 from four subfamilies: Pompilinae (26 genera, 54%), Pepsinae (19, 40%), Ceropalinae (2, 4%), and Notocyphinae (1, 2%) (Fig. 5, Table 1). The level of endemism is the lowest among the all regions —

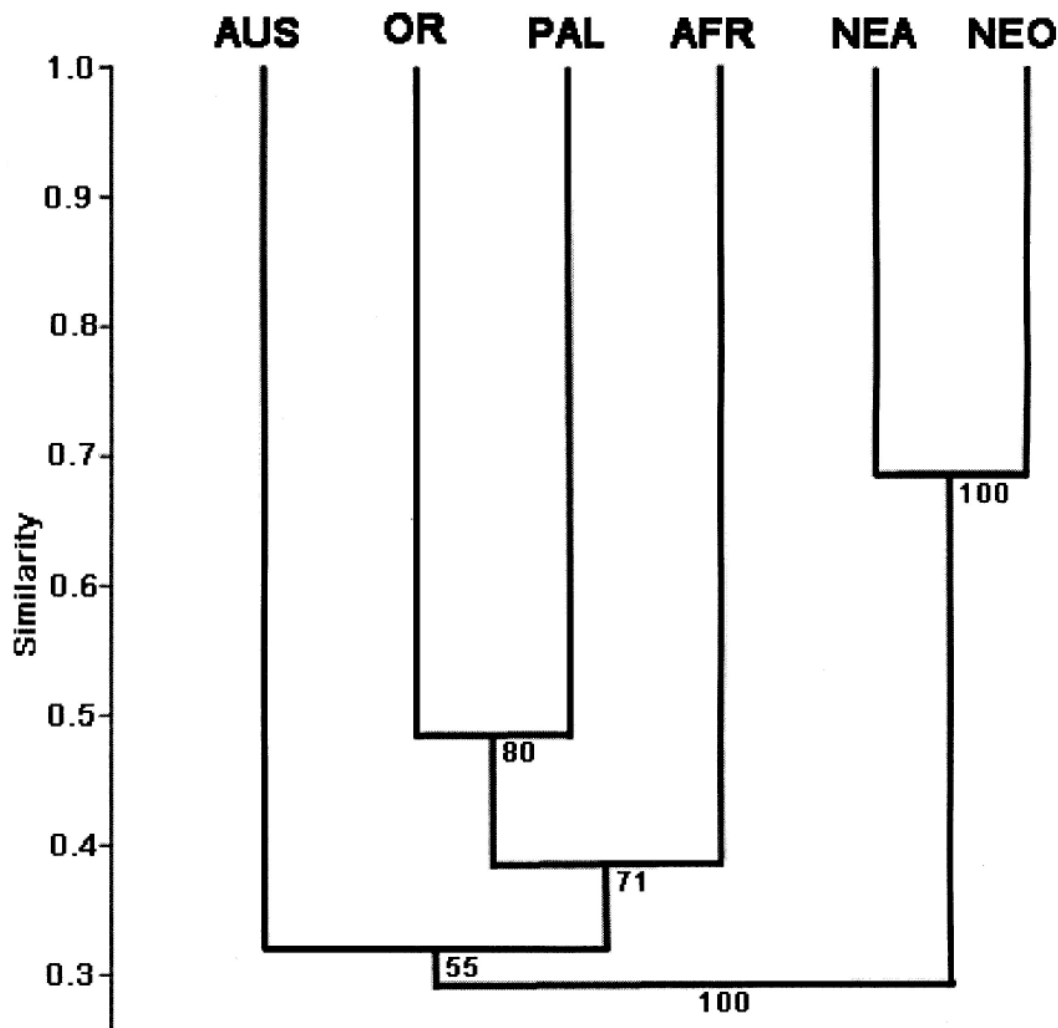


Fig. 4. Dendrogram of the similarity of spider wasp faunas of biogeographic regions at the genus level based on the Sørensen–Dice coefficient of similarity. Bootstrap support for 1000 replications is shown at the base of branches. Abbreviations of biogeographic regions as in Fig. 1.

Рис. 4. Дендрограмма сходства фаун дорожных ос зоогеографических областей мира на родовом уровне на основе меры сходства Чекановского–Сьеренсена. В основании ветвей указана бутстреп-поддержка для 1000 повторностей. Сокращения названий зоогеографических областей как на рис. 1.

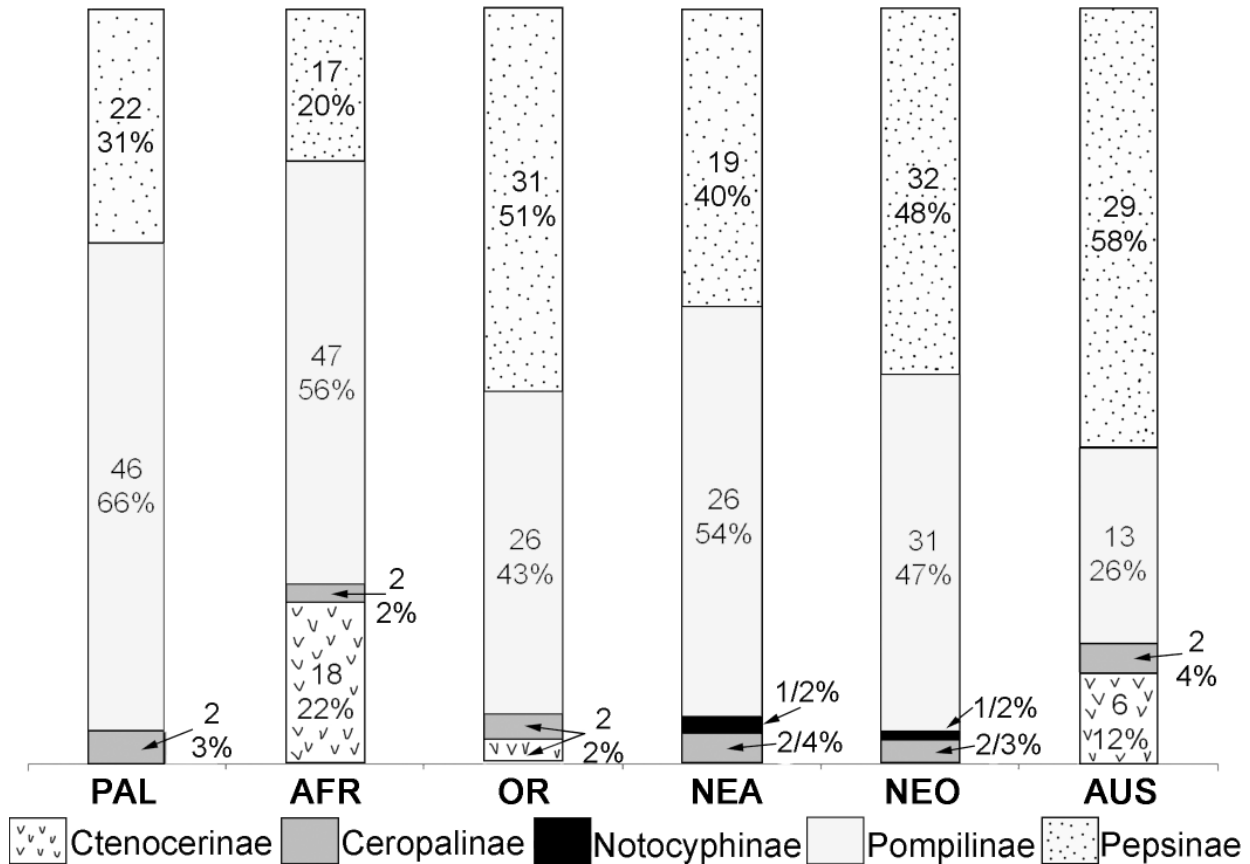


Fig. 5. Composition of faunas of spider wasps in biogeographic regions at the subfamily level. The sector labels denote the numbers of genera in the subfamily and percentages of genera in the subfamily of total fauna of the region (in the numerators and denominators respectively). Abbreviations of biogeographic regions as in Fig. 1

Рис. 5. Состав фаун дорожных ос зоогеографических областей мира на уровне подсемейств. В подписях секторов дано число родов в подсемействе (в числителе) и процент родов подсемейства от общей фауны области (в знаменателе). Сокращения названий зоогеографических областей как на рис. 1.

5 genera (10%) (Table 1). The highest level of similarity was revealed here, between the faunas of the Nearctic and Neotropical regions (coeff. 0.68, a unique common subfamily Notocyphinae and 14 UCG: *Allaporus*, *Allochares*, *Anoplioides*, *Chelaporus*, *Chirodamus*, *Dipogon*, *Entypus*, *Eragenia*, *Notocyphus*, *Priocnemella*, *Priocnessus*, *Psorthaspis*, *Xenopompilus*, and *Xerochares*) (Figs 1, 3, 4). The similarity with the faunas of other regions is noticeably lower: the Palaearctic region (coeff. 0.37, with a single UCG given above), Oriental (coeff. 0.35, no UCG), and Australasian regions (coeff. 0.31, no UCG). The lowest similarity is revealed with fauna of the Afrotropical region (coeff. 0.26, no UCG).

The **Neotropical region** is represented by 66 genera from four subfamilies: Pepsinae (32 genera, 48%), Pompilinae (31, 47%), Ceropalinae (2, 3%), and Notocyphinae (1, 2%) (Fig. 5, Table 1). 25 genera (38%) are endemic (Table 1). The fauna is most similar to that of the Nearctic region (see above) (Figs 1, 3, 4). The similarity with faunas of other regions is very low, the coefficient of similarity varies from 0.20 (the Afrotropical region) to 0.30 (the Oriental region); the only two UCG (*Calo-*

pompilus and *Leptodialepis*) are known for the fauna of the Australasian region.

The **Australian region** comprises 50 genera from four subfamilies: Pepsinae (29 genera, 58%), Pompilinae (13, 26%), Ctenocerinae (6, 12%), and Ceropalinae (2, 4%) (Fig. 5, Table 1). 22 genera (44%) are endemic (Table 1). The pompilid fauna of the region is the most distinctive (Fig. 3). The highest similarity is revealed with the fauna of the Oriental region (coeff. 0.36, with two UCG, see above) (Fig. 1). The coefficient of similarity with faunas of other regions varies from 0.28 to 0.32. There are UCG with the Afrotropical region (*Spiridiophorus*) and the Neotropical region (two UCG, see above).

Pepsinae is the largest cosmopolitan subfamily comprising approximately 2600 species from 82 genera (new updated data) (Table 1). It is represented by 22 genera in the Palaearctic region (31% of all subfamilies in the region), of them four genera (18%) are endemic; 17 genera in the Afrotropical region (22%), of them seven genera (41%) are endemic; 31 genera in the Oriental region (51%), of them 10 genera (32%)

are endemic; 19 genera in the Nearctic region (40%), of them one genus (5%) is endemic; 32 genera in the Neotropical region (48%), of them 12 genera (38%) are endemic; and 29 genera in the Australasian (58%), of them 13 genera (45%) are endemic (Table 1). The proportion of the subfamily Pepsinae in the different regions varies from 22 to 58% (Fig. 5).

According to molecular data, the subfamily Pepsinae originated approximately 31.4 Ma [Waichert *et al.*, 2015]. Until recently, fossil representatives of the subfamily were known from the Eocene and Miocene (47–5 Ma) [Rodríguez *et al.*, 2017]. The recently described fossil, which belongs to extant genus *Cryptochelilus*, is the oldest record of Pompilidae to date (early Eocene, 56–54 Ma) [Waichert *et al.*, 2019].

Pompilinae is the second largest subfamily, the fauna of which comprises approximately 2000 species [Rodríguez *et al.*, 2016] from 107 genera (new updated data). It is distributed in six biogeographic regions (Fig. 5): the Palaearctic region (46 genera, 66% of all subfamilies in the region, of them 18 genera, 39% are endemic), the Afrotropical region (47 genera, 56%, of them 22 genera, 47% are endemic), the Oriental region (26 genera, 43%, of them eight genera, 31% are endemic), the Nearctic region (26 genera, 54%, of them four genera, 15% are endemic), the Neotropical region (31 genera, 47%, of them 13 genera, 42% are endemic), and the Australasian region (13 genera, 26%, of them three genera, 23% are endemic) (Table 1). The proportion of the subfamily in the different regions varies from 26 to 66% (Fig. 5).

According to molecular data, the subfamily originated approximately 30.5 Ma [Waichert *et al.*, 2015]. Fossil representatives of the subfamily are known from the Eocene and Miocene (37–13 Ma) [Rodríguez *et al.*, 2017].

Ctenocerinae is a small subfamily including 140 species from 25 genera (new updated data). It is distributed in three biogeographic regions: the Afrotropical region (18 genera, 22% of all subfamilies in the region, of them 17 genera, 94% are endemic), the Oriental region (two genera, 2%, of them one genus, 50% are endemic), and the Australasian region (six genera, 12%, all genera, 100% are endemic) (Table 1). In these regions, Ctenocerinae occupies from 2 to 22% (Fig. 5). 24 of 25 genera of the subfamily are endemic.

According to molecular data, the subfamily originated approximately 27.9 Ma [Waichert *et al.*, 2015]. No fossil representatives of the subfamily are known.

Ceropalinae is a small kleptoparasitic subfamily. It includes two genera (*Ceropales* and *Irenangelus*) and 130 species distributed worldwide [Shimizu, Wahis, 2007; Waichert *et al.*, 2022]. Both genera are known in all biogeographic regions, and their share among other subfamilies varies in the different regions from 2 to 4% (Fig. 5).

According to molecular data, the Ceropalinae originated approximately 28.4 Ma [Waichert *et al.*, 2015], but recent data suggest 7 Ma [Waichert *et al.*, 2022]. No fossils are known.

Notocyphinae is the smallest subfamily represented by the only genus, *Notocyphus*, which is distributed exclu-

sively in the Nearctic and Neotropical regions (Table 1), it includes 74 species [Krombein, 1979; Fernández *et al.*, 2022]. The share of the Notocyphinae among other subfamilies in the different regions is 2% (Fig. 5).

According to molecular data, the Notocyphinae originated approximately 23.1 Ma [Waichert *et al.*, 2015]. No fossils are known.

Conclusion

The present analysis showed that the faunas of spider wasp genera of the Nearctic and Neotropical regions are the most similar (Figs 1–4), and the latter fauna is associated with that of the Palaearctic region (Fig. 2). The faunas of the Palaearctic, Afrotropical and Oriental regions obviously cluster together (Figs 1–4). The fauna of the Australasian region is the most isolated and specific (Figs 1, 3), having maximum similarity only with the fauna of the Oriental region, through which it is connected to that of the Palaearctic region (Fig. 2).

The two largest subfamilies, Pepsinae and Pompilinae, with their joint share among other subfamilies being 78 to 95%, constitute the main bulk of the faunas of all biogeographic regions. The subfamily Ceropalinae is equally represented in all regions, with the shares of 2 to 4%. Ctenocerinae are known from the Afrotropical, Oriental, and Australasian regions, with the shares of 2 to 22%. Notocyphinae are distributed only in the Nearctic and Neotropical regions, with the share of 2%.

Supplementary data. The following Supplementary Table is available online.

Supplementary Table 1. Distribution of 217 genera of spider wasps by biogeographic regions.

Acknowledgments. I thank all collectors as well as curators of Russian and foreign collections for possibility to study spider wasps from their materials. Many thanks to the editor, Vladimir E. Gokhman (Botanical Garden, Moscow State University, Moscow, Russia) and the reviewer, Alexander V. Fateryga (A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Feodosiya, Russia) for critically reviewing the manuscript and making important suggestions which have improved it. I am especially grateful to Dr. Arkady S. Lelej (FSC Biodiversity FEB RAS, Vladivostok, Russia) for the permanent support of my research. The current paper was carried out within the state assignment of Ministry of Science and Higher Education of the Russian Federation (project No. 121031000151-3).

References

- Aguiar A.P., Deans A.R., Engel M.S., Forshage M., Huber J.T., Jennings J.T., Johnson N.F., Lelej A.S., Longino J.T., Lohrmann V., Mikó I., Ohl M., Rasmussen C., Taeger A., Yu D.S.K. 2013. Order Hymenoptera. Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness (Addenda 2013) // *Zootaxa*. Vol.3703. P.51–62. <https://doi.org/10.11646/zootaxa.3703.1.12>
- Al-Jahdhami A., Schmid-Egger C. 2020. A new species of *Microcurgus* Haupt, 1950 (Hymenoptera, Pompilidae) from Oman // *Zootaxa*. Vol.4728. No.4. P.498–500. <http://dx.doi.org/10.11646/zootaxa.4728.4.9>

- Banks N. 1934. The Psammocharidae of the Philippines // *Proceedings of the American Academy of Arts and Sciences*. Vol.69. No.1. P.1–117. <https://doi.org/10.2307/20023025>
- Bingham C.T. 1896. New and little-known species of Indo-Malayan Hymenoptera, with a key to the genera of Indian Pompilidae, and a note on *Sphex flava* of Fabricius, and allied species // *Journal of the Bombay Natural History Society*. Vol.10. P.195–215.
- Branstetter M.G., Danforth B.N., Pitts J.P., Faircloth B.C., Ward, P.S., Buffington, M.L. et al. 2017. Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees // *Current Biology*. Vol.27. No.7. P.1019–1025. <https://doi.org/10.1016/j.cub.2017.03.027>
- Day M.C. 1974a. A contribution to the taxonomy of the genus *Anoplius* Dufour (Hymenoptera: Pompilidae) including a revision of the Palaeotropical subgenus *Orientaloplius* Haupt // *Bulletin of the British Museum (Natural History), Entomology*. Vol.30. No.8. P.375–404.
- Day M.C. 1974b. A revision of *Atopompilus* Arnold, with a note on the identity of *Anoplinellus* Banks (Hymenoptera: Pompilidae) // *Bulletin of the British Museum (Natural History), Entomology*. Vol.31. No.3. P.45–70.
- Day M.C. 1981. A revision of *Pompilus* Fabricius (Hymenoptera: Pompilidae), with further nomenclatural and biological considerations // *Bulletin of the British Museum (Natural History), Entomology*. Vol.42. No.1. P.1–42.
- Elliott M.G. 2007. Annotated catalogue of the Pompilidae (Hymenoptera) of Australia // *Zootaxa*. Vol.1428. P.1–83.
- Enayatnia M., Rakhshani E., Kroupa A.S., Schmid-Egger C. 2018. Updated catalogue of Pompilidae (Hymenoptera) in Iran // *Zootaxa*. Vol.4394. No.4. P.451–489. <https://doi.org/10.11646/zootaxa.4394.4.1>
- Fernández F., Rodríguez J., Waichert C., Decker B., Pitts J. 2022. Twenty two years later: An updated checklist of Neotropical spider wasps (Hymenoptera: Pompilidae) // *Zootaxa*. Vol.5116. No.4. P.451–503. <https://doi.org/10.11646/zootaxa.5116.4.1>
- Hammer Ø., Harper D.A.T., Ryan P.D. 2006. Paleontological statistics (Version 1.57). 78 pp.
- Haupt H. 1935a. Schwedisch-chinesische wissenschaftliche Expedition nach den nordwestlichen Provinzen Chinas, unter Leitung von Dr. Sven Hedin und Prof. Sü Ping-Chang. Insekten gesammelt vom schwedischen Arzt der Expedition Dr. David Hummel 1927–1930. 24. Hymenoptera. 2. Psammocharidae // *Arkiv för Zoologi*. Bd.27A. H.10. S.1–21.
- Haupt H. 1935b. Hymenoptera aus den Sundainseln und Nordaustralien. Psammocharidae // *Revue Suisse de Zoologie*. T.42. Fasc.9. S.306–321.
- Haupt H. 1941. Neues über mitteleuropäische Psammochariden (Hym.) // *Stettiner Entomologische Zeitung*. Bd.102. S.177–191.
- Haupt H. 1959. Elemente einer systematischen Aufteilung der Macromerinae m. (Hymenoptera–Sphecoidea) Fam. Pompilidae, Subfam. Macromerinae // *Nova Acta Leopoldina*. Bd.21. H.141. S.5–74.
- Haupt H. 1962. The Pompilidae of Israel // *Bulletin of the Research Council of Israel (Section B. Zoology)*. Vol.11. P.3–70.
- Krogmann L., Austin A.D. 2012. Systematics of Australian *Agenioideus* Ashmead (Hymenoptera: Pompilidae) with the first record of a spider wasp parasitizing *Latrodectus hasselti* Thorell (redback spider) // *Australian Journal of Entomology*. Vol.51. P.166–174. <https://doi.org/10.1111/j.1440-6055.2011.00850.x>
- Krombein K.V. 1979. Superfamily Pompiloidea // K.V. Krombein, P.D.Jr. Hurd, D.R. Smith, B.D. Burks (eds.). *Catalog of Hymenoptera in America North of Mexico*. Vol.2. Apocrita (Aculeata). Washington, D.C.: Smithsonian Institution Press. P.1523–1571.
- Legendre L., Legendre P. 1983. Numerical Ecology. Developments in Environmental Modelling. Amsterdam–Oxford–N.Y.: Elsevier. 419 pp.
- Lelej A.S., Loktionov V.M. 2008. A review of the genus *Poecilagenia* Haupt, 1927 (Hymenoptera, Pompilidae) of the Russia with the world catalogue of the species // *Far Eastern Entomologist*. No.190. P.1–16.
- Lelej A.S., Loktionov V.M. 2012. Phylogeny and classification of the tribe Deuterageniini (Hymenoptera, Pompilidae: Pepsinae) // *Far Eastern Entomologist*. No.254. P.1–15.
- Loktionov V.M. 2021. A review of the spider wasp genus *Austrosalius* Turner, 1917 (Hymenoptera, Pompilidae), with the description of a new species // *Zootaxa*. Vol.5006. No.1. P.121–126. <https://doi.org/10.11646/zootaxa.5006.1.16>
- Loktionov V.M., Lelej A.S. 2014. Spider wasps (Hymenoptera: Pompilidae) of the Russian Far East. Vladivostok: Dalnauka. 472 pp.
- Loktionov V.M., Lelej A.S. 2015. Keys to genera of the spider wasps (Hymenoptera: Pompilidae) of Russia and neighbouring countries, with check-list of genera // *Zootaxa*. Vol.4034. No.1. P.87–111. <http://dx.doi.org/10.11646/zootaxa.4034.1.4>
- Loktionov V.M., Lelej A.S. 2017. An annotated catalogue of the spider wasps (Hymenoptera: Pompilidae) of Russia // *Zootaxa*. Vol.4280. No.1. P.1–95. <https://doi.org/10.11646/zootaxa.4280.1.1>
- Loktionov V.M., Lelej A.S. 2018. Discovery of the spider wasp genus *Sphictostethus* Kohl, 1884 (Hymenoptera: Pompilidae: Pepsinae) in New Guinea, with description of two new species // *Zootaxa*. Vol.4429. No.2. P.295–302. <https://doi.org/10.11646/zootaxa.4429.2.5>
- Loktionov V.M., Lelej A.S. 2019. The spider wasp genus *Telostholus* Haupt, 1929 (Hymenoptera, Pompilidae) in Indonesia, with the description of three new species // *Zootaxa*. Vol.4648. No.2. P.260–272. <https://doi.org/10.11646/zootaxa.4648.2.3>
- Loktionov V.M., Lelej A.S., Liu J.-X. 2018. Contribution to the knowledge on the spider wasps genus *Morochares* Banks, 1934 (Hymenoptera: Pompilidae) from China // *Zootaxa*. Vol.4462. No.4. P.497–510. <https://doi.org/10.11646/zootaxa.4462.4.3>
- Loktionov V.M., Lelej A.S., Liu J.-X. 2019. A new genus of spider wasps (Hymenoptera, Pompilidae) from China // *Far Eastern Entomologist*. No.376. P.1–14. <https://doi.org/10.25221/fee.376.1>
- Loktionov V.M., Lelej A.S., Vasilenko D.V., Perkovsky E.E. 2023. Discovery of a new extinct spider wasp (Hymenoptera, Pompilidae) from Eocene Rovno amber // *Zootaxa*. Vol.5352. No.3. P.426–432. <https://doi.org/10.11646/zootaxa.5352.3.6>
- Loktionov V.M., Lelej A.S., Xu Z.-F. 2017. Discovery of the genus *Nipponodipogon* Ishikawa in the Oriental region, with description of two new species from China (Hymenoptera, Pompilidae) // *ZooKeys*. Vol.692. P.103–127. <https://doi.org/10.3897/zookeys.692.12062>
- Noort van S. 2023. WaspWeb: Hymenoptera of the Afrotropical region. <http://www.waspweb.org>
- Pesenko Yu.A. 1982. [Principles and methods of quantitative analysis in faunal studies]. Moscow: Nauka. 136 pp. [In Russian]
- Peters R.S., Krogmann L., Mayer C., Donath A., Gunkel S., Meusemann K. et al. 2017. Evolutionary history of the Hymenoptera // *Current Biology*. Vol.27. P.1013–1018. <https://doi.org/10.1016/j.cub.2017.01.027>
- Priesner H. 1966. Einiges über Pompiliden (Hymenoptera) // *Nachrichtenblatt der Bayerischen Entomologen*. Bd.15. H.7–8. S.57–60.
- Rodríguez J., Pitts J.P., Florez J.A., Bond J.E., von Dolhen C.D. 2016. Molecular phylogeny of Pompilinae (Hymenoptera: Pompilidae): Evidence for rapid diversification and host shifts in spider wasps // *Molecular Phylogenetics and Evolution*. Vol.94. P.55–64. <http://dx.doi.org/10.1016/j.ympev.2015.08.014>
- Rodríguez J., Waichert C., von Dohlen C.D., Pitts J.P. 2017. The geological record and phylogeny of spider wasps (Hymenoptera: Pompilidae): A revision of fossil species and their phylogenetic placement // *PLoS ONE*. Vol.12. No.10. Art.e0185379. <https://doi.org/10.1371/journal.pone.0185379>
- Shimizu A. 1994. Phylogeny and classification of the family Pompilidae // *Tokyo Metropolitan University, Bulletin of Natural History*. Vol.2. P.1–142.
- Shimizu A., Broad G., Yoshimura J., Pitts J.P. 2022. First records of the spider wasps *Ctenocerus* Dahlbom and *Paraclavelia* Haupt from Asia, with discussions on the systematics of Ctenocerinae (Hymenoptera: Pompilidae) // *European Journal of Taxonomy*. Vol.845. P.101–131. <https://doi.org/10.5852/ejt.2022.845.1957>
- Shimizu A., Lelej A.S., Loktionov V.M., Nishimoto Y., Endo T. 2018. Revision of the subgenus *Stigmatodipogon* Ishikawa of the genus *Dipogon* Fox (Hymenoptera: Pompilidae: Pepsinae) // *Zootaxa*. Vol.4514. No.1. P.1–22. <https://doi.org/10.11646/zootaxa.4514.1.1>
- Shimizu A., Pitts J., Rodríguez J., Wahis R., Yoshimura J. 2021. Systematics and convergent evolution in three Australian genera of Pepsinae spider wasps (Hymenoptera: Pompilidae) // *Austral Entomology*. Vol.60. P.301–316. <http://dx.doi.org/10.1111/aen.12530>

- Shimizu A., Terayama M. 2016. Pompilidae // M. Terayama, H. Suda (eds). A Guide to the Aculeate Wasps of Japan. Minamiyama: Tokai University Press. P.178–247 + pls.39–53 + P.594–599.
- Shimizu A., Wahis R. 2004. Systematic study of the genus *Cyphononyx* (Hymenoptera: Pompilidae) occurring in Japan // Entomological Science. Vol.7. P.171–181.
- Shimizu A., Wahis R. 2005. A new genus and species of Japanese Pompilidae (Hymenoptera, Pompilidae) // Journal of Hymenoptera Research. Vol.14. No.1. P.115–120.
- Shimizu A., Wahis R. 2007. Systematic studies on the Pompilidae occurring in Japan: genus *Irenangelus* Schulz (Hymenoptera: Pompilidae: Ceropalinae) // Journal of Hymenoptera Research. Vol.16. No.2. P.311–325.
- Shimizu A., Wahis R. 2013. Systematic studies on the Pompilidae occurring in Japan: Genus *Platydialepis* Haupt (Hymenoptera: Pompilidae: Pepsinae) // Entomological Science. Vol.16. P.316–325.
- Shimizu A., Wahis R., Harris A.C., Pitts J.P. 2016. An extraordinary new genus and species of spider wasps (Insecta: Hymenoptera: Pompilidae) from Southeast Asia // Journal of Natural History. Vol.50. No.25–26. P.1549–1559. <https://doi.org/10.1080/00222933.2016.1155781>
- Tsuneki K. 1988. Pompilidae recently collected in the Philippines (Hymenoptera) // Special Publications of the Japan Hymenopterists Association. Vol.34. P.1–55, 61–62.
- Tsuneki K. 1989. A study on the Pompilidae of Taiwan (Hymenoptera) // Special Publications of the Japan Hymenopterists Association. Vol.35. P.1–180.
- Wahis R. 1981. Revision du genre *Minotocyphus* Banks (Hym., Pompilidae) // Bulletin de la Societe Entomologique Suisse. Vol.54. P.399–414.
- Wahis R. 2000. Sur quelques Pompilides afrotropicaux décrits par G. Gribodo en 1894 (Hymenoptera: Pompilidae) // Notes Fauniques de Gembloux. Vol.40. P.77–81.
- Wahis R. 2018. Ajustements nomenclatoriels de la Monographie de Bingham «The Fauna of British India, Hymenoptera», 1897 (Hymenoptera, Pompilidae) // Entomologie Faunistique–Faunistic Entomology. Vol.71. P.1–20.
- Wahis R., Durand F., Villemant C. 2009. Pompiles de l'île d'Espiritu Santo, Vanuatu (Insecta, Hymenoptera, Pompilidae) // Zoosystema. Vol.31. No.3. P.707–718. <https://doi.org/10.5252/z2009n3a15>
- Wahis R., Lelej A.S., Loktionov V.M. 2018. Contribution to the knowledge of the genus *Eopompilus* Gussakovskij, 1932 (Hymenoptera, Pompilidae) // Far Eastern Entomologist. No.361. P.1–11. <http://dx.doi.org/10.25221/fee.361.1>
- Wahis R., Schmid-Egger C. 2002. The genus *Eoferreola* Arnold, 1935 in the Palaearctic with description of a new species (Hymenoptera: Pompilidae) // Notes Fauniques de Gembloux. Vol.46. P.39–73.
- Waichert C., Rodriguez J., Lelej A.S., von Dohlen C.D., Pitts J.P. 2022. Revealing diagnostic characters through morphological evolution in cleptoparasitic spider wasps (Hymenoptera, Pompilidae, *Ceropales*) // Zoologica Scripta. Vol.51. P.365–380. <https://doi.org/10.1111/zsc.12530>
- Waichert C., Rodriguez J., Rapoza M., Wappler T. 2019. The oldest species of Pompilidae to date, a new fossil spider wasp (Hymenoptera: Pompilidae) // Historical Biology. Vol.33. No.7. P.1008–1011. <https://doi.org/10.1080/08912963.2019.1675056>
- Waichert C., Rodriguez J., Wasbauer M.S., von Dohlen C.D., Pitts J.P. 2015. Molecular phylogeny and systematics of spider wasps (Hymenoptera: Pompilidae): redefining subfamily boundaries and the origin of the family // Zoological Journal of the Linnean Society. Vol.175. P.271–287. <http://dx.doi.org/10.1111/zoj.12272>
- Waldren G.C., Sadler E.A., Murray E.A., Bossert S., Danforth B.N., Pitts J.P. 2023. Phylogenomic inference of the higher classification of velvet ants (Hymenoptera: Pompilidae) // Systematic Entomology. Vol.48. No.3. P.463–487. <https://doi.org/10.1111/syen.12588>
- Wilson J.S., von Dohlen C.D., Forister M.L., Pitts J.P. 2012. Family-level divergences in the stinging wasps (Hymenoptera: Aculeata), with correlations to angiosperm diversification // Evolutionary Biology. Vol.40. P.101–107. <http://dx.doi.org/10.1007/s11692-012-9189-0>
- Wolf H. 1968. Beiträge zur Kenntnis der fauna Afghanistans. Pompilidae, Hym. // Časopis Moravského Musea, Brno. Vol.53. S.233–248.
- Wolf H. 1978. Systematik, Morphologie und Verbreitung der westpaläarktischen Arten der Wegwespen-Gattungen *Arachnotheutes* und *Stolidia* (Hymenoptera: Pompilidae) // Entomologia Generalis. Vol.4. No.2. S.164–182.
- Wolf H. 1990. Zur Kenntnis der Wegwespen-Gattung *Gonaporus* Ashmead 1902 und verwandter Gattungen (Hym., Pompilidae) // Linzer Biologische Beiträge. Bd.22. H.2. S.619–716.
- Yuan D., Rodriguez J. 2020. Three new species of *Epipompilus* Kohl (Hymenoptera, Pompilidae, Pepsinae) from Australia // Zootaxa. Vol.4743. No.4. P.575–584. <https://doi.org/10.11646/zootaxa.4743.4.7>
- Zonstein I., Zonstein S. 2015. Revision of the Palaearctic genus *Gonaporus* Ashmead, 1902 of spider wasps (Hymenoptera: Pompilidae) // Zootaxa. Vol.4018. No.4. P.451–505. <http://dx.doi.org/10.11646/zootaxa.4018.4.1>