

Eocene and not Cretaceous origin of spider wasps: Fossil evidence from amber

JUANITA RODRIGUEZ, CECILIA WAICHERT, CAROL D. VON DOHLEN, GEORGE POINAR JR.,
and JAMES P. PITTS



Rodriguez, J., Waichert, C., von Dohlen, C.D., Poinar, G. Jr., and Pitts, J.P. 2016. Eocene and not Cretaceous origin of spider wasps: Fossil evidence from amber. *Acta Palaeontologica Polonica* 61 (1): 89–96.

Spider wasps had long been proposed to originate in the Late Cretaceous based on the Burmese amber fossil *Bryopompilus intersector*. We performed a morphological examination of this fossil and determined that it does not belong to Pompilidae or any other described hymenopteran family. Instead, we place it in the new family Bryopompilidae. The oldest verifiable member of the Pompilidae is from Baltic amber, which suggests that the crown group of the family probably originated in the Eocene, not in the Late Cretaceous as previously proposed. The origin of spider wasps appears to be correlated with an increase in spider familial diversity in the Cenozoic. We also add two genera to the extinct pompilid fauna: *Tainopompilus* Rodriguez and Pitts gen. nov. and *Paleogenia* Waichert and Pitts gen. nov., and describe three new species of fossil spider wasps: *Anoplius planeta* Rodriguez and Pitts sp. nov., from Dominican amber (Burdigalian to Langhian); *Paleogenia wahisi* Waichert and Pitts sp. nov., from Baltic amber (Lutetian to Priabonian); and *Tainopompilus argentum* Rodriguez and Pitts sp. nov., from Dominican amber (Chattian to Langhian).

Key words: Hymenoptera, Pompilidae, solitary wasps, amber, Eocene, Dominican Republic, Baltic sea, Russia.

Juanita Rodriguez [juanitarodrigueza@gmail.com], Cecilia Waichert [cwaichert@gmail.com], Carol D. von Dohlen [Carol.vonDohlen@usu.edu], and James P. Pitts [james.pitts@usu.edu], Utah State University, Department of Biology, 5305 Old Main Hill, Logan, UT 84322-5305, USA.

George Poinar Jr. [poinarg@science.oregonstate.edu], Oregon State University, Department of Zoology, 3029 Cordley Hall, Corvallis, OR 97331, USA.

Received 26 February 2014, accepted 8 December 2014, available online 28 January 2015.

Copyright © 2016 J. Rodriguez et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see <http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Spider wasps (Hymenoptera: Pompilidae) are solitary ectoparasitoids that show a wide variety of hunting, nesting, and prey-carrying behaviors as adults. Females specialize in hunting spiders, which they typically paralyze permanently, then lay a single egg on their body. A few species lay multiple eggs on the spider (Shimizu et al. 2012). The resulting larva consumes the spider host. In several lineages of spider wasps the spider is only temporarily paralyzed and the spider wasp larva feeds on it as the spider behaves normally. Cleptoparasitoid pompilids, like *Evaetes* (Wasbauer and Kimsey 1985) and *Poecilagenia* (Shimizu 2000), use the host of another spider wasp as their own hosts. Although behavior is not recorded for all spider wasp species, a certain degree of ecological or taxonomical host specificity has been reported (Evans and Yoshimoto 1962).

Approximately 5000 species of Pompilidae are described and are currently classified into five subfamilies (Waichert et al. 2015). Presently there are 21 species of fossil

Pompilidae described (Rodriguez 2014). The taxonomy of extinct spider wasps is challenging, because many of the descriptions (mostly published from Tertiary compression fossils in the late 1800s and early 1900s) lack necessary details and figures that could facilitate the placement of specimens in appropriate genera (Engel and Grimaldi 2006). The accuracy of identification of Pompilidae fossils is tenuous at best, especially for compression fossils, for which a thorough revision is needed. Compared to compression fossils, amber-preserved fossils are much easier to identify to genus and even to species.

The age of Pompilidae is currently based on the description of a fossil in Cenomanian (Late Cretaceous) Burmese amber (Engel and Grimaldi 2006). This date conflicts with a recent estimate based on molecular data, which dated the origin of crown-group Pompilidae to the early Paleogene (Wilson et al. 2013; Waichert et al. 2015). Here we clarify the identity of the Cenomanian Burmese fossil, describe two new genera and three new species of spider wasps and provide a discussion on the evolutionary implications of these new fossils.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, New York, USA; OSAC, Oregon State Amber Collection, Oregon State University, Corvallis, Oregon, USA.

Other abbreviations.—LA3, length of third antennal segment, LC, maximum height of clypeus, WA3, width of third antennal segment; WC, width of clypeus (measured between the widest points). Abbreviations for cell and vein names: A, anal; C, costal; Cu, cubital; M, medial; R, radial; Rs, radial sector; Sc, subcostal.

Material and methods

The Dominican amber fossils studied derive from deposits found in mines between the cities of Santiago and Puerto Plata (Dominican Republic). One of the Baltic amber fossil derives from the Kaliningrad region (Russia). The specimens newly described here were preserved in Baltic and Dominican amber. The holotypes are deposited in the Oregon State Arthropod Collection (OSAC). The amber fossil of *Bryopompilus interfactor* has been loaned from the American Museum of Natural History (AMNH).

Terminology used in the descriptions follows Wasbauer and Kimsey (1985). Wing venation terminology follows Huber and Sharkey (1993: figs. 19, 20).

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758

Family Pompilidae Latreille, 1804

Remarks.—The species treated here were assigned to the family Pompilidae based mainly on wing venation features, which are relatively uniform for the family (Day 1988). These were placed in the family Pompilidae based on the following combination of characters: presence of ten closed cells in the forewing, the hind wing with the veins C+Sc+R+Rs fused basally, and the second abscissa of 1A lost. Marginal cell with vein Rs rounded and attached to anterior margin of wing. Vein Rs of cell 1Rs attached to the base of cell 2R1. Costal cell ending on the anterior margin of the wing.

Subfamily Pompilinae Latreille, 1804

Genus *Anoplius* Dufour, 1834

Type species: *Sphex fusca* Linnaeus, 1751 (Latreille, 1803), type by subsequent designation; Recent, England.

Anoplius planeta Rodriguez and Pitts sp. nov.

Fig. 1.

Etymology: From Latin *planeta*, planet (noun in apposition), a nickname used by the first author's parents (Iomara Arrieta and Francisco Manuel Rodriguez).

Holotype: Complete male inclusion, OSAC Hy-10-45.

Type locality: Cordillera Septentrional, between Puerto Plata and Santiago, Dominican Republic.

Type horizon: Dominican amber, Early Miocene.

Diagnosis.—Wings hyaline; maximum width 0.18× its length; 2Rs cell as long as 1Rs; 2m-cu vein slightly curved, meeting 2Rs cell 0.70× distance from base to apex of cell; and 2M cell with an inflection at the base of the vein Cu.

Description.—Male. Body length 6.20 mm. Forewing 4.80 mm. Integument dark on head and mesosoma, light on metasoma. Body pubescence short and scattered on entire body. Mandible glabrous. Erect, long setae, present on second half of mandible. Pygidium bare, polished. Punctuation inconspicuous. Antenna elongate; ratio of length of segments two to four 6:15:16; WA3 0.40× LA3; WA4 0.26× LA4. Pronotum short, width 2.35× length, posterior margin slightly angulate; pronotal disc well defined. Length of 2R1 cell 0.71× distance from its margin to wing apex; 2Rs cell as long as 1Rs; 2m-cu slightly curved, meeting 2Rs cell 0.70× distance from base to apex of cell. Tibiae and tarsi with few spines present, short, acute, sparse; pulvillar comb strong; metasoma 1.33× as long as mesosoma.

Remarks.—This is the first species of *Anoplius* described from Dominican amber. We are confident about the placement of this species into *Anoplius* due to the good preservation of the specimen. The characters that place this specimen in *Anoplius* are: the postnotum is a transverse band with parallel anterior and posterior margins, the 2m-cu vein arises on the Cu less than half the distance from the base of the 2M cell to the outer wing margin, the clypeus is emarginated, the strong pulvillar comb, and the claws bifid. The only other genus with which it could be confused is *Arachnospila* Kincaid, 1900, which occurs in the Nearctic region, but *Arachnospila* does not have a strong pulvillar comb. *Anoplius planeta* does not fit the diagnosis of any of the *Anoplius* subgenera; on the contrary, it shows a combination of characters that belong to many of them. The two subgenera that *Anoplius planeta* best fits are *Anoplioides* Banks, 1939 and *Arachnoproctonus* Howard, 1901. In the first case, members of the subgenus have a 2Rs cell wider anteriorly than 1Rs, but *A. planeta* lacks this character. Also, extant members of *Anoplioides* do not show light colouration on the metasoma as does *A. planeta*. The light orange colouration on the metasoma could place *A. planeta* in the subgenus *Arachnoproctonus*. Nevertheless, members of this subgenus have a fifth tarsomere in the front leg with the inner margin slightly produced, while in *A. planeta* it is parallel sided. Given these reasons, we are not placing this species in an extant subgenus, rather, this is considered a desiomorph species, i.e., a fossil that possesses morphological characters found in two or more fossil or extant groups. Desiomorphs have been found in amber, and are known in species of Coleoptera, Diptera, Hemiptera, Hymenoptera, and Neuroptera (Poinar 2012).

The age of Dominican amber is controversial, with various published dates: 54–40 Ma (Landis and Snee 1991),

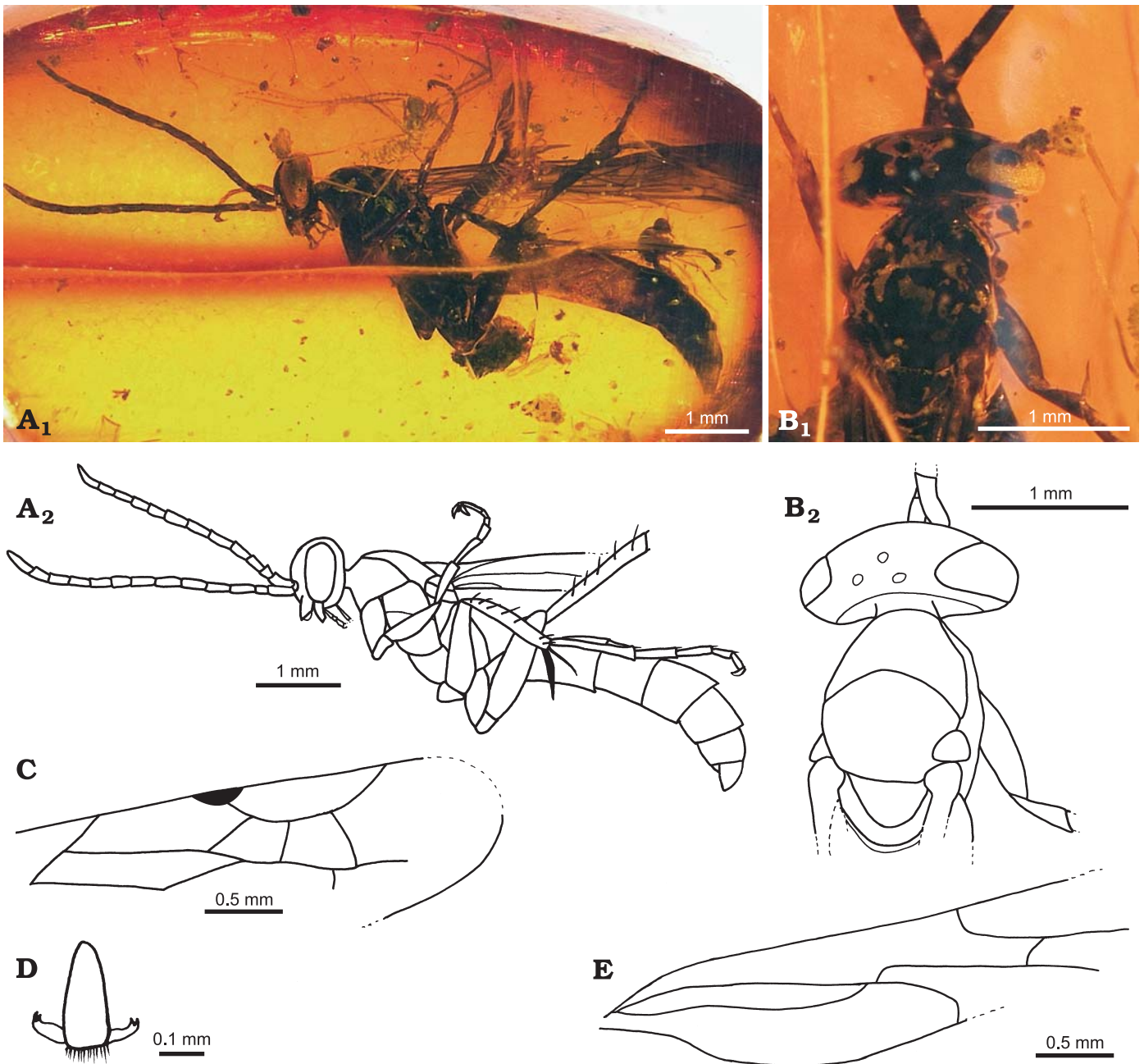


Fig. 1. Spider wasp *Anoplius planeta* Rodriguez and Pitts sp. nov., holotype, OSAC Hy-10-45, male specimen, from Early Miocene Dominican amber, Cordillera Septentrional, between Puerto Plata and Santiago, Dominican Republic. **A**. Habitus in lateral view. **B**. Mesosoma in dorsal view. **C**. Forewing. **D**. Pulvillus. **E**. Hindwing. Photographs (A₁, B₁), camera lucida illustrations (A₂, B₂, C–E).

45–30 Ma (Cepek in Schlee 1990), 23–30 (Grimaldi 1995), and 20–15 Ma (Iturralde-Vinent and MacPhee 1996) (for a comprehensive review see Penney 2010). Amber from the northern region of Dominican Republic has been found to be from 40 to 26 Ma (Lambert et al. 1985), but Iturralde-Vinent and MacPhee (1996) argue that all Dominican amber should be dated to the same age as the deposits bearing it, because evidence suggests that the fragments have not been emplaced by re-deposition. Therefore, Iturralde-Vinent and MacPhee (1996) proposed an age of 20–15 Ma for all Dominican amber, based on biostratigraphic and palaeogeographic data from Hispaniola. Later, Iturralde-Vinent

(2001) constrained the age of Amber to approximately 16 Ma (Penney 2010).

Insect inclusions have also been observed in Dominican copal (Brown 1999). This material is similar to amber in appearance and composition, and for this reason has sometimes been mistakenly reported as Pliocene–Pleistocene amber. Radiocarbon dating has suggested ages of less than 50 000 years for copal, while ambers are out of the radiocarbon age range (Burleigh and Whalley 1983).

Stratigraphic and geographic range.—Early Miocene of the northern of Dominican Republic.

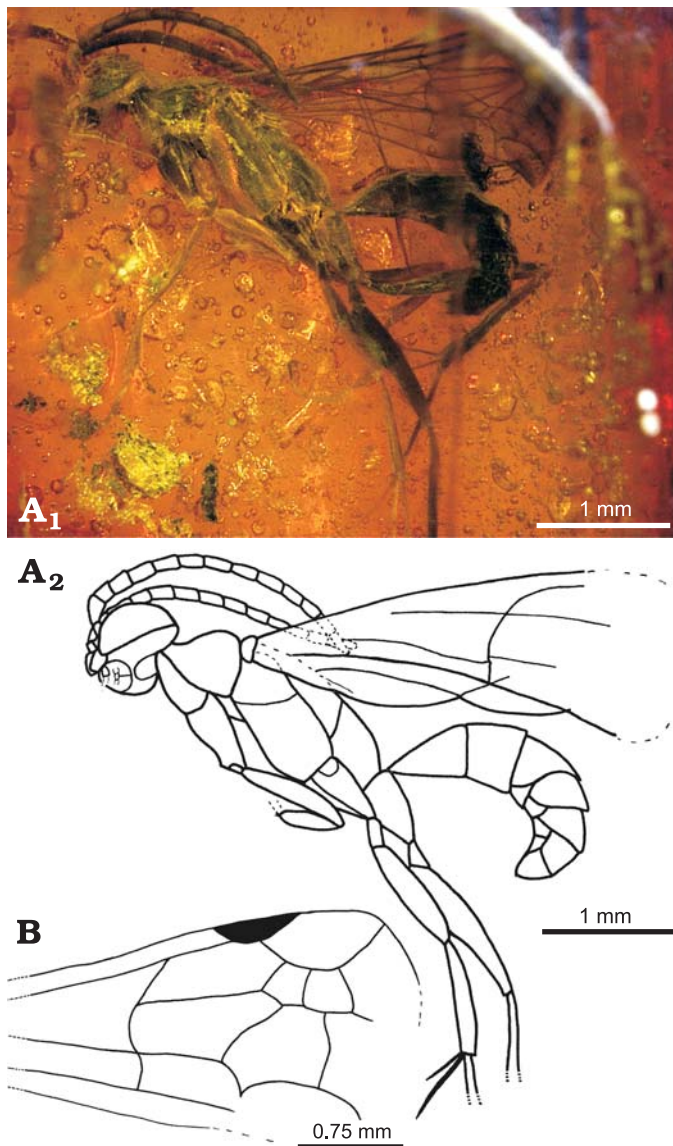


Fig. 2. Spider wasp *Tainopompilus argentum* sp. nov., holotype, OSAC Hy-10-45, male specimen, from Early Miocene Dominican amber, Cordillera Septentrional, between Puerto Plata and Santiago, Dominican Republic. A. Specimen in lateral view. B. Forewing. Photograph (A₁), camera lucida illustrations (A₂, B).

Genus *Tainopompilus* Rodriguez and Pitts nov.

Etymology: From Tainos, a pre-columbian indigenous culture that populated the Dominican Republic; and Latin *pompilus*, pilot fish; widely used for Pompilidae taxa. The gender is masculine.

Type species: *Tainopompilus argentum* Rodriguez and Pitts sp. nov., monotypic.

Diagnosis.—Antennal flagellum crenulate; postnotum is a narrow band, with parallel anterior and posterior margins; metatibia with apical spine-like setae of uniform length, the setae not splayed; 2M cell with an inflection on the base of vein Cu; 2m-cu vein arising on the Cu less than half the distance from the base of the 2M cell to the outer wing margin.

Remarks.—This genus resembles *Priochilus* Banks, 1943 in its general morphology. Nevertheless, the presence of

spine-like setae of uniform length on the metatibia, and the presence of an inflection at the base of vein Cu of the 2M cell, separate the two genera. *Tainopompilus* is placed in the subfamily Pompilinae by the presence of an inflection at the base of the Cu vein on 2M cell. This is the only genus in the subfamily that has spine-like setae of uniform length on the metatibia.

Stratigraphic and geographic range.—Early Miocene of the Dominican Republic.

Tainopompilus argentum Rodriguez and Pitts sp. nov.

Fig. 2.

Etymology: From Latin *argentum*, silver; in reference to the city Puerto Plata (silver port), close to where the holotype was collected.

Holotype: Complete male inclusion, OSAC Hy-10-45.

Type locality: Cordillera Septentrional, between Puerto Plata and Santiago, Dominican Republic.

Type horizon: Dominican amber, Early Miocene

Diagnosis.—Wing hyaline; maximum width $0.31\times$ its length; 2Rs cell as long as 1Rs; 2m-cu vein curved, meeting 2Rs cell $0.55\times$ distance from its base to apex of cell; and 2M cell with an inflection at the base of Cu vein.

Description.—Male. Body length 3.95 mm. Forewing 2.50 mm. Pubescence sparse and short on entire body including the mandible. Pygidium covered with short pubescence. Punctuation conspicuous on mesosoma. Antennae elongate, crenulate; ratio of segments two to four 6:9:10; WA3 $0.8\times$ LA3; WA4 $0.4\times$ LA3. Pronotum short, width $8.3\times$ length, posterior margin concave; pronotal disc well defined. Wing long; length of 2R1 cell $0.50\times$ distance from its edge to wing apex; 2Rs cell as long as 1Rs; 2m-cu vein curved, meeting 2Rs cell $0.55\times$ distance from base to apex of cell. Tibiae and tarsi with few short, sharp, sparse spines; metasoma $0.78\times$ as long as mesosoma.

Remarks.—This is the only described species of *Tainopompilus* gen. nov.

Stratigraphic and geographic range.—Early Miocene of the northern of Dominican Republic.

Subfamily Pepsinae Lepelletier, 1845

Genus *Paleogenia* Waichert and Pitts nov.

Etymology: From Greek *paleo*, ancient; and *Agenia*, a proper name widely used for Pepsinae taxa. The gender is feminine.

Type species: *Paleogenia wahisi* Waichert and Pitts sp. nov., monotypic.

Diagnosis.—Antennal segments short; propodeum smooth, with a lateral carina; tibia with apical spine-like setae short, regular; fore, mid and hind tibia not spinose; first metasomal segment with a lateral carina; wing hyaline; forewing with cells short, 2M cell without an inflection on the base of Cu vein; 1Rs and 2Rs about the same size; 1R1 and 1M about the same size; 1M $1/3$ as wide as long; 2m-cu vein arising on the Cu more than half the distance from the base of the 2M cell to the outer wing margin.

Remarks.—This genus is morphologically similar to the cosmopolitan genus *Minagenia* Banks, 1934. These genera resemble each other by having cells 1Rs and 2Rs small and about the same size, a short clypeus, straight stinger, and bulging eyes. However, *Paleogenia* gen. nov. differs from *Minagenia* by having dentate claws, short antennal segments, and subgenital plate S6 not laterally compressed. Additionally, the 2R1 cell in *Paleogenia* is large, with length 2.5× its width, and it almost touches the apical margin of the forewing. Usually in pompilids, the 2R1 cell ends somewhere in the anterior margin of the wing, never the apical margin.

Paleogenia is assigned to the subfamily Pepsinae due to the absence of an inflection at the base of the Cu vein in 2M cell and the presence of regular, apical spine-like setae on the tibia. Additionally, *Paleogenia* gen. nov. has the metasomal sternum 2 with a distinct sharp transverse groove. This genus is placed in the tribe Pepsini, because it has a defined carina on the first metasomal segment. This is the only genus in the tribe with short antennal segments. The wing venation also resembles that of *Poecilagenia* and *Nipponodipogon* Ishikawa, 1965 species. However, *Poecilagenia* has an elongated body and punctuated integument that differs from the short body and polished integument shown on *P. wahisi* Waichert and Pitts sp. nov. Besides, *P. wahisi* has a transversal carina on the first metasomal segment, which is absent on *Poecilagenia* species. *Paleogenia* cannot be placed on *Nipponodipogon*, because it has two apical mandibular teeth, whereas in *Nipponodipogon* three teeth are present. Moreover, *Paleogenia* has hyaline wings, lacking basal or apical fascia on forewing, as present on *Nipponodipogon*.

Remarks.—Baltic amber deposits have been obtained for more than 100 years, and their age is controversial. Microfaunistic dating of the deposits containing the largest amount of amber suggest they are from the Priabonian, Eocene (37.7 Ma) (Kaplan et al. 1977), whereas radiometrically dated glauconite dates them as Lutetian, Eocene (47.0 to 44.1 Ma) (Ritzkowski 1997). Perkovsky et al. (2007) considered the Ritzkowski (1997) data insufficient to disprove Kaplan et al. (1977), because the former was based on two samples and the latter on seven samples. Novel data indicate that the age of Baltic Amber can be narrowed to 34–38 Ma (Aleksandrova and Zaporozhets 2008; Kosmowska-Ceranowicz 2012).

Stratigraphic and geographic range.—Eocene Baltic amber of the Kaliningrad region of Russia.

Paleogenia wahisi Waichert and Pitts sp. nov.

Fig. 3.

Etymology: In honour of Raymond Wahis who has greatly contributed to our knowledge of Pompilidae biodiversity.

Holotype: Complete male inclusion, OSAC Hy-10-80a.

Type locality: Kaliningrad Region, Baltic Sea, Russia.

Type horizon: Baltic amber, late Eocene.

Material.—Five specimens: 4 male, 1 female (OSAC Hy-10-80a–e), all from the type locality and horizon.

Diagnosis.—Wing hyaline; maximum width 0.45× its length; cells short and rounded; 2Rs cell about the same size as 1Rs; 2m-cu vein slightly curved, meeting 2Rs cell 0.5× distance from base to apex of cell; 2R1 ending on apex of the forewing instead of anterior margin; mid and hind tarsi pale brown with apex black; and 2M cell without an inflection at the base of the Cu vein.

Description.—Male. Body length 2.55 mm. Forewing 2.04 mm. Integument black; tarsomeres, fore and mid tibia brown; mid and hind tarsi pale brown, apex black; metasoma black. Punctuation inconspicuous. Head with sides convergent ventrally, vertex much broader than frons; clypeus short, trapezoidal; mandible with two sharpened apical teeth. Antennae short; ratio of first four segments 7:5:6:7; WA3 0.8× LA3; WA4 0.8× LA4. Pronotum short, width 2.0× length, posterior margin concave; pronotal disc well defined. Tibiae and tarsi with short sparse spines, almost smooth. Wing long; length of 2R1 cell 0.8× distance from edge to apex of wing; 2Rs as long as 1Rs; 2m-cu vein curved, meeting 2Rs cell 0.4× distance from base to apex of cell. Metasoma 0.9× as long as mesosoma.

Allotype.—Complete female inclusion OSAC-Hy-10-80b. Body length 3.8 mm. Forewing ~2.5 mm (forewing is folded). Integument black; front and mid tibia and tarsi, hind tarsi pale brown; palpi pale brown. Clypeus, antennae, mesosoma and wing as described for male. Metasoma 1.2× as long as mesosoma; stinger straight.

Remarks.—This species was probably a cleptoparasitoid pompilid. It shares characteristics of other pompilid cleptoparasitoids, such as short antennal segments with thick conspicuous setae. No extant species of Pepsini are known to act as cleptoparasites; the only representatives of the subfamily with this behaviour recorded or suspected are placed within Ageniellini (*Poecilagenia*), Deuterageniini (*Nipponodipogon*), and within Psoropempulini (*Psoropempula* Evans, 1974).

Stratigraphic and geographic range.—Eocene Baltic amber of the Kaliningrad region of Russia.

Family Bryopompilidae nov.

Type genus: *Bryopompilus* Engel and Grimaldi, 2006 with type species *Bryopompilus interfector* Engel and Grimaldi, 2006 based on the holotype (AMNH Bu-051), complete female inclusion from Tanai Village (on Ledo Road 105 km NW Myitkyna), Kachin, Burma, early Cenomanian.

Diagnosis.—Presence of an angularly protruding, rounded lobe on the posterior margin of the pronotum; the lobe is deeply incised, overlapping the anterior and posterior margins of the wing base. The mesepisternal groove is interrupted, not reaching the mesopleural margin. The fore wing has the Rs vein straight and attached to the distal wing margin; the costal vein reaches the wing distal margin, and the Rs vein of cell 1Rs is attached to the base of 1R1.

Remarks.—The single known specimen from Burmese am-

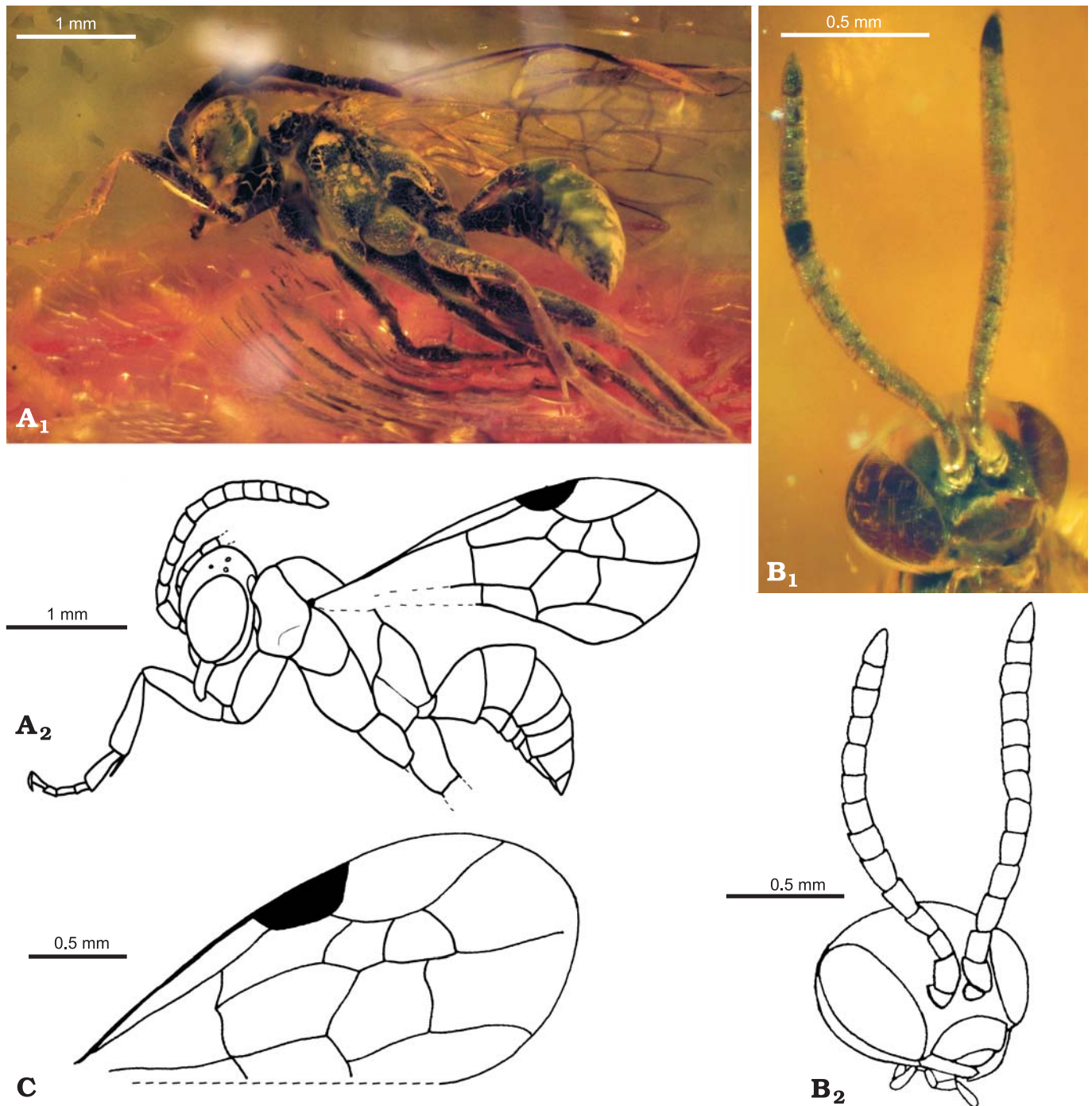


Fig. 3. Spider wasp *Paleogenia wahisi* Waichert and Pitts sp. nov. holotype, OSAC Hy-10-80, male specimen, from late Eocene Baltic amber, Kaliningrad Region, Baltic Sea, Russia. **A.** Habitus in lateral view. **B.** Head. **C.** Forewing. Photographs (A₁, B₁), camera lucida illustrations (A₂, B₂, C).

ber, *Bryopompilus interfector* Engel and Grimaldi, 2006, is unusual as it is so much older than all other described Pompilidae fossils. Upon re-examining this specimen (not figured in this paper), we discovered that it does not have the diagnostic characters of Pompilidae (see Engel and Grimaldi 2006: figs. 1–5). The specimen exhibits a conspicuous, angularly protruding, rounded lobe on the posterior margin of the pronotum, which is absent in Pompilidae. Moreover, the jugal lobe is absent from the wing of this specimen, while present in Pompilidae, and the wing venation greatly differs

from that of Pompilidae. In *Bryopompilus interfector* the Rs vein is not rounded and is attached to the distal wing margin, the costal vein reaches the wing distal margin, and the Rs vein of the cell 1Rs is not attached to the base of the cell 2R1 but to the base of 1R1. The presence of a mesepisternal groove in *Bryopompilus interfector* could be confused with the same structure that defines Pompilidae. Nevertheless, the mesepisternal groove covers the whole mesopleuron in Pompilidae, while in *B. interfector* it does not reach the mesopleural margin. The placement of this fossil in extinct or

extant Hymenoptera families is dubious. *Bryopompilus intersector* is considered herein as a member of a new fossil family Bryopompilidae. This fossil has a rounded posterior lobe on the pronotum, which resembles the lobe observed in Apoidea. Nevertheless, this lobe is deeply incised and overlaps the wing base both above and below, whereas in Apoidea it is entire, rounded, and somewhat inflated, and only extremely rarely reaches the wing base and never overlaps it from above.

The age of Burmese amber has been assigned to the late Albian (106 to 100 Ma) based on palynology, insect and ammonite inclusions (Ross et al. 2010). A more recent study places the deposits in the early Cenomanian (ca. 98 Ma) using U-Pb zircon dating (Shi et al. 2012).

Stratigraphic and geographic range.—Kachin state of Burma, early Cenomanian Burmese Amber.

Concluding remarks

Because the Burmese amber specimen dating Pompilidae to the Late Cretaceous is no longer recognised as a member of the family, we reconsider the age of Pompilidae based on confirmed fossil and molecular data. The oldest fossils assigned with confidence to the family are from Baltic amber, which is dated from the Eocene; these taxa can be attributed to extant (crown-group) lineages and, thus, represent crown-group Pompilidae. These fossils are thus somewhat younger than the age (55–43 Ma) proposed for the common ancestor of crown-group Pompilidae by recent molecular dating analyses (Wilson et al. 2013; Waichert et al. 2015). Therefore, the common ancestor of extant Pompilidae must have existed prior to the Eocene, but more recently than 85 Ma (divergence of Pompilidae and Mutillidae), which was estimated as the age of the stem-group Pompilidae by molecular dating analyses of Aculeata (Wilson et al. 2013). Compared to the fossil record of other Hymenoptera (Grimaldi and Engel 2005), crown-group Pompilidae diversified more than 140 Myr after the origin of Hymenoptera, and more than 100 Myr after the origin of Aculeata. The oldest fossils of the sole hosts of Pompilidae, spiders (Araneae), are found in the Carboniferous (360–290 Ma) (Selden et al. 2013), with extant suborders and many sub-lineages found in Lower Jurassic fossils, ca. 175 Ma (Vollrath and Selden 2007; Penney and Selden 2011). Recent divergence-time estimation studies support the origin of crown-group spiders in the Late Devonian, and an origin for the majority of spider families before 100 Ma (Bond et al. 2014).

To compare the origin of pompilids with that of their prey, it is necessary to study the age of spiders used by pompilids as hosts. Many pompilids use wolf spiders (Lycosidae), Theridiidae, and jumping spiders (Salticidae), which originated after the beginning of the Palaeogene according to fossil data (Penney 2004), and diverged from their sister families before 50 Ma (Bond et al. 2014). Moreover, some other pompilids use older spider taxa such as velvet spiders

(Eresidae) (Raemakers and Helsdingen 1999) and crevice weaver spiders (Filistatidae) (Deyrup et al. 1988). Thus, the origin and diversification of at least the majority of Pompilidae must have occurred long after the origin of some of their host-spider lineages.

Pompilidae are unique among Hymenoptera in constituting a diverse, Palaeogene-aged lineage, in which all members preyed solely on spiders. These wasps most generally attacked hunting spiders and sheet-web spiders, but many species preyed on tarantulas and trap-door spiders. Use of spiders occurs only sporadically in other, younger hymenopteran taxa, e.g., *Trypoxylon* Latreille, 1796 (Crabronidae) wasps. The closest relatives of Pompilidae, Mutillidae, and Sapygidae (Pilgrim et al. 2008; Wilson et al. 2013), are predatoids (following the terminology of Evans 1963) of solitary wasp and bee larvae, and occasionally other insects. The ancestral prey type of Aculeata as a whole may have been beetle larvae and probably other concealed insect larvae. Thus, at some point after their divergence from Mutillidae and Sapygidae, pompilids shifted their prey specialization to spiders exclusively. This shift must have been accompanied by specialized behaviour to deal with potentially dangerous (venomous) prey capable of defense, which are often much larger than their attackers (Evans 1953; Evans and Shimizu 1996).

The fossil record of spiders documents an increase in family-level diversity (Penney et al. 2003) since the origin of Araneae in the Carboniferous (Selden et al. 2013), which, based on fossil data, correlates with insect diversification (Penney 2004). Family-level spider diversity shows episodes of diversification in both the Mesozoic and Paleogene, and appears to have been unaffected by the Cretaceous–Paleogene extinction event (Penney et al. 2003). It is challenging, however, to infer spider diversification based solely on the fossil record, given the bias in spider species descriptions to certain ages, depending on how well spiders are preserved in different types of deposits and how extensively different deposits have been studied (Penney and Selden 2011; Penney et al. 2012). Nevertheless, it is possible to suggest that spiders constituted a ubiquitous, diverse, and abundant source of prey after pompilids split from their sister group in the Late Cretaceous. Once stem-group pompilids evolved the skills to prey on spiders, the continued increase in spider diversity may have played a role in radiation of their pompilid predators in the early Paleogene, similar to the implied influence of insect radiations in general on the diversification of spiders (Penney 2004). This affirmation, however, should be tested using diversification models within a phylogenetic framework.

Acknowledgements

We are grateful to Frank Parker (formerly U.S. Department of Agriculture Agricultural Research Service, Logan, Utah, USA) for helping with the examination of the Bryopompilidae specimen, David Grimaldi (AMNH) for loaning amber specimens. We also thank Kimberly Sullivan, Susanne Janecke, Edward Evans (all Utah State University, Logan, USA), Lars Krogmann (Staatliches Museum

für Naturkunde, Stuttgart, Germany), Denis Brothers (University of KwaZulu-Natal, Durban, South Africa), Jason Dunlop (Museum für Naturkunde, Berlin, Germany), Anthony Harris (Otago Museum-Entomology, New Zealand), and other anonymous reviewers for their comments on the manuscript. The Utah Agricultural Experiment Station, Utah State University UAES #8490, supported this research. The National Science Foundation award DEB-0743763 to JPP and CDvD also supported this work.

References

- Aleksandrova, G.N. and Zaporozhets, N.I. 2008. Palynological characteristics of Upper Cretaceous and Paleogene deposits on the west of the Sambian Peninsula (Kaliningrad region), Part 2. *Stratigraphy and Geological Correlation* 16: 528–539.
- Bond, J.E., Garrison, N.L., Hamilton, C.A., Godwin, R.L., Hedin, M., and Agnarsson, I. 2014. Phylogenomics resolves a spider backbone phylogeny and rejects a prevailing paradigm for orb web evolution. *Current Biology* 24: 1765–1771.
- Brown, B.V. 1999. Re-evaluation of the fossil Phoridae (Diptera). *Journal of Natural History* 33: 1561–1573.
- Burleigh, R. and Whalley, P. 1983. On the relative geological ages of amber and copal. *Journal of Natural History* 17: 919–921.
- Day, M.C. 1988. *Spider Wasps. Hymenoptera: Pompilidae. Handbooks for the Identification of British Insects*. 66 pp. Royal Entomological Society, London.
- Deyrup, M., Cronin, J.T., and Kurczewski, F.E. 1988. *Allochares azureus*: an unusual wasp exploits unusual prey (Hymenoptera: Pompilidae; Arachnida: Filistatidae). *Psyche* 95: 265–282.
- Engel, M.S. and Grimaldi, D.A. 2006. The first Cretaceous spider wasp (Hymenoptera: Pompilidae). *Journal of the Kansas Entomological Society* 79: 359–368.
- Evans, H.E. 1953. Comparative ethology and the systematics of spider wasps. *Systematic Zoology* 2: 155–172.
- Evans, H.E. 1963. Predatory wasps. *Scientific American* 208 (4): 144–155.
- Evans, H.E. and Shimizu, A. 1996. The evolution of nest building and communal nesting in Ageniellini (Insecta: Hymenoptera: Pompilidae). *Journal of Natural History* 30: 1633–1648.
- Evans, H.E. and Yoshimoto, C.M. 1962. The ecology and nesting behavior of the Pompilidae (Hymenoptera) of the Northeastern United States. *Miscellaneous Publications of the Entomological Society of America* 3: 67–119.
- Grimaldi, D.A. 1995. The age of Dominican amber. In: K.B. Anderson and J.C. Crelling (eds.), *Amber, Resinite, and Fossil Resins. ACS Symposium Series* 617: 203–217.
- Grimaldi, D. and Engel, M.S. 2005. *Evolution of the Insects*. 755 pp. Cambridge University Press, Cambridge.
- Huber, J.T. and Sharkey, M.J. 1993. Structure. In: H. Goulet and J.T. Huber (eds.), *Hymenoptera of the World: An Identification Guide to Families*, 13–59. Research Branch Agriculture Canada Publication, Ottawa.
- Iturralde-Vinent, M.A. 2001. Geology of the amber-bearing deposits of the Greater Antilles. *Caribbean Journal of Science* 37: 141–167.
- Iturralde-Vinent, M.A. and MacPhee, R.D.E. 1996. Age and paleogeographical origin of Dominican amber. *Science* 273: 1850–1852.
- Kaplan, A.A., Grigelis, A.A., Strelnikova, N.I., and Glikman, L.S. 1977. Stratigraphy and correlation of Palaeogene deposits of South-Western cis-Baltic region [in Russian]. *Sovetskaâ Geologiâ* 4: 30–43.
- Kosmowska-Ceranowicz, B. 2012. *Bursztyn w Polsce i na świecie*. 299 pp. Wydawnictwa Uniwersytetu Warszawskiego, Warszawa.
- Lambert, J.B., Frye, J.S., and Poinar, G.O. 1985. Amber from the Dominican Republic—analysis by nuclear magnetic-resonance spectroscopy. *Archaeometry* 27: 43–51.
- Landis, G.P. and Snee, L.W. 1991. AR-40/AR-39 systematics and Argon diffusion in amber—implications for ancient earth atmospheres. *Global and Planetary Change* 97: 63–67.
- Penney, D. 2004. Does the fossil record of spiders track that of their principal prey, the insects? *Transactions of the Royal Society of Edinburgh, Earth Sciences* 94: 275–281.
- Penney, D. 2010. Dominican Amber. In: D. Penney (ed.), *Biodiversity of Fossils in Amber From the Major World Deposits*, 23–166. Siri Scientific Press, Manchester.
- Penney, D. and Selden, P.A. 2011. *Fossil Spiders: the Evolutionary History of a Mega-diverse Order. Monograph Series, Vol. 1*. 128 pp. Siri Scientific Press, Manchester.
- Penney, D., Dunlop, J.A., and Marusik, Y.M. 2012. Summary statistics for fossil spider species taxonomy. *ZooKeys* 192: 1–13.
- Penney, D., Wheeler, C.P., and Selden, P.A. 2003. Resistance of spiders to Cretaceous–Tertiary extinction events. *Evolution* 57: 2599–2607.
- Perkovsky, E.E., Rasnitsyn, A.P., Vlaskin, A.P., and Taraschuk, M.V. 2007. A comparative analysis of the Baltic and Rovno amber arthropod faunas: representative samples. *African Invertebrates* 48: 229–245.
- Pilgrim, E.M., Von Dohlen, C.D., and Pitts, J.P. 2008. Molecular phylogenetics of Vespoidea indicate parphyly of the superfamily and novel relationships of its component families and subfamilies. *Zoologica Scripta* 37: 539–560.
- Poinar, G., Jr. 2012. Desiomorphs in amber. *American Entomologist* 58: 214–222.
- Raemakers, I.P. and Helsdingen, P.J. van 1999. De vuurspindoder *Eoferreola rhombica*, een voor Nederland nieuwe spinnendoder, en haar bijzondere waard: de Lentevuurspin *Eresus sandaliatus* (Hymenoptera: Pompilidae; Araneae: Eresidae). *Nederlandse Faunistische Mededelingen* 9: 1–6.
- Ritzkowski, S. 1997. K-Ar-alternbestimmung der bernsteinführenden sedimente des samlandes (Paläogen, Bezirk Kaliningrad). *Metalla (Sonderheft)* 66: 19–23.
- Rodriguez, J. 2014. *Molecular Systematics, Historical Biogeography, and Evolution of Spider Wasps (Hymenoptera: Pompilidae)*. 340 pp. Ph.D. Thesis, Department of Biology, Utah State University, Logan.
- Ross, A., Mellish, C., York, P., and Crighton, B. 2010. Burmese Amber. In: D. Penney (ed.), *Biodiversity of Fossils in Amber From the Major World Deposits*, 23–166. Siri Scientific Press, Manchester.
- Schlee, D. 1990. *Das Bernstein-Kabinett: Begleitheft zur Bernsteinausstellung im Museum am Löwentor, Stuttgart*. 100 pp. Staatliches Museum für Naturkunde, Stuttgart.
- Selden, P., Shcherbakov, D., Dunlop, J., and Eskov, K. 2013. Arachnids from the Carboniferous of Russia and Ukraine, and the Permian of Kazakhstan. *Paläontologische Zeitschrift* 88: 297–307.
- Shi, G.H., Grimaldi, D.A., Harlow, G.E., Wang, J., Yang, M.C., Lei, W.Y., Li, Q.L., and Li, X.H. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37: 155–163.
- Shimizu, A. 2000. Cleptoparasitic behavior and flagellar sensilla of *Poecilagenia sculpturata* (Hymenoptera: Pompilidae). *Entomological Science* 3 (3): 499–510.
- Shimizu, A., Nishimoto, Y., Makino, S., Sayama, K., Okabe, K., and Endo, T. 2012. Brood parasitism in two species of spider wasps (Hymenoptera: Pompilidae, *Dipogon*), with notes on a novel reproductive strategy. *Journal of Insect Behavior* 25: 375–391.
- Vollrath, F. and Selden, P. 2007. The role of behavior in the evolution of spiders, silks, and webs. *Annual Review of Ecology, Evolution, and Systematics* 38: 819–846.
- Waichert, C., Rodriguez, J., Wasbauer, M.S., von Dohlen, C.D., and 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* 175: 271–287.
- Wasbauer, M.S. and Kimsey, L.S. 1985. California spider wasps of the subfamily Pompilinae (Hymenoptera: Pompilidae). *Bulletin of the California Insect Survey* 26: 1–130.
- Wilson, J.S., Von Dohlen, C.D., Forister, M.L., and Pitts, J.P. 2013. Family-level divergences in the stinging wasps (Hymenoptera: Aculeata), with correlations to Angiosperm diversification. *Evolutionary Biology* 40: 101–107.