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REVIEW OF HAWAIIAN VESPIDAE (HYMENOPTERA)

JAMES M. CARPENTER

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Cover: *Vespula pensylvanica* queen. Photo: David Foote

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Review of the Hawaiian Vespidae (Hymenoptera)

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Abstract. A key to the genera of Vespidae occurring in Hawai'i is presented. New generic synonymies include *Chelodynerus* Perkins, 1902, and *Pseudopterocheilus* Perkins, 1901, = *Nesodynerus* Perkins, 1901. All Hawaiian species presently placed in the genus *Odynerus* Latreille are transferred either to *Euodynerus* Dalla Torre (four species) or to *Nesodynerus* (94 species).

Introduction

Hawai'i is celebrated for its profusion of species flocks, and within Hymenoptera, a notable example is in wasps of the family Vespidae. More than 100 endemic species are known, all in the subfamily Eumeninae, commonly known as potter wasps. These species were largely described by R.C.L. Perkins (1899, 1901, 1902, 1906, 1910, 1912b), with the great majority in the genus *Odynerus* Latreille. Recent checklists (Nishida, 1992, updated in 1994 and 1997; the fourth edition also online: Nishida, 2002) follow Perkins's generic assignments. However, Perkins's concept of *Odynerus* was the very broad genus that was decisively challenged by Blüthgen (1938), who began a process of splitting the genus that has prevailed since (see Carpenter, 1986; van der Vecht & Carpenter, 1990). That trend never reached Hawai'i, although Giordani Soika (1958: 198) noted that the majority of Hawaiian species belonged to *Parodynerus* de Saussure, which he elevated to genus. Nothing formal followed, but that is rectified here. Giordani Soika's view was not correct, but none of the Hawaiian species belong in *Odynerus* as it is presently construed.

In addition to describing many species of *Odynerus*, Perkins (1901, 1902) described three genera of endemic Hawaiian wasps: *Chelodynerus*, *Nesodynerus* and *Pseudopterocheilus*. All were described in keys, and the characters diagnosing them are evidently autapomorphies: *Chelodynerus* was distinguished by the elongate malar space (Fig. 24) and mandibular teeth reduced, *Nesodynerus* by loss of the midtibial spur (Fig. 4), and *Pseudopterocheilus* by having a psammophore (the labial[1] palpi enlarged and it and the mandibles fringed with long hairs, used in other eumenines having this feature as a basket to carry sandy soil; Fig. 23). However, all three genera share with the majority of the Hawaiian "*Odynerus*" the same features of a laterally semicircular tegula (Fig. 6), female lacking cephalic foveae, usually weak impressions on the anterior pronotal face (Fig. 18), valvulae fused to the submarginal carina but with a notch between them and slightly projecting posteriorly (variable in development), and slightly narrowed first metasomal tergum (Fig. 13). Some of these are certainly derived features, and indicate that these wasps form a single lineage. *Parodynerus* differs from that lineage in three important characters: (1) the shape of the tegula, which is not curved and evenly expanded laterally, instead

1. Perkins incorrectly gave "maxillary" in his keys, as he later noted (Perkins, 1912a).

being largely straight then narrowed; (2) females having cephalic foveae, and (3) valvulae not slightly projecting. *Odynerus* in the modern sense is basically a Holarctic genus with just 45 species, differing in all the characters just mentioned. The Hawaiian species currently placed in *Odynerus* must be transferred, then, but not to *Parodynerus*. Their relationships to other genera of Eumeninae are not clear (see below), and so they should not be transferred to one of the described genera outside of Hawai'i. Moreover, there is nothing to define the species currently placed in *Odynerus* as a group versus the three endemic genera save absence of the respective autapomorphies of those genera. Thus, those "genera" are but small subgroups of the main lineage of Hawaiian Eumeninae, and recognition of them results in paraphyly. Accordingly, the most efficient course is to synonymize all three genera, and transfer most of the species currently placed in *Odynerus* to that genus. That course is taken here. *Nesodynerus* and *Pseudopterocheilus* were described in the same publication, one year before *Chelodynerus*; as first reviser I select *Nesodynerus* as the name for the genus.

Although most of the endemic species of Hawai'i are the lineage that may be termed *Nesodynerus*, that is not true of all of them. Four of the species are part of another lineage, that corresponds to the genus *Euodynerus* Dalla Torre. These are quite different from the species of *Nesodynerus*, as shown in the key.

It is noteworthy that these conclusions were anticipated by Perkins (1913: lxxxix) himself:

> "This family is represented by a greater number of species than any other of the indigenous Hymenoptera, and all, to the number of 102, belong to the ubiquitous genus *Odynerus, sensu latiori*. From this interesting complex I have split off some small groups of species and considered them as distinct genera, as indeed they are, although they appear to be derivatives of the same stock, as the Hawaiian *Odynerus* proper. *Odynerus nigripennis* and its three allies are of different descent from that of all the others, and certainly are sprung from a quite different[2] ancestral immigrant. If the classification of the *Odynerus* of the world were not in such a chaotic state, these four species would not be placed in the same genus as the others, and a number of genera or subgenera, allied to one another, would also be formed for the dispersion of the bulk of the Hawaiian species."

Finally, it should be observed that, while the endemic fauna is part of just two lineages, for more than a century species of Vespidae have been introduced into Hawai'i from many places, and now the main generic diversity is adventive. Although that encompasses few species, they can be much more abundant than native species, and their number can only be predicted to increase.

Key to Genera of Hawaiian Vespidae

The key presented here allows separation of the genera so far recorded from Hawai'i. The checklist of Hawaiian arthropods (Nishida, 2002) listed another genus not included here, *Ropalidia* (in Nishida, 1992, as *Icaria*, a synonym). The *Ropalidia* record is *marginata* Lepeletier, from Midway, which is part of the Hawaiian archipelago but not the state. The fauna of Midway consists entirely of introduced species (see list in Nishida & Beardsley, 2002), and *R. marginata* is the most widespread species of *Ropalidia* in the Pacific Islands (Kojima & Carpenter, 1997). The genus would key to the Polistinae in the key presented

2. No doubt Asiatic; since allied Japanese species exist.

here; *R. marginata* differs from all taxa considered here in having the second metasomal tergum and sternum completely fused (and see Carpenter & Nguyen, 2003). Nishida & Beardsley (2002) also listed *Parancistrocerus fulvipes* (de Saussure) from Midway; that American species would key to *Nesodynerus* in the key presented here, but has deep pits on the anterior face of the pronotum, not shallow impressions. The online version of the checklist also listed the genus *Eumenes* from Hawai'i, however that is dated, as the taxa recorded are now placed in the genus *Delta*, and so the records are duplicates.

1. Midtibia with two spurs (Figs. 1–2); scutum posterolaterally without parategula (Fig. 5); claws toothless (Figs. 1–2); eusocial 2
–. Midtibia with one spur (Fig. 3) or none (Fig. 4); scutum posterolaterally with parategula (Figs. 6–8); claws bifid (cleft at tip; Figs. 3–4); solitary ... (Eumeninae) 4

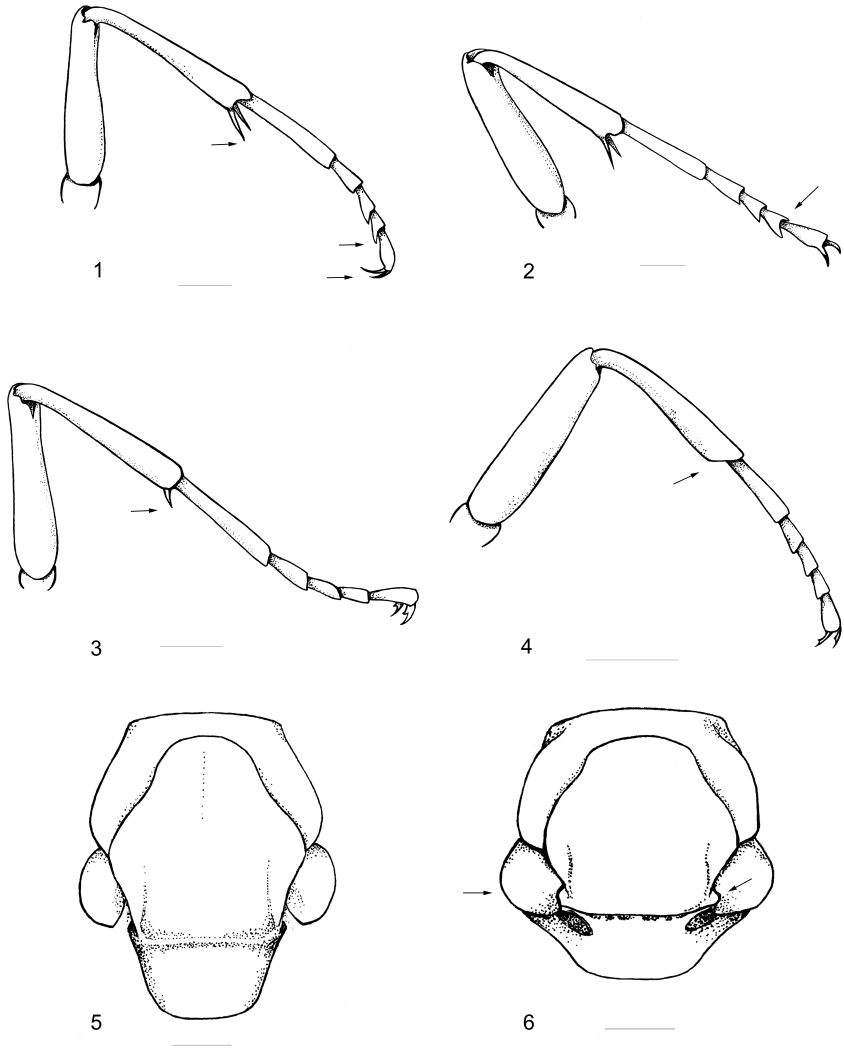
2. First metasomal segment anteriorly truncate in dorsal view (Fig. 9), sharply angular in lateral view (Fig. 14); hindwing lacking jugal lobe (Fig. 16) ... (Vespinae) ... . **Vespula** Thomson
–. First metasomal segment not anteriorly truncate in dorsal view (Figs. 10–11), gradually sloping in lateral view (Fig. 15); hindwing with jugal lobe (Fig. 17) ... (Polistinae) 3

3. First metasomal segment petiolate: in dorsal view with width half or less that of II, and at least twice as long as wide (Fig. 10); mid- and hindtarsi with third and fourth segments asymmetrical, inner lobe longer than outer lobe (Fig. 1) .... **Mischocyttarus** de Saussure
- First metasomal segment subsessile: funnel-shaped in dorsal view (Fig. 11); mid- and hindtarsi with third and fourth segments symmetrical (Fig. 2) ... **Polistes** Latreille

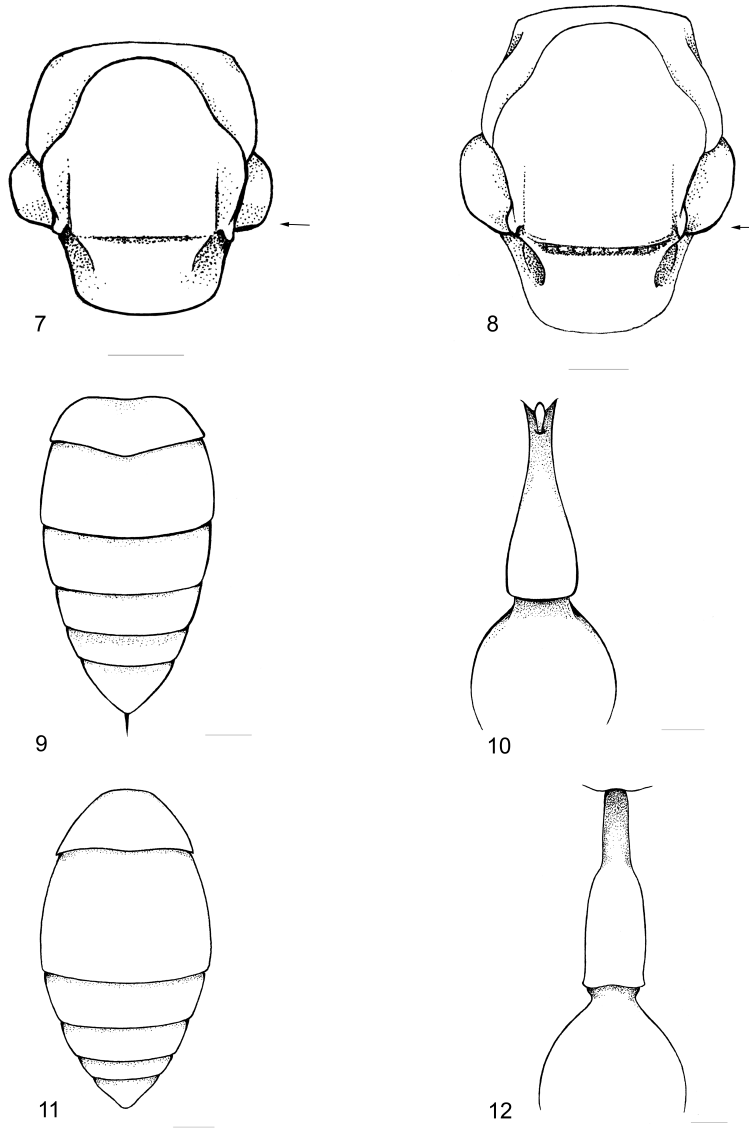
4. First metasomal segment petiolate: in dorsal view with width half or less that of II, and more than twice as long as wide (Fig. 12) ..... **Delta** de Saussure
- Metasoma not petiolate: segment I with width more than half that of II, much less than twice as long as wide (Fig. 13) 5

5. Tegula laterally semicircular, about as long as wide and evenly rounded (Fig. 6); anterior face of pronotum usually with weak impressions medially (Fig. 18) .... **Nesodynerus** Perkins
- Tegula with length exceeding width, little curved laterally (Figs. 7–8); anterior face of pronotum smooth (Figs. 19–20) 6

6. Pronotum with oblique humeral carina (Fig. 19); tegula truncate posteriorly (Fig. 7); second metasomal sternum truncate basally and not depressed medially (Fig. 21) ..... **Pachodynerus** de Saussure
- Pronotum without oblique humeral carina (Figs. 18, 20); tegula narrowed posteriorly (Fig. 8); second metasomal sternum curving basally and depressed medially (Fig. 22) ..... **Euodynerus** Dalla Torre



Figs. 1–4. Midleg. 1, *Mischocyttarus flavitarsis*. **2**. *Polistes fuscatus*. **3**. *Euodynerus localis*. **4**. *Nesodynerus rudolphi*. **Figs. 5–6.** Scutum and tegulae. **5.** *Polistes fuscatus*. **6**. *N. rudolphi*. Scale bars = 1 mm.



Figs. 7–8. Scutum and tegulae. **7**. *Pachodynerus nasidens*. **8**. *Euodynerus localis*. **Figs. 9–12.** First metasomal segment in dorsal view. **9**. *Vespula pensylvanica*. **10**. *Mischocyttarus flavitarsis*. **11**. *Polistes fuscatus*. **12**. *Delta campaniforme*. **13**. *Nesodynerus rudolphi*. Scale bars = 1 mm.

Taxonomic Notes

Subfamily Eumeninae
Genus ***Delta*** de Saussure

Delta de Saussure, 1855: 130, 132, 143. Type species: *Vespa maxillosa* De Geer, 1775 [= *Vespa emarginata* Linnaeus, 1758], by subsequent designation of Bequaert, 1925: 137 [erroneously as *Sphex maxillosus* De Geer].

Erinys Zirngiebl, 1953: 173, subgenus of *Eumenes* Latreille. Type species: *Vespa unguiculata* Villers, 1789, by monotypy. [Junior homonym of *Erinys* Rye, 1876 (Coleoptera).]

The genus is adventive in Hawai‘i. Its taxonomy is currently in a confused state, but there are nearly 50 species recognized, and near again as many subspecies, distributed throughout the Old World, with one species adventive in North America and the Antilles.

There are four entries for the genus *Delta* in Nishida (2002): *campaniforme campaniforme* (Fabricius), *campaniforme esuriens* (de Saussure), *latreillei* and *latreillei petiolare* (Schulz). There are also two entries for the genus *Eumenes*: *latreillei* and *pyriformis*, both of which are now placed in the genus *Delta*. Both the record for *latreillei* and that for *latreillei petiolare* evidently refer to the same taxon, which was first recorded from Hawai‘i as *Eumenes pyriformis petiolaris* by Townes (1947) and Maehler (1947a), and then by Williams (1948) as *Eumenes latreillei petiolaris*; it is now known as *Delta latreillei petiolare*, from New Guinea, the Solomon Islands, and the Admiralty Islands. The record for *pyriformis* evidently refers to the taxon recorded as *Eumenes pyriformis philippinensis* by Williams (1948); it is now known as *Delta pyriforme philippinense* (Bequaert), from the Philippines. The record for *campaniforme campaniforme* evidently refers to the taxon recorded as *Eumenes campaniformis* by Maehler (1947b); now known as *Delta campaniforme campaniforme*, ranging from Australia to Southeast Asia. The record for *campaniforme esuriens* perhaps refers to the same taxon; *esuriens* is now considered a species (Giordani Soika, 1992), but has frequently been misidentified in the literature.

Delta curvatum (de Saussure) was also recorded from Hawai‘i, as *Eumenes curvatus* by Beardsley (1978). It was listed in Nishida (1992, 1994, 1997) but is not in Nishida (2002), and thus may no longer occur in Hawai‘i. It is actually assignable to the genus *Phimenes* Giordani Soika, but in my opinion that genus should be synonymized with *Delta*, and therefore *Phimenes* is not included in the key.

Wasps of the genus *Delta* make nests of free mud cells attached a variety of substrates. The likely mode of transport of these wasps to the Hawaiian Islands was described by Weber (1948: 206) for *D. latreillei petiolare*; he reported arriving in O‘ahu by steamship from South Pacific islands, and finding “many nests of this wasp on the rudder, propellers and cradles of two motorboats carried on the deck cargo.” Prey consist of Microlepidoptera, the most common prey of Eumeninae.

Genus ***Euodynerus*** Dalla Torre

Euodynerus Dalla Torre, 1904: 38; declared available from date of publication by Opinion 893 (International Commission on Zoological Nomenclature, 1970). Type species: *Vespa dantici* Rossi, 1790, by subsequent designation of Blüthgen, 1938: 277; confirmed by Opinion 893.

The genus is cosmopolitan, and comprises more than 100 species, with the majority of the species being Holarctic. There are four endemic Hawaiian species presently placed in *Odynerus* and now assigned to *Euodynerus* as **new combinations**: *Euodynerus episeustes* (Perkins), *E. localis* (Smith), *E. nigripennis* (Holmgren) and *E. radula* (Fabricius). These belong to the nominotypical subgenus. Their relationships are unclear: they have overall resemblance to Japanese species such as *Euodynerus dantici* (Rossi), but do not share specific, derived features.

Euodynerus nigripennis and *E. radula* nest in a variety of pre-existing cavities (Perkins, 1913; Williams, 1927), which is commonly referred to as "renting" behavior (see Iwata, 1976), and which is the predominant mode of nesting in the genus worldwide. Prey consist of Microlepidoptera.

It is worth mentioning that, as discussed by Swezey (1929), *E. radula* is the earliest described Hawaiian insect. It was evidently collected in Cook's voyage of discovery, during the landing at Waimea in Kaua'i on 21 January 1778. The type became part of the Banks collection in London, and was described as *Vespa radula* by Fabricius in 1787. Just one other insect was ever described from that voyage, also from the Banks collection, the ichneumonid described as *Ichneumon fuscator* by Fabricius in 1793.

Genus ***Nesodynerus*** Perkins

Nesodynerus Perkins, 1901: 267, genus, in key (3 species). Type species: *Odynerus rudolphi* Dalla Torre, 1889 (replacement name for *Odynerus cardinalis* Blackburn, 1886, *non* Morawitz, 1885), by subsequent designation of Carpenter, 1986: 76.

Pseudopterocheilus Perkins, 1901: 266, genus, in key. Type species: *Odynerus pterocheiloides* Perkins, 1899, by original designation. **New synonymy.**

Chelodynerus Perkins, 1902: 136, genus, in key. Type species: *Odynerus chelifer* Perkins, 1899, by monotypy. **New synonymy**.

The genus is endemic to Hawai'i. Bohart (1940: 165) stated of *Pseudopterocheilus*: "It appears to be most closely related to the subgenus *Stenodynerus* and may be a specialized offshoot from it." The comment applies to the entire lineage including *Pseudopterocheilus*, that is, the genus *Nesodynerus* in the present, revised sense. The laterally semicircular tegula does support a relationship with the *Leucodynerus-Stenodynerus* component of Carpenter and Cumming (1985), but the absence of deep pits or foveae on the anterior pronotal face casts doubt on a particularly close relationship with *Stenodynerus* itself, although the typically faint impressions in *Nesodynerus* could be derived from deep pits, as may be the case with some Caribbean species of *Stenodynerus*, in which the females also lack cephalic foveae. *Nesodynerus* does not appear to be closely related to Oriental representatives of the worldwide *Leucodynerus-Stenodynerus* clade such as the genus *Paraleptomenes*, which lacks female cephalic foveae and also lacks pits on the anterior pronotal face, but is punctate there, and also has the submarginal carina well developed.

Nishida (1992, 1994, 1997, 2002) listed 12 species in *Nesodynerus*. One of these, *N. conifer* (Perkins) was transferred to the genus from *Odynerus* by Perkins (1906: 69), although he later (Perkins, 1912b: 727) stated that this was a mistake. Another, *N. floscu-*

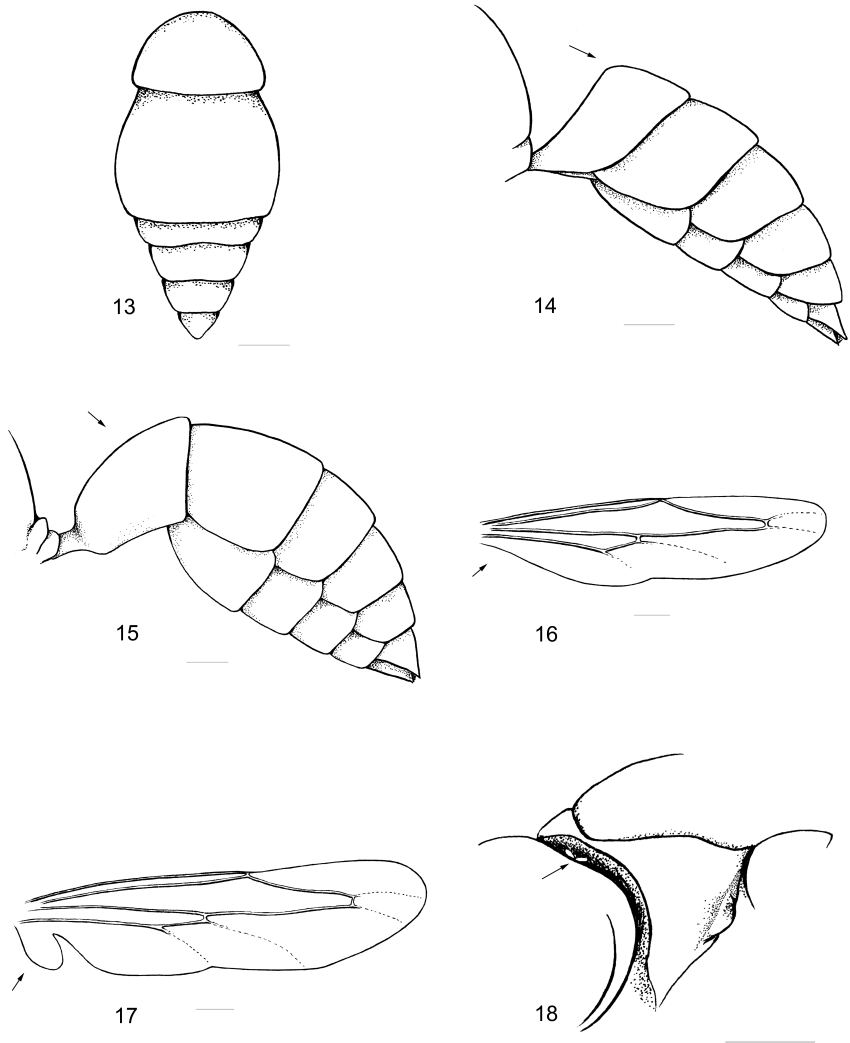
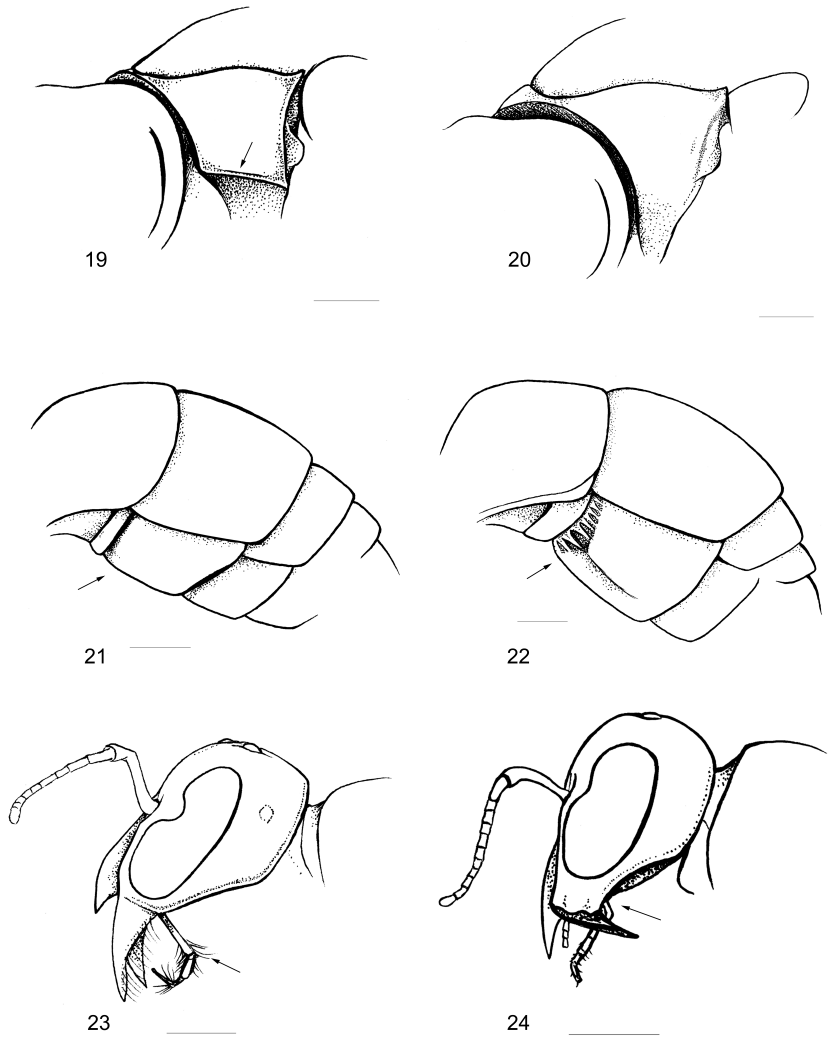


Fig. 13. *Nesodynerus rudolphi*, first metasomal segment in dorsal view. **Figs. 14–15**. First metasomal segment in lateral view. **14**. *Vespula pensylvanica*. **15**. *Polistes fuscatus*. **Figs. 16–17**. Hindwing. **16**. *Vespula pensylvanica*. **17**. *Polistes fuscatus*. **Fig. 18**. *Nesodynerus rudolphi*, pronotum in oblique anterior view. Scale bars = 1 mm.



Figs. 19–20. Pronotum in oblique anterior view. **19**. *Pachodynerus nasidens*. **20**. *Euodynerus localis*. **Figs. 21–22**. Second metasomal sternum in oblique lateral view. **21**. *Pachodynerus nasidens*. **22**. *Euodynerus localis*. **Figs. 23–24.** Head in lateral view. **23**. *Nesodynerus congruus*. **24**. *Nesodynerus chelifer*. Scale bars = 1 mm.

lus (Perkins) was treated as a variety of *O. waianaeanus* Perkins by Perkins (1901), which itself was never placed in *Nesodynerus*, and I can find no other references to *N. flosculus* until Nishida (1992). Evidently *N. flosculus* is to be considered a synonym of *O. waianaeanus*. The other 10 species consist of two described in *Nesodynerus* (*N. optabilis* Perkins and *N. paractias* Perkins) and eight transferred from *Odynerus* by Perkins (1901, 1906, 1910, 1913) and Giffard (1913): *N. acyanus* (Perkins), *N. cooki* (Perkins), *N. dilatatipes* (Perkins), *N. egens* (Perkins), *N. eupteryx* (Perkins), *N. oblitus* (Perkins), *N. rudolphi* (Dalla Torre) and *N. vittativentris* (Perkins). Finally, *O. brevicostatus* Perkins was stated by Perkins (1906: 67, footnote) to belong very probably to *Nesodynerus*, but was never formally transferred.

Chelodynerus is monobasic; *Nesodynerus chelifer* (Perkins) is a **new combination**. *Pseudopterocheilus* includes three species; **new combinations** transferred from it are *N. congruus* (Smith), *N. pterocheiloides* (Perkins) and *N. relictus* (Perkins).

The assignment of four species of Hawaiian "*Odynerus*" to *Euodynerus* leaves a total of 93 listed in the genus in Nishida (2002). The list is different from Nishida (1992), in that the following species are in the earlier list but not the later version: *O. blackburni* Smith, *O. nautarum* (de Saussure), *O. obscurepunctatus* (Blackburn) and *O. rubropustulatus* (Blackburn). These species are listed in both the second and third editions of the checklist (Nishida, 1994, 1997), and have not been synonymized, hence must have been omitted through oversight. All four versions of the list also omit a species: *O. illudens* Perkins. Two of the remaining entries in all versions of the list are actually synonyms: *O. ecostatus* Perkins was stated by Perkins (1912b: 726) to be identical with the type of *O. haleakalae* Blackburn, and *O. venator* Perkins was stated by Perkins (1912b: 726) to be identical with the type of *O. hawaiiensis* Blackburn. *Odynerus instabilis* Perkins, 1899, is listed in all versions, but it is a primary junior homonym of *O. instabilis* Smith, 1857, and was replaced by *O. ganahli* Dalla Torre, 1904. Nishida (1992, 2002) also listed *O. brevithorax* de Saussure, which is a species of *Pachodynerus*; it was not listed in Nishida (1994, 1997), and was not recorded from Hawai‘i in Willink and Roig-Alsina (1998). Finally, Nishida (2002) listed *O. luzonensis* Rohwer, a species now placed in the genus *Antepipona*, which was not recorded from Hawai‘i in Giordani Soika (1982).

With the foregoing corrections, there are a total of 94 species and one additional subspecies to be transferred from *Odynerus* to the genus *Nesodynerus* (see Appendix). With the 11 species already placed in *Nesodynerus*, and the four brought in because of new generic synonymy, there are 109 endemic species plus one additional subspecies in *Nesodynerus*. This is a remarkable number, and all the more so as nearly all were described in the course of a couple of decades, and none have been described in almost 50 years (the last was by Yoshimoto, 1959).

Nesting behavior is known for relatively few species, but these show marked diversity in behavior, ranging from burrowing in soil, to renting a variety of pre-existing cavities, to making free mud cells (Perkins, 1913; Williams, 1927). The majority are renters: burrowing is known in *N. sociabilis* and free mud cells in *N. oahuensis*, while renting is known in *N. eucharis*, *N. hiloensis*, *N. montanus*, *N. obscurepunctatus*, *N. paludicola*, *N.*

pseudochromoides, *N. pseudochromus, N. rudolphi* and *N. unicus*. Williams (1927: plate XVI) figures the nests of some of these species. Prey consist of Microlepidoptera.

Genus ***Pachodynerus*** de Saussure

Pachodynerus de Saussure, 1870: 56, division of subgenus *Odynerus* of genus *Odynerus* Latreille (4 species); declared available from date of publication by Opinion 893. Type species: *Odynerus californicus* de Saussure, 1870, by subsequent designation of Bohart, 1951: 892; confirmed by Opinion 893.

Monobiella Ashmead, 1900: 312, genus. Type species: *Vespa atrata* Fabricius, 1798, by monotypy.

The genus is adventive in Hawai‘i; its 45 species are primarily Neotropical, with a few in North America. One species, *Pachodynerus nasidens* (Latreille), was first recorded from Hawai‘i by Giffard (1913a), as *Odynerus nasidens*; he later (Giffard, 1913b) referred to it as *P. simplicicornis* (de Saussure), now considered a synonym (Willink, 1972). This species is now widespread throughout the Pacific; see the recent summary in Yamane *et al.* (1996).

The genus shows considerable plasticity in nesting behavior, but most species known are renters (Willink & Roig-Alsina, 1998). *Pachodynerus nasidens* has been found to use such cavities as abandoned mud dauber cells, but also to make mud cells behind wooden siding of buildings, etc., thus it is easily transported. Nishida & Beardsley (2002) gave the amusing common name “keyhole wasp” in obvious reference to its nesting habits. Prey consist of Microlepidoptera.

Subfamily Polistinae
Tribe Mischocyttarini
Genus ***Mischocyttarus*** de Saussure

Mischocyttarus de Saussure, 1853: 19, genus (2 species). Type species: *Zethus labiatus* Fabricius, 1804, by subsequent designation of Ashmead, 1902: 166.

The genus is adventive in Hawai‘i; it is primarily Neotropical, with a few Nearctic species, and with 245 species is the largest genus in the Vespidae.

Richards (1978a) mentioned that *Mischocyttarus flavitarsis idahoensis* Bequaert was introduced in the Hawaiian Islands, but gave no further details. Nishida (2002), where the taxon is listed both as *M. flavitarsis* and *M. flavitarsis idahoensis*, gave O‘ahu as locality. The subspecies was sunk by Snelling (1983). The species is Nearctic.

As with the other social wasps, introduction of *Mischocyttarus* presumably occurred through transport of overwintering queens, which are inseminated and found colonies on their own upon emergence. Prey of the social wasps consist of a variety of arthropods, which are masticated and fed directly to the larvae.

Tribe Polistini
Genus ***Polistes*** Latreille

Polistes Latreille, 1802: 363, genus. Type species: "*Polistes gallica*, Fab." [=*Vespa gallica* Linnaeus, 1767], by subsequent designation of Latreille, 1810: 438.

Eupolistes Dalla Torre, 1904: 68, name for "Premiere division" of *Polistes* Latreille in de Saussure, 1853: 45 (61 species). Type species: *Vespa gallica* Linnaeus, 1767, by subsequent designation of Richards, 1973: 86.

Pseudopolistes Weyrauch, 1937: 266, 274, genus (3 species). Unavailable; name proposed after 1930 with no type species designated.

Sulcopolistes Blüthgen, 1938: 273, subgenus of *Polistes* Latreille. Type species: *Polistes semenowi* Morawitz, 1889 [= *semenowii*], by original designation.

Polistula Weyrauch, 1938: 273, genus (5 species). Unavailable; name proposed after 1930 with no type species designated.

Polistula Weyrauch, 1939: 148, genus. Type species: *Polistes kohli* Dalla Torre, 1904 [= *Polistes biglumis* Linnaeus, 1758], by original designation.

Pseudopolistes Weyrauch, 1939: 195, genus. Type species: *Polistes sulcifer* Zimmermann, 1930, by original designation.

Leptopolistes Blüthgen, 1943: 99, 121, subgenus of *Polistes* Latreille. Type species: *Polistes associus* Kohl, 1898, by original designation.

The genus is adventive in Hawai'i; it is cosmopolitan, and comprises 211 species. Nishida (1992) listed four species in Hawai'i, but in Nishida (2002) the total is seven taxa: *P. aurifer* (de Saussure), *P. carnifex* (Fabricius), *P. carnifex carnifex* (Fabricius), *P. exclamans* Viereck, *P. fuscatus* (Fabricius), *P. jokahamae* Radoszkowski (as *P. jadwigae*, a synonym) and *P. olivaceus* (De Geer). The records for *P. carnifex* and *P. fuscatus* presumably refer to *P. carnifex carnifex* and *P. aurifer*, respectively (*P. aurifer* was considered a subspecies of *P. fuscatus* for much of the last century, e. g., Richards, 1978a). Richards (1978b: 21) mentioned that a form like *P. tepidus religiosus* Cheesman is found in Hawai'i, but that name is a *nomen nudum*, and according to Snelling (1997) the specimens on which the *nomen nudum* is based are *P. hebridensis* Giordani Soika[3] with misinterpreted labels, hence *P. tepidus* is mistakenly recorded from Hawai'i.

Species of this genus are the oldest records of introduced Vespidae in Hawai'i. Blackburn & Kirby (1880: 88) recorded *P. aurifer* as "Plentiful all over the islands" and noted it as "A well-known Californian species." Blackburn & Cameron (1886) added *P. hebraeus* (Fabricius), a synonym of *P. olivaceus*, which they stated was common in Oahu; they were uncertain as to whether it was introduced by human agency or in driftwood, but considered *P. aurifer* to have been introduced in timber from America. These two species were all that were listed in Perkins (1899), but he later (Perkins, 1913) listed a third, *P. macaensis* (Fabricius). Perkins (1913: xcix) stated that *P. macaensis* and *P. aurifer* were present in Hawai'i more than 30 years before, but that *P. hebraeus* was a later introduction, not generally distributed in 1892. However, *P. macaensis* is like *P. hebraeus* presently considered a synonym of *P. olivaceus*. Perkins referred to differences in the processes of the terminal metasomal sternum in the male, and to judge from the illustrations of these processes in Williams (1947: figs. 2a–b) *P. macaensis* was a misidentification for *P. jokahamae*: the figure of *P. macaensis* corresponds to these structures in *P. jokahamae*. *Polistes jokahamae* was also mentioned from Hawai'i by Richards (1978a, as *P. jadwigae*). Other species of *Polistes* were reported much later (Clagg, 1952: *P. exclamans*; Nishida, 1992: *P. carnifex* — not listed in Nishida, 1994, 1997).

3. Snelling did not say to which of the four described subspecies of *P. hebridensis* the specimens corresponded; based on locality, it would presumably be *P. hebridensis vilensis* Giordani Soika.

The majority of the introduced species are from the New World: *P. aurifer* is from western North America and *P. exclamans* from the Southeast, while *P. carnifex* is found from Argentina to the southwestern USA. *Polistes jokahamae* is from East Asia, and *P. olivaceus* is distributed circum-Indian Ocean and across Asia, but both species are now found on many Pacific islands (Carpenter, 1996).

Subfamily Vespinae
Genus ***Vespula*** Thomson

Vespula Thomson, 1869: 79, subgenus of *Vespa* (8 species). Type species: *Vespa austriaca* Panzer, 1799, by subsequent designation of Ashmead, 1902: 164.

Pseudovespa Schmiedeknecht, 1881: 314, subgenus of *Vespa* Linnaeus. Type species: *Vespa austriaca* Panzer, 1799, by monotypy.

Paravespula Blüthgen, 1938: 271, subgenus of *Dolichovespula* Rohwer. Type species: *Vespa vulgaris* Linnaeus, 1758, by original designation.

Allovespula Blüthgen, 1943: 149, subgenus of *Paravespula* Blüthgen. Type species: "*Paravespula rufa* (Linné)" [= *Vespa rufa* Linnaeus, 1758], by monotypy.

Rugovespula Archer, 1982: 261, 264, subgenus of *Vespula* Thomson. Type species: *Vespa koreensis* Radoszkowski, 1887, by original designation.

The genus is adventive in Hawai'i; the 26 species are primarily Holarctic, with a few species extending into Central America and Southeast Asia. Two species have been reported as established in Hawai'i, *Vespula pensylvanica* (de Saussure) and *V. vulgaris* (Linnaeus). The former is from western North America, while the latter is Holarctic. *Vespula pensylvanica* was first reported by Williams (1921, as *Vespa occidentalis*, a synonym), while *V. vulgaris* was recorded much later (Howarth, 1975). *Vespula pensylvanica* is widespread while *V. vulgaris* has been reported only from Maui (Nishida, 2002), and it is likely no longer present in Hawai'i, having not been seen since 1991 (N. Evenhuis, *in litt.*). A higher elevations *V. pensylvanica* may achieve high population densities, with numerous perennial colonies (Gambino *et al.*, 1990; Gambino, 1991), exerting extensive predation pressure on the endemic fauna (Gambino, 1992). Recent introductions of yellowjackets were in shipments of Christmas trees (W. Gagné, pers. comm.)!

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Appendix. The taxa listed below are all transferred from the genus *Odynerus* as **new combinations** in the genus *Nesodynerus.*

Nesodynerus acoelogaster (Perkins)
Nesodynerus aprepes (Perkins)
Nesodynerus axestes (Perkins)
Nesodynerus blackburni (Kirby)
Nesodynerus brevicostatus (Perkins)
Nesodynerus caenosus (Perkins)
Nesodynerus camelinus (Perkins)
Nesodynerus cephalostictus (Perkins)
Nesodynerus charadrophilus (Perkins)
Nesodynerus crypterythrus (Perkins)
Nesodynerus cyanopteryx (Perkins)
Nesodynerus cyphotes (Perkins)
Nesodynerus cypris (Perkins)
Nesodynerus deinogaster (Perkins)
Nesodynerus dromedarius (Blackburn)
Nesodynerus dryas (Perkins)
Nesodynerus dubiosus (Smith)
Nesodynerus dyserythrias (Perkins)
Nesodynerus eludens (Perkins)
Nesodynerus erro (Perkins)
Nesodynerus erythrognathus (Perkins)
Nesodynerus erythrostactes (Perkins)
Nesodynerus eucharis (Perkins)
Nesodynerus eutretus (Perkins)
Nesodynerus frater (Dalla Torre)
Nesodynerus ganahli (Dalla Torre)
Nesodynerus halaekalae (Blackburn)
Nesodynerus hawaiiensis (Blackburn)
Nesodynerus heterochromus (Perkins)
Nesodynerus hiloensis (Perkins)
Nesodynerus holomelas (Perkins)
Nesodynerus homochromus (Perkins)
Nesodynerus homoeogaster (Perkins)
Nesodynerus homoeophanes (Perkins)
Nesodynerus hylophilus (Perkins)
Nesodynerus illudens (Perkins)
Nesodynerus insulicola (Blackburn)
Nesodynerus iopteryx (Perkins)
Nesodynerus kauaiensis (Perkins)
Nesodynerus kauensis (Giffard)
Nesodynerus kirbyi (Dalla Torre)
Nesodynerus konanus (Perkins)
Nesodynerus koolauensis (Giffard)
Nesodynerus laevisulcatus (Perkins)
Nesodynerus lanaiensis (Perkins)
Nesodynerus leiodemas (Perkins)
Nesodynerus leucozonias (Perkins)
Nesodynerus lipocharis (Perkins)
Nesodynerus litoralis (Giffard)
Nesodynerus melanognathus (Perkins)
Nesodynerus mesospilus (Perkins)
Nesodynerus microdemas (Perkins)
Nesodynerus mimus (Perkins)
Nesodynerus molokaiensis (Perkins)
Nesodynerus monas aenus (Giffard)
Nesodynerus monas monas (Perkins)
Nesodynerus monobius (Perkins)
Nesodynerus montanus (Smith)
Nesodynerus montivagus (Perkins)
Nesodynerus naiadum (Perkins)
Nesodynerus nautarum (de Saussure)
Nesodynerus nesiotes (Perkins)
Nesodynerus newelli (Perkins)
Nesodynerus niihauensis (Yoshimoto)
Nesodynerus nivicola (Perkins)
Nesodynerus nubicola (Perkins)
Nesodynerus oahuensis (Dalla Torre)
Nesodynerus obscurepunctatus (Blackburn)
Nesodynerus orbus (Perkins)
Nesodynerus paludicola (Perkins)
Nesodynerus paranaias (Perkins)
Nesodynerus peles (Perkins)
Nesodynerus perkinsi (Giffard)
Nesodynerus petrobius (Perkins)
Nesodynerus potamophilus (Perkins)
Nesodynerus pseudochromoides (Perkins)
Nesodynerus pseudochromus (Perkins)
Nesodynerus pterophaennes (Perkins)
Nesodynerus purpurifer (Perkins)
Nesodynerus rubropustulatus (Blackburn)
Nesodynerus sandwichensis (de Saussure)
Nesodynerus scoriaceus (Perkins)
Nesodynerus smithii (Dalla Torre)
Nesodynerus sociabilis (Perkins)
Nesodynerus soror (Perkins)
Nesodynerus subegens (Perkins)
Nesodynerus tempe (Perkins)
Nesodynerus thersites (Perkins)
Nesodynerus threnodes (Perkins)
Nesodynerus unicus (Perkins)
Nesodynerus vulcanus (Blackburn)
Nesodynerus waianaeanus (Perkins)
Nesodynerus xanthorhoes (Perkins)
Nesodynerus xerobius (Perkins)
Nesodynerus xerophilus (Perkins)