

# The New World tarantula-hawk wasp genus *Pepsis* Fabricius (Hymenoptera: Pompilidae).

## Part 1. Introduction and the *P. rubra* species-group

C.R. Vardy

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C.R. Vardy, Yarina, Springwell Lane, Harefield, Middlesex UB9 6PG, U.K.

Key words: spider-hunting wasps; Pompilidae; *Pepsis*; systematic revision; new species; Neotropical; natural history.

The genus *Pepsis* is diagnosed and described, and its taxonomic and natural history reviewed. The following are newly synonymized under this genus: the genera *Abripepsis* Banks, 1946 and *Brethesia* Schrottky, 1909; and all the existing subgenera of *Pepsis*, viz. *Chrysopepsis* Haupt, 1952; *Cirripepsis* Banks, 1945 & 1946; *Deropepsis* Banks, 1946; *Dinopepsis* Banks, 1945; *Dinopepsis* Haupt, 1952; *Gigantopepsis* Lucas, 1919 of Pate, 1946; *Gigantopepsis* Lucas, 1919; *Nannopepsis* Banks, 1945 & 1946; *Ovatopepsis* Haupt, 1952; *Stenopepsis* Banks, 1945; *Titanopepsis* Haupt, 1952; and *Trichopepsis* Banks, 1945.

The *Pepsis rubra* species-group, with 18 species, including the type-species of *Pepsis*, is defined and described; keys to both sexes are provided. In this group, 3 species-names are newly proposed: *P. cooperi*, *P. inbio*, and *P. roigi*; and the following 32 names are newly synonymized under the names indicated: *P. albocincta* Smith, 1855 = *P. abrupta* Brèthes, 1908; = *P. ameghinoi* Brèthes, 1908; = *P. annaerdmuthae* Lucas, 1919; = *P. chrysothorax* Brèthes, 1908; = *P. copelloi* Brèthes, 1914; = *P. echeverriai* Brèthes, 1908; = *P. ichesi* Brèthes, 1908; = *P. lycaste* Banks, 1946; = *P. nutrix* Brèthes, 1914; = *P. pertyi* Lucas, 1895; = *P. prixii* Brèthes, 1908; = *P. rubescens* Lucas, 1895; = *P. ruficornis* Lucas, 1897 (not Fabricius, 1781); = *P. staudingeri* Enderlein, 1901; = *P. sulcata* Brèthes, 1908. *P. caridei* Brèthes, 1908 = *P. pampeana* Brèthes, 1908. *P. chrysothemis* Lucas, 1895 = *P. lucasii* Fox, 1898. *P. decorata* Perty, 1833 = *P. incompleta* Brèthes, 1908; = *P. opposita* Banks, 1946. *P. foxi* Lucas, 1897 = *P. flaminia* Brèthes, 1914; = *P. gemella* Banks, 1946. *P. heros* (Fabricius, 1798) = *P. atrata* Lepeletier, 1845; = *P. magnifica* Montet, 1921. *P. mexicana* Lucas, 1895 = *P. messerschmidti* Lucas, 1895. *P. pallidolimbata* Lucas, 1895 = *P. smithi* Hurd, 1948. *P. rubra* (Drury, 1773) = *P. papiliopennis* (Christ, 1791); = *P. stellata* (Fabricius, 1793). *P. sericans* Lepeletier, 1845 = *P. decepta* Banks, 1928; = *P. domingensis* Lepeletier, 1845; = *P. ignicornis* Cresson, 1865. *P. thisbe* Lucas, 1895 = *P. sayi* Banks, 1926. *P. vinipennis* Packard, 1869 = *P. insignis* Mocsáry, 1885. A single name, *P. albocincta* Smith, 1855, is revalidated. The name *P. inca* Banks, 1946 [*Abripepsis*], does not belong in the *P. rubra*-group, but is here synonymized under *P. chiliensis* Lepeletier, 1845 [*Pepsis*] because of its new generic status.

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**Preface**

In the present paper are included only the basic items necessary to introduce the genus, together with a detailed treatment of one species-group which includes the type of the genus. The full treatment of phylogenetics, biogeography, mimicry-groups and some other general subjects will follow in subsequent parts of this work.

**Introduction**

For sheer variety of size and colour, the spectacular wasps of the genus *Pepsis* Fabricius, 1804, including 133 known species, are unrivalled by any aculeate group in the world. Their diversity of colour approaches that of butterflies, often with extreme variation between sexes and within species; the members vary from the gigantic, brassy-haired females of the *P. sumptuosa*-group whose astonishing size (65 mm long) instantly commands respectful attention, to the slender, comparatively diminutive (11 mm long), brilliant green males of *P. purpurea*. The members of this genus, making their nests in burrows in the ground and provisioning them exclusively with mygalomorph spiders (usually Theraphosidae, i.e. tarantulas), are found everywhere in the New World from the USA and West Indies to Chilean and Argentine Patagonia; in all habitats from rainforest to desert, and in the High Andes reaching altitudes of around 3,400m. The very diversity of these conspicuous wasps has made them attractive to collectors; unfortunately no reliable, comprehensive key (except to the few species of the USA) has ever been published.

An overall total of 32,071 specimens of *Pepsis* from the Neotropical region, as well as much material from the Nearctic, has been examined in the course of this work. Of an initial overall total of 612 names, 546 remain in the genus, and of these latter 419 (77%) will be synonymized (including those in the present part); a species-name from another genus has also been included in *Pepsis* as a synonym. Sixteen species have not been recognized from the descriptions, while a single name is a *nomen nudum*. Details of these, and names excluded from the genus (together with their current placement), will appear in a later part of this work. A total of 24 species of *Pepsis* (including 3 in the present work) are new to science.

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 AMNH = American Museum of Natural History, New York (Dr E.L. Quinter)  
 ANSP = Academy of Natural Sciences, Philadelphia (Dr D. Azuma)  
 BMNH = British Museum (Natural History) [now: Natural History Museum, London] (Mr T. Huddleston)  
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### Abbreviations

- AC = Apical carina (transverse) of male SGP  
 AE index = Antennal/eye index: AS3 divided by UID, multiplied by 100; exceptional values are given in parentheses, e.g. (82-)91-108  
 AP = Apical projection of digitus (figs 52, 53).  
 APT = Anterior propodeal tubercle (paired projection at junction of dorsal and lateral face, associated with spiracle)  
 AS3 = Antennal segment 3 (or its length)  
 BL = Body length, given in millimetres (exceptional values are given in parentheses, as under AE index)  
 DTC = Dorsal transverse carinae of propodeum  
 Lacuna = A bubble-like space, found in sub-basal pairs inside some SGPs.  
 MG = Median groove of propodeum  
 MPN = Metapostnotum (between postscutellum and propodeum)  
 MT = Mesopleural tubercle  
 ND = No data  
 NFD = No further data  
 NFL = No further locality  
 NL = No locality  
 PAC = Pre-apical carina of SGP (transverse, in *P. rubra*-group)

PPV =	Postero-proximal veinlet of SMC2 in forewing (fig. 1)
PTC =	Posterior transverse carina of propodeum (at junction of dorsal and posterior faces)
PPT =	Posterior propodeal tubercle (paired projection more or less in line with PTC)
PST =	Postscutellum
S =	Sternite
SGP =	Subgenital plate (last visible ventral segment of gaster) in male (only that part visible without dissection is described, so that "base" refers to about the mid-point of the entire structure)
SMC =	Submarginal cell of forewing
T =	Tergite
UID =	Upper interocular distance (minimum, at level of ocelli)

### Biogeography and biodiversity

Despite the intention to treat these subjects in greater detail in a later part of this work, it seems desirable at least to give an outline of the already-established basic facts here. To judge from present distributional and phylogenetic evidence, it seems likely that the genus *Pepsis* originated in Amazonia, becoming a discrete genus sometime after the breakup of Gondwanaland. At the same time *Hemipepsis* (its sister-group, *teste* M.C. Day, pers. comm.), became its counterpart in the Old World. Remarkably, *Hemipepsis* is today represented by several species in the New World; it is intended to treat the interesting biogeographical implications of this in a separate paper. The area of highest endemism in the genus *Pepsis*, i.e. the greatest concentration of species with a small distributional range, is south-eastern Brazil; other areas of high endemism are Central America, the Guianas and Argentina. It is noteworthy that all of these more important areas are outside of Amazonia proper; the reason appears to be that they are regions where the results of successive peripheral vicariance events have accumulated. This situation would imply that these areas therefore harbour a majority of older species, which is indeed the case (see discussion Biogeography under *P. rubra*-group). In other areas, either the species found there are more widespread, or there are fewer of them.

Increasing concern about the conservation of biodiversity on planet Earth makes revisions of large groups, which provide the means of assessing that biodiversity, ever more relevant. The genus *Pepsis* is an excellent indicator of biodiversity, since it is large, diverse, and occupies all terrestrial habitats within its very extensive New World range; furthermore, it is well collected because the wasps are so conspicuous. The species' ranges will probably be more or less direct reflections of those of their (mainly tarantula) prey, which are known to be poor self-distributors (P. Hillyard, pers. comm.). Clearly, a better measure of biodiversity is provided by relatively static species of restricted range, than by mobile, widely ranging ones, such as, for example, araneid spiders whose young can travel great distances on silk threads carried by the wind. Generally, differences between distribution mechanisms are reflected by considerable differences in distributional range; an excellent illustration of this is given by the late Alwyn H. Gentry (1979) concerning the Neotropical members of the plant

family Bignoniaceae, in which the seeds of some groups are dispersed by wind, and of others by animals. However, the degree of coincidence between ranges of wasp and spider host is influenced by several other factors; first, the degree of specificity to spider hosts. Although much more work needs to be done properly to assess how specific *Pepsis* species are to their spider hosts, the scanty evidence so far available (see under Host records below) suggests a fairly high degree of specificity. The Nearctic species of *Pepsis* alone are numerous enough, and sufficiently diverse in phylogenetic composition, for their study to afford considerable insight into this matter. Second, the degree to which a wasp's range is as extensive as that of its host. This probably depends on such things as climatic or other environmental factors, which may prevent the wasp's distributional range being as great as that of its host. For example, the sawfly *Sciapteryx consobrina* Klug, 1811, rare in Britain, is by no means present in all the localities where its sole foodplant, *Adoxa moschatellina* Linnaeus occurs (Woollatt, 1945, 1946; Benson, pers. comm.). Several comparable cases are also known in British butterflies (*teste* G.R. Else, pers. comm.). If this proves to be the case in *Pepsis* species, they would be particularly sensitive indicators of biodiversity.

### History and classification of the genus *Pepsis*

Since Hurd (1952) has summarized most of the chaotic taxonomic and nomenclatorial history of the genus, the subject is treated only in outline here. The work of some previous workers fell outside the classical mould of taxonomy based mostly on colour differences. For example Lucas (1895) went into extreme structural detail; but given the extent of intraspecific variation which exists, it is hardly surprising that the result of his rubricity was that his descriptions pertain more to individuals than to species (some of his undoubted syntypes strongly disagree with his descriptions). Most other authors went into the same kind of detail with colour differences, which at least was more the mode in those days. Banks (1946: 312) made a laudable plea, "... I feel that a more intensive study should be made of external structures ...". Despite this, he then says (p. 313) "... species that have a rather small [subgenital] plate with the cross-ridge parallel to the raised tip are certainly not more closely related to one another than they are to species with a different subgenital plate." Thus confused at the outset, most of the rest of his work is likewise self-contradictory, even to the point of separating syntopic species solely on the basis of minute colour differences. His subgenera (mostly proposed in 1945) were, like those of other authors, each based on distinctive species; however, they became much less uniform when he subsequently (1946) enlarged them by including all manner of heterogeneous additions. One result of this confusion was that sometimes opposite sexes of a species (and occasionally even the same sex of a single species!) were simultaneously placed in different subgenera. Furthermore, his microscope slides of subgenital plates unfortunately include three-dimensional structures broken by a cover-slip rammed down on top.

A ray of light eventually entered the scene with the publication of Hurd's (1952) revision of the Nearctic species and review of the genus, including a virtually complete nomenclatorial catalogue, although he was unaware of Haupt's (1952) nearly simultaneous publication. Despite the fact that Hurd apparently saw no type-specimens, his interpretations of the species were remarkably accurate, though he was of

course dealing with a very limited fauna. Furthermore, his lists of species-names and other additions have proved to be of the greatest value.

In ignorance of the work of both Banks and Hurd, Haupt (1952) compounded chaos yet again by proposing a whole new series of subgenera, as well as describing yet more “new” species. The situation becomes understandable, though nonetheless regrettable, on reading Haupt’s introduction: he stated that his work was mainly carried out before World War II and finished under difficult conditions during the war. He added that he had no access to any publications other than those he cited (he did not cite Banks; clearly, scientific communications between the USA and Germany were then at a low ebb). Later (presumably after the war ended), when for the first time he saw Lucas’ abundant material in Berlin, he realized to what extent he had been misled and confused by that author’s publications. However, rather than carry out the extensive re-working which he realized was necessary, he went ahead and published with the comment “something had to be left for his successors to do”. Little did he realize just how much!

The use of subgenera was misleading since it gave the undue importance of formal status to a minority of small species-groups while leaving many species in the classical “dustbin” - the heterogeneous assemblage perforce known as *Pepsis sensu stricto*. A further shortcoming of subgenera as used by previous authors is that they did not take account of as many characters as possible of both sexes, even in the relatively few cases where the latter had been associated. All the subgenera hitherto proposed are here synonymized and replaced by an expanded and complete system of species-groups (few of which correspond with the old subgenera), and their inter-relationships are discussed. The sexes of all species have been associated in the present work, except that only a single sex is known for five species; the past failure to do this is of major importance, since the characters of both sexes of a species together are often needed to assess phylogenetic placement. Many new characters have been discovered, especially in females; and all previously known characters have been re-assessed. As a result, many of the characters formerly used to distinguish “species” have proved to constitute no more than intraspecific variation.

### *Pepsis* Fabricius, 1804

*Pepsis* Fabricius, 1804: 207. Type-species: *Sphex stellata* Fabricius, 1793: 219 (= *P. rubra* Drury, 1773), by subsequent designation (Latreille, 1810: 437). Fabricius included 16 newly described species, as well as many previously described (mainly as *Sphex*), divided into 2 groups: “with sessile abdomen” and “with petiolate abdomen”; none of the latter now remain in the genus (most belong to Sphecinae); Latreille, 1809: 61 (included species: *P. stellata* Fab., *P. ruficornis* [no author]; Banks, 1945: 81, “type-species: *Pepsis (Pepsis) ruficornis* (L.)”; Haupt, 1952: 320, “type-species: *Pepsis (Pepsis) ruficornis* (L.)”). (Haupt placed this species simultaneously in the *P. marginata*-group on p. 357, and in the *P. ruficornis*-group on p. 387!).

*Brethesia* Schrottky, 1909: 243. Type-species: *Pepsis dimidiata* Fabricius, 1804: 216, by original designation. **Syn. nov.** Schrottky also included *P. limbata* Guérin, *P. chrysoptera* Burmeister and *P. caridei* Brèthes (the last overlooked by Hurd, 1952); but Banks (1945) used *P. limbata* as the type of his new subgenus *Trichopepsis* (see below) and indicated (1946) that *P. chrysoptera* belongs in *Pepsis sensu stricto*.

*Abripepsis* Banks, 1946: 314. Type-species: *Abripepsis inca* Banks, 1946 by original designation and monotypy (= *Pepsis chiliensis* Lepeletier, 1845). **Syn. nov.**

Notes on generic synonymy.— *Abripepsis* Banks. Banks proposed this genus on the basis of the following characters. Although he saw both sexes, he did not distinguish to which one these characters pertained; the following discussion is annotated with this information.

The first recurrent vein (= 1m-cu) ends nearly one-third way out to plainly more than one-third way out on the second submarginal cell (= SMC2) [both sexes]. This is indeed the case, but specimens at the early end of this range are normal for the genus! Furthermore, the variation found in *Pepsis tolteca* Lucas (like *P. chiliensis*, an inhabitant of high altitudes) is just as great; the only difference is that the range is shifted slightly along the scale, i.e. the variation begins well within the range normal for the genus and ends at a lesser extreme than that in *P. chiliensis*. Other species, especially those found in montane habitats, also display much variation in this respect. Furthermore, even the greatest extreme found in *P. chiliensis* does not equal the condition found in other genera of Pompilidae (this species also differs from those in other genera in that its forewing radial cell does not end in an acute point on the costa). Thus this character is of no generic significance.

Maxillary cardines with hair on under side [both sexes]. Banks stated that *Pepsis* has no such hair. The cardines of *P. tolteca*, a high-altitude Andean species whose body is almost as densely hairy as that of *P. chiliensis*, has very similar hairs; so also do those of an undescribed species of the *P. hymenaea*-group which occupies a similar habitat to that of *P. tolteca*. Indeed, examination of almost any *Pepsis* found at high altitude shows that its cardines bear a greater or lesser amount of hair, albeit often less coarse and dense than that in *P. chiliensis*.

Antenna long and tapering [female]. This character is found in several species of *Pepsis* belonging to various species-groups.

Clypeus with transverse ridge close to margin [female]. In comparison with the extraordinary development of the clypeus in *Pepsis deaurata* Mocsáry and *P. frivaldszkyi* Mocsáry, to which species no author has accorded full generic status, this modification appears insignificant.

Clypeus is double just below this ridge [female]. Banks was presumably referring to the lower margin of the ridge, and an integral part of it, rather than a separate structure. Certainly the clypeus is not double-edged in the usual sense, i.e. where the edge is strongly thickened and sharply bevelled, so he may have been referring to the two lobes produced by the deeply arcuate emargination of the clypeus. Whatever the case, the comments under the previous heading apply equally here.

Hind tibia without teeth [female]. Banks admitted that this character is found also in *Pepsis*.

Maxillary palp with last 3 joints subequal, short [female]. Banks contrasted this character with "most" *Pepsis* only. In female *P. tolteca*, for example, the last two segments are equal in length, the previous one slightly longer. This condition is intermediate between that of *P. chiliensis* and of other *Pepsis*, where the last 3 segments gradually decrease in length.

The basal vein ends a little further forward than in most *Pepsis*. It is uncertain what Banks meant by this; in any case, he admitted that it is not an exclusive character.

In summary, the general habitus of this species places it in the genus *Pepsis*. Banks' proposal of a new genus may have been useful in drawing attention to its

unusual concomitance of characters, but the more comprehensive evaluation given above makes it evident that these are insufficient to support generic status; either comparable characters are found (albeit often in isolation) in other species which are undoubted members of the genus, or the characters are small extrapolations of variation in characters normal for the genus. Indeed, many of the so-called generic characters of *Abripepsis* appear to owe almost as much to generalized montane phenotypic expression as they do to its genotype.

*Brethesia* Schrottky. The status of this genus, originally proposed as a replacement name for *Pepsis*, has been the subject of some controversy, as discussed by Hurd (1952: 324) who reduced the name to the status of subgenus. Whatever the merits of the case, the name *Brethesia* has been employed by only one (Malaise, 1937) of the numerous authors who have published on the group. In the unlikely event of the name being shown to be valid, it would have to be suppressed by reason of lack of usage.

Notes on subgeneric synonymy.— The following subgenera are listed alphabetically, not chronologically, in order to facilitate appreciation of repeated proposals of the same names (Banks, 1945 & 1946) and objective synonymy (Banks, 1945 and Haupt, 1952). Where multiple species were included, the names of the species additional to the type of the subgenus are only given where they are of exceptional interest; they were sometimes very numerous, particularly in Banks' work, and the species were often not closely related to each other.

*Pepsis (Chrysopepsis)* Haupt, 1952: 323. Type-species: *Pepsis speciosissima* Lucas, 1919: 26 by original designation. **Syn. nov.** Firstly, *P. speciosissima* is not a Lucas name; the latter mentioned it on p. 16 (not 26), correctly ascribing its authorship to Schulz, 1906: 16, who proposed it as a replacement name for *P. speciosa* Smith, 1855 not Fabricius, 1804. Secondly, Haupt misidentified his material, so that his description disagreed with his designation. On p. 400 he gave reasons for specifically excluding *P. deaurata* Mocsáry (and its synonym *auricoma* Lucas) from *Chrysopepsis*, without knowing that his type species *P. speciosissima* is also a synonym of *P. deaurata*! In fact a female *P. sumptuosa* Smith from Colombia in MLU, although not bearing any Haupt identification label, agrees with his "*speciosissima*".

*Pepsis (Cirripepsis)* Banks, 1945: 82. Type-species: *Pepsis planifrons* Lucas, 1895: 684 [= *auriguttata* Burmeister, 1872], by original designation (two other included species). **Syn. nov.** Banks applied this name correctly. Banks, 1946: 353. Repeated proposal, with type-species as before. Banks included a new total of 13 species.

*Pepsis (Deropepsis)* Banks, 1946: 336. Type-species: "*Pepsis frivaldszkyi* Erichson", by original designation (25 other species included). **Syn. nov.** *Pepsis frivaldszkyi* is not an Erichson name: it was proposed by Mocsáry, 1885: 259. Although Banks correctly applied this name, he incorrectly stated that the male possesses no modified sternal hairs, thus causing ambiguity in his definition of the subgenus.

*Pepsis (Dinopepsis)* Banks, 1945: 83. Type-species: *Sphex grossa* Fabricius, 1798: 245, by original designation (only one other species included: *P. theresiae* Kriechbaumer, 1800) [= *P. grossa*]. **Syn. nov.** This name was correctly applied by Banks, who (1946) included two further names, one of which was another synonym of *P. grossa*.

*Pepsis (Dinopepsis)* Haupt, 1952: 322, not Banks, 1945 (q. v.). Type-species: *Pepsis frivaldszkyi* Mocsáry, 1885: 259, by original designation (one other species included). **Syn. nov.** This name was correctly applied by Haupt.

*Pepsis (Gigantopepsis)* Lucas, 1919: 10. Type-species: *Pepsis gigantea* Lucas, 1895: 575 [= *P. hyperion* Mocsáry, 1894], by original designation (four other species included, of which one is another synonym of *P. hyperion*). **Syn. nov.** Banks (1945) included a further three species, and in 1946, 12 altogether. Haupt (1952) included four species apart from the type.

*Pepsis* (*Giganteopepsis*) Pate, 1946: 88. [Lapsus for *Giganteopepsis* Lucas, 1919].

*Pepsis* (*Nannopepsis*) Banks, 1945: 82. Type-species: "*Pepsis pruinoso* Lucas", by original designation (one other included species). **Syn. nov.** In fact *P. pruinoso* was described by Mocsáry, 1894: 5 [= *P. nitida* Lepeletier, 1845], although Banks correctly applied this name. The other included species was given as "*P. consors* Brèthes". No such Brèthes name exists: a species of this name was later described as new by Banks (1946: 352). Banks, 1946: 351; this repeated proposal, with the type-species as before but with the correct author's name, included a new total of seven species.

*Pepsis* (*Ovatopepsis*) Haupt, 1952: 321. Type-species: *Pepsis elevata* Fabricius, 1804: 213, by original designation (only one other included species, *P. cristata* Haupt, 1952 [= *P. elevata*]). **Syn. nov.** Haupt correctly applied this name.

*Pepsis* (*Stenopepsis*) Banks, 1945: 82. Type-species: *Pepsis hymenaea* Mocsary 1885: 257, by original designation (six other included species). **Syn. nov.** Banks applied this name correctly. In 1946 he included a total of 25 species.

*Pepsis* (*Titanopepsis*) Haupt, 1952: 323. Type-species: *Pepsis optimus* Smith, 1879: 157, by original designation (monobasic). **Syn. nov.** Haupt applied this name correctly.

*Pepsis* (*Trichopepsis*) Banks, 1945: 82. Type-species: *Pepsis limbata* Guérin, 1831, by original designation (seven other species included). **Syn. nov.** Banks applied this name correctly; he added a further ten species in 1946.

Definition of the genus *Pepsis* Fabricius.— The genera of Pompilidae are notoriously difficult to define. However, almost all species of *Pepsis* are easy to recognize because the SMC2 of the forewing (fig. 1) possesses a very short PPV, usually much less than 1/3 the total posterior length of the cell; and a more or less rounded radial cell apex (i.e. never sharply pointed). Only some specimens of two species (*P. chilienensis* and *P. tolteca*) (see remarks under *Abripepsis* above) have the PPV longer, approaching the condition in *Hemipepsis* Dahlbom, 1843 (the sister-genus of *Pepsis*, *teste* M.C. Day, pers. comm.), but do not have the radial cell pointed on the costa as in most species of that genus. Also, all members of *Hemipepsis* have a strong bulla in the base of the first discoidal cell, unlike any *Pepsis*.

Shimizu (1994: 34) lists "several unique characteristics" of *Pepsis*. Amongst these are the following alleged new ones: the last abscissa of forewing vein Rs is strongly recurved toward the wing margin; he figures the wing of *P. grossa* to illustrate this. He has chosen the most extreme example in the genus; this configuration is characteristic only of the *P. rubra*- and *P. grossa*-groups (it is found fortuitously in a very few other species of the genus). Most species of *Pepsis* have this vein curved less strongly, while in some (e.g. the *P. hymenaea*-group) it meets the wing margin virtually at a right angle (a character found also in some species of *Hemipepsis*). He further states that in the hind wing, crossvein cu-a meets vein CuA far beyond the separation of vein M from vein M+CuA, about as far as the width of the sub-basal cell. This is true, but it is not unique to *Pepsis*; it is shared with, for example, *Hemipepsis* (both New and Old World species), *Entypus* Dahlbom, 1843 and *Anacyphononyx* Haupt, 1950 (although in some species of these genera the condition is less extreme, i.e. cu-a and M are almost interstitial). He gives also some mouthpart characters, still under the "unique" heading, but then implies that they are shared with *Anacyphononyx* and *Aimatocare* Roig, 1989! That leaves as unique only the forewing venation character he (correctly) ascribes to Townes (1957), and which is already mentioned above.

Description.— Body colour usually black, rarely testaceous; but almost always

completely covered by pubescence in the form of extremely fine, silvery, golden, golden-green, green, blue or violet metallic scale-hairs, varying to extremely long, coarse and dense, most often black, hair. Antennae most commonly with at least the two basal segments black and the rest orange; sometimes entirely black, males usually with more segments orange than corresponding females. Wing colour extremely variable: apart from the amber-orange to dark transition common in Hymenoptera, milk-white, crimson, silvery and golden all occur. Sexual dimorphism is often very strong; the males usually possess the brighter body colour, but the females often the brighter wing colour.

Body small and slender (BL 11mm) to extremely large and robust (BL 65mm); males smaller than corresponding females. Head shape very variable, from very strongly constricted behind the eyes to extremely strongly swollen (especially in females), when the vertex is often also swollen. Clypeus shallowly, arcuately emarginate in both sexes; in females rarely more strongly so, or very deeply, rectangularly emarginate. Occipital carina variable in length, sometimes meeting preular suture. Male antenna usually markedly thicker than female. Pronotal shoulders rounded, occasionally pointed. Mesopleuron with a more or less strong posterolateral tubercle. The MPN varies between 1.5 times as long as the PST, to extremely short (less than 0.5 PST) and has few strong to several weak, transverse carinae; its median furrow varies from suture-like to very broad, deep and shining. Propodeum more or less elongate in males, shorter and more convex in females; parallel-sided with PTC and PPT very strong, to strongly tapered and virtually without posterior projections (dorsal and posterior faces merging); with variable dorsal, transverse carinae. Gaster slender and more or less dorsoventrally flattened in males, more robust and only occasionally flattened in females, when dorsum often shining and apical tergal margins shallowly, arcuately emarginate. The male sternites 3 and 4, sometimes others, possess strongly modified hairs and the SGP is virtually unmodified; otherwise, modified sternal hairs are minimal and the SGP is more or less strongly modified, with spines, teeth, carinae, tubercles, polished areas, etc. The female S.2 always with strong, transverse groove; the lateral, posterad extension of this is most often well developed, occasionally weak or absent; pygidium convex and densely hairy, sometimes partly polished. Male hindlegs, especially in larger species, strongly flattened, most strongly towards the extremities; tibia with strong dorsal hair fringe only, the spurs very long, reaching to about half basitarsus length; claws strongly, usually evenly curved. In females, the foreleg apical spur is usually pointed, rarely spatulate, the basitarsus with 8-11 rake spines; hindleg tibia with dorsal teeth (sometimes absent), a spine behind each and a bristle (often curved backwards) on the inner side of each; the apical spurs, especially the inner one, vary from extremely short and robust (slightly shorter than the apical width of the tibia), to extremely long (reaching to just over half the basitarsus length), sometimes apically hooked; last tarsal segment straight to strongly curved, its claw with a sharp tooth usually near the mid-point but occasionally pre-apical, when the setae overlying it are sinuate rather than straight.

#### Notes on generic and other characters in the Pompilidae

Comparisons with other genera.— The following assessments were made inde-

pendently of those of Roig (1987: 282); it is interesting to compare them with the characters he regarded as apomorphic in the genus *Sphictostethus* Kohl, 1885 (also a member of the subfamily Pepsinae). Females of all the Pompilidae in the BMNH named collection (141 genera, comprising 2,136 species) were investigated; the results are given below. Males were not surveyed because there are few sexual differences in the characters concerned, except for the MPN length which is often greater in males.

1. Last 3 palpal segments approximately equal in length. This condition is found only in very few species of this genus, but in many other genera. In most *Pepsis* species the last 3 segments are progressively shorter apicad.

2. Postero-proximal veinlet (PPV) of SMC2 very short (less than one-third of posterior cell length). This is the principal apomorphy of *Pepsis*; the veinlet varies up to a little longer than one-third posterior cell length in very few species of the genus. In all other Pompilidae it is longer than one-third, usually considerably so (a single male specimen of the pepsine genus *Chirodamus* Haliday, 1836 from Mexico (BRIO) has the PPV only a quarter of the total cell length; the radial cell is sharply pointed).

3a. Radial cell pointed on costa. This condition is not found in *Pepsis*; it is characteristic of most other Pompilidae (136 genera, 1,785 species).

3b. Radial cell more or less right-angled on costa. Found only in a few species groups (13 species) of *Pepsis*, a few species of both Old and New World *Hemipepsis*, *Cryptocheilus* Panzer, 1806, *Java* Pate, 1946 and all of the (few) species of *Macromeris* Lepageletier, 1831 (pointed to right-angled in most species: 3 genera, 221 species; more or less right-angled in all species: 1 genus, 4 species).

3c. Radial cell rounded on costa. Exclusive to *Pepsis*, where it is found in most species (extreme in two groups: 120 of 133 species).

4. Female MPN short, its median furrow often deep. Restricted to a very few species in *Pepsis*; found in most *Hemipepsis* and most other pompilids. (MPN always shorter than PST: 112 genera, 1,153 species; MPN shorter than or equal to PST in most species: 20 genera, 806 species; MPN equal to or longer than PST: 3 genera, 42 species; species more or less evenly distributed between all three character-states: 5 genera, 9 species).

5. Female propodeum rounded in profile, lacking a PTC. In a few groups of *Pepsis*; here, as in other Pompilidae, often found in conjunction with (4) above. In most groups in *Pepsis* the propodeum is divided into more or less flat dorsal and posterior faces, with a strong carina at the angle. The MPN length and propodeal shape appear to be related: where the propodeum is short and rounded in profile, the MPN is usually short as well. Both are here regarded as "ground-plan" characters in Pompilidae. In species displaying these character-states, the junction between dorsal and posterior faces is sometimes distinguished by a more or less sharp, angular ridge. In some cases the surface has transverse carinae, one of which may be stronger at the above-mentioned junction. In most species of *Pepsis*, and some species in the most closely related genera such as *Hemipepsis*, the propodeum is elongate with strong transverse carinae, one of which is developed to form a sharp PTC.

6. Other characters. The following characters, found in a few, possibly older, *Pepsis* species are shared with various other genera and may therefore be plesiomorphic: a. Body with long, dense hair, especially on legs (densest below front femur); b. Female hind tibia with long inner spur; c. Female hind tibia without teeth; d. Hind femur with sharp carina on inner, posterior edge.

Anomalous structural characters in *Pepsis* and *Hemipepsis*.— At first sight, similar combinations of certain structural characters in *Pepsis* and its sister-group *Hemipepsis* are extremely confusing. However, each genus has its own well defined apomorphy (a very short PPV in *Pepsis*, and a strong bulla in the base of the 1st discoidal cell in *Hemipepsis*). In *Pepsis*, only a few of the species have an extremely short MPN (probably an ancestral character in Pompilidae) while most New World species of *Hemipepsis* have it thus. Furthermore, a few species of both *Pepsis* and *Hemipepsis* share the character of the radial vein forming more or less a right angle with the costa; whereas most species of *Pepsis* have the radial cell apex rounded on the costa, most *Hemipepsis* have it pointed. The simplest explanation of this situation would be that a common ancestor developed the specializations of a long MPN and an apically right-angled radial cell and that many *Hemipepsis* subsequently lost these, reverting to the primitive form, and while a few *Pepsis* secondarily lost the long MPN, most species became even more specialized and developed the rounded radial cell apex. This explanation seems more likely in view of the fact that the characters of long/short MPN and pointed/rounded radial cell are combined in various ways in Old World *Hemipepsis*. Such self-contradictory cross-correspondences caused by character reversals likewise produce confusing anomalies throughout the genus *Pepsis*.

### The diverse kinds of variation in the genus *Pepsis*

The phylogenetic significance of aberration.— Apart from the normal variation in venation (see Structural variation below), there are two further kinds of variation:

1. Additional veins, often incomplete and sometimes asymmetrical in opposite wings, appear to occur at random and are not uncommon. These may be the results of chance mutations or errors of development.

2. Veins which are normally present but which take a different course from the usual. This kind of change can be of phylogenetic significance; for example, the apparent close relationship of *Pepsis chiliensis* Lepeletier (which often has the PPV longer than normal for the genus) to the *P. brevicornis*-group was substantiated by the later discovery of an aberrant male *P. cassiope* Mocsáry, 1889 (belonging to the latter group) with a PPV very similar to that of *P. chiliensis*.

Variation in other characters may also be significant; for example, the *P. sumptuosa*-group is characterized by, among other things, a very short inner spur of the hind tibia in females; the only other group with this tendency is the *P. sommeri*-group. A female *P. xanthocera* Dahlbom, 1889 (belonging to the latter group) has been seen with the dense, black pubescence, which is normal for the species, replaced on the face by bright brassy hair, a colour almost exclusive to the *P. sumptuosa*-group.

Structural variation.— Structural variation in this genus is almost always a matter of degree, within certain parameters according to species. The more obvious forms concern variation in the shape of SMC3 in the forewing, the shape of the median furrow of the MPN and the projections and surface sculpture of the propodeum, especially in the female where the latter structure is more strongly developed. One remarkable case of localized structural variation concerns the female of *Pepsis terminalata* Dahlbom, 1844. This is an extremely widespread species, but where it occurs in the High Andes females often display a small, lateral, vertical groove on T.2; its function

is unknown. One important aspect of simultaneous variation in structure and colour concerns convergence in sympatric areas (see discussion under The problem of phenotypic convergence below).

Unusual pubescence.— In this phenomenon, very rare in most species of the genus, the entire body is covered by short, yellowish-silvery or tawny pubescence. In certain species it is evidently the norm; fresh males of *P. egregia* Mocsáry show it, and in *P. elongata* Lepeletier it is one of the normal extremes of variation, where it occurs more commonly in males and with all intermediate stages to normal pubescence. However, among the many thousands of specimens of *Pepsis* examined in the rest of the genus, only 9 such individuals have been seen. These pertain to both sexes and to phylogenetically widely separated species groups. (*viz.*, *Pepsis chrysoptera*, ♂, Brazil (MNHNPS); *P. chrysothemis*, ♀, USA (AMNH); *P. defecta*, ♀, Brazil (MZUSP); *P. festiva*, ♀, Costa Rica (BMNH); *P. foxi*, ♀, Bolivia (USNM); *P. gracillima*, ♀, Ecuador (USNM); *P. inclyta*, ♀, Brazil (NMV), and another, ♀ [no locality] (MACN); and *P. seladonica*, ♀, Brazil (AMNH)). Surely, *Pepsis marginata* var. *sericata* Cresson, 1872, must be concerned here. Hurd (1952: 300) discussed this name, considering it unlikely to belong in *Pepsis*. However, Cresson's description, "silvery-sericeous pile", sounds appropriate to this phenomenon, and he did not otherwise fail to recognize species of this genus correctly. Neither *P. egregia* nor *P. elongata* figure in the Nearctic fauna (the subject of Hurd's work). I agree with Hurd that *P. marginata* ("10 specimens from Texas") is surely a misidentification and that var. *sericata* will therefore have been a variety of a different species. In summary, this phenomenon is generalized and extremely rare in the vast majority of species-groups in the genus. It may represent an ancestral condition and study of other genera may elucidate this.

The problem of phenotypic convergence.— The convergence of structure and colour between closely related species where their territories overlap seriously hinders correct identification. This phenomenon is the exact opposite of the situation in Sphecidae, for example, where species are more distinct, not less, where they meet (this phenomenon is known as "character displacement"). Two male specimens of *P. terminata* Dahlbom, 1844 (*P. elevata*-group) from Brazil, Uypiranga, Rio Negro 14 k from Manaus have the white forewing apex broader and the SMC3 shorter than usual, converging with *P. vinipennis* Packard, 1869 (*P. rubra*-group), which is sympatric in that area. This creates great difficulties in distinguishing between females, whose taxonomic characters are variable to begin with (see for example the table given below for distinguishing between females of *P. decorata*, *P. foxi* and *P. roigi*). Brown & Wilson (1956: 59) state, "It is interesting to note that the tendency towards displacement of characters is opposed by the pressure for mimicry. One can imagine some elaborate interactions between the two tendencies, particularly in the evolutionarily fertile tropics." Presumably convergence of characters is aided, not opposed, by mimicry pressure. In the case of the *P. discolor* mimicry-group, there is unlikely to be any displacement of characters due to biological competition, since most of the species belonging to it are not closely related. Grant (1972: 40) gives the name "sympatric convergence" to the opposite phenomenon, but says disappointingly little about it. The subject of mimicry-groups will be treated more fully in a subsequent part of this work.

A remarkable equilibrium in male sexual modifications and comments on females.— The great variety of male, non-genitalic, sexual structures found in this genus exhibits a well defined equilibrium. In the *P. rubra*-group, for example, the sub-genital plate is more strongly modified than in any other, while all the sternal hairs are very weak. In species of other groups where the SGP is little more than a flat strap-shape, certain sternal hairs are very strongly modified; intermediate combinations of the two extremes are found in various other groups or species of the genus, albeit much less commonly. Where the sternal hairs are modified, a further, more detailed balance is often found: in some species-groups the hairs of sternite 4 alone are greatly enlarged, forming specific patterns; while in other groups the hairs are instead shorter and denser on sternites 5 and 6. Again, a variety of intermediate stages is found, each variation being usually peculiar to a species-group. Males of all New World and many Old World species of *Hemipepsis* in BMNH have been examined; in this genus a comparable situation exists, but on average the modifications both of structure and sternal hairs are much less pronounced than in *Pepsis*. However, S.6 is often also involved, being structurally modified or bearing modified hairs, or even both simultaneously.

These highly species-specific modifications of non-genitalic structures are especially interesting in view of Eberhard's (1985) theory of sexual selection by female choice because the above-described equilibrium must be involved in any changes mediated according to the theory; and each change must be accompanied by another in compensation. Furthermore, it may be that the need for this equilibrium to be maintained has a braking effect on the rate of change in these modifications. Circumstantial evidence favouring this idea is that most species in the genus are more or less close to one of the two extremes, so that any secondary changes which need to be made to keep the balance are minimal and therefore perhaps easier to accomplish; the intermediates which exist between the two extremes are comparatively few in number. Although the genitalia themselves are species-specific in *Pepsis*, they usually furnish less distinct characters than the non-genitalic structures. Eberhard (1985), using as an example the sexual adornments of male fiddler crabs, stated that apparently insignificant structures can have highly specialized functions, which were quite unsuspected until recently. Studies of mating behaviour may help to explain the basis of this equilibrium phenomenon in *Pepsis*; but will be difficult to carry out in view of the very short duration of copulation in Pompilidae (often a few seconds).

In contrast to the males, female Pompilidae are remarkably uniform in structure. M.C. Day (pers. comm.) has suggested that this is because the females are so well adapted to dealing with dangerous and powerful prey, that there is a very strong selection pressure against further change. Day's idea may represent one of the mechanisms responsible for Raup's (1993: 189) concept of phylogenetic constraint, referring to "the finding that evolutionary groups tend, in time, toward anatomical stability". The fact that pompilids are a very ancient group (as of course are their spider prey) is consistent with this. Those relatively small differences which do exist between females (the most obvious of which are species-group characters) may well reflect specialization on structurally different groups of spiders. This putative limitation on divergence among females would mean that evolution has been able to "progress" away from ancestral characters only very slowly, the effect of this being that ancestral

characters may be expected to occur with more than usual frequency, which is indeed the case in Pompilidae. Gauld & Mound (1982: 76) state that, "If we accept that many characters are under polygenic control, it is perhaps not surprising that development *de novo* of a character will be far rarer than the 'loss' of a character. The latter effect can result from the loss of any one of the multiple genes needed for that character's full expression, and this process probably underlies the frequency of homoplasy and reversals involving such characters". However, character reversal is also commonplace in males. These "retrograde" changes may adhere to a pattern; their frequency seems to be in proportion to degree of relationship, inasmuch as the more recently an ancestral character was present, the more likely it is to recur (see also discussion under Anomalous colour resemblances, below). Parallelism may also contribute to the phenomenon, but this is a less satisfactory explanation of why characters are replicated in such detail (e.g. colour patterns). Although exact replication is perhaps more likely to occur in parallelism than in convergent evolution, it is much less likely in either than in character reversal based on pre-existing genes.

The different kinds of colour variation in *Pepsis*.

Normal colour variation.— Although the wings of many *Pepsis* remain dark or pale according to species, others exhibit light-dark colour variation in accordance with Gloger's Rule (see Müller, 1986: 98); rarely, melanic specimens of normally pale-winged species occur (see e.g. *P. thisbe* Lucas, 1895). In specimens with more or less dark wings, there exists a fine balance: the stronger the infuscation, the stronger the metallic reflections; this is presumably a device to counteract the increased heating effect of darker wings. Among the species which always have entirely dark wings, a few, especially *P. xanthocera* Dahlbom and *P. vitripennis* Smith, in which the wings are extremely dark, also exhibit very strong, almost mirror-like, metallic reflections, which may enable these species to fly under hotter conditions than others can tolerate. In some species whose wings vary in colour, most individuals are either distinctly light or dark, with few intermediates; in others, a more or less complete range of transitional forms exists, starting with pale amber, darkening to orange, then becoming increasingly infuscate (sometimes passing through a strikingly beautiful deep crimson, e.g. in *P. terminata* Dahlbom), and finally becoming completely black. The infuscation either extends inwards from both ends of the wings or, more commonly, gradually increases over the whole wing surface. The situation in which a range of transitional forms exists is well exemplified in certain species ranging across northern Argentina (e.g. *P. discolor* Taschenberg), where a gradual colour change cline, becoming lighter from east to west, can be observed. This phenomenon is marked by changing proportions of light/dark individuals, so that even in the far west (e.g. Salta) a few specimens with mainly dark wings still occur. This is probably caused by variation of humidity between the emergence dates of individuals of a population, as well as between one year and another. It seems likely that in those species with few intermediate individuals, the critical range of humidity which causes the production of those intermediates must be extremely small, analogous to an over-sensitive thermostat. However, the entire situation is far from clear. Among the colour changes found in certain North American species, some (e.g. *P. grossa* Fabricius) are dark-winged in the west and pale in the east, whereas in others (e.g. *P. menechma* Lepelletier) the exact

reverse is true. Hurd did not attempt to explain these facts, merely regarding the colour forms as representing distinct taxa in his 1952 monograph. Bohart & Menke's (1963: 124-125) explanation for the one situation (exemplified by *Sphex ichneumoneus* (Linnaeus)) cannot hold good for the opposite, and must therefore be regarded as an over-simplification. Bohart himself must have been aware of this because he wrote "most [i.e. not all] of the ... species have light wings in the east and dark in the west".

"Fading".— Although normal fading of wing colour is fairly common, it is invariably accompanied by abrasion of wing tips, mandibles and coarse hairs. However, occasionally, specimens occur which are not abraded but nevertheless appear extremely faded (see e.g. *P. mexicana* Lucas). This phenomenon occurs in various groups of Hymenoptera; it may be an artefact due either to the use of an unusual killing agent, or to long exposure to light or other storage conditions after death of the insect.

The strange phenomenon of lygarochromy.— Something intriguing is happening in South America. The phenomenon (fig. 2) is focussed on the coastal plain from Guayaquil (Ecuador) to Chiclayo (northern Perú), up to about 500m via the Reque and Chotano valleys as far as Bagua Grande (in a low pass in the northern Andes of Peru). The area approximates to the western watershed, and includes the transition zone from tropical rain-forest to desert. In this area alone, the species gravitate towards two distinct colour forms; they do not comprise mimicry-groups because there is insufficient similarity between most of the species concerned; furthermore, no such situation is found in other insect groups which normally mimic wasps. This phenomenon is so distinct from other kinds of colour variation that the name lygarochromy is here proposed to distinguish it.

The various species react diversely to this local influence, yet are in accord with two themes set by the endemics, one theme (or occasionally both simultaneously) being followed by each species or sex. The first theme is the acquisition of white wing tips (or extension of existing ones); the second is loss of certain areas of infuscation, producing a pattern of pale amber markings distinctive for each species and sometimes augmented by bright, metallic pubescence. These themes are represented in the endemic species as follows: white wing tips are present in *P. lycaon* Banks and *P. cooperi* spec. nov. whereas *P. petiti* Guérin and a smaller, undescribed species of the *P. lampas*-group represent the amber theme. Only the last-mentioned varies in colour: at around 500m, the wings are amber-orange with a broad, dark border; at sea level almost the entire wing is silver-sandy in the female, which closely resembles that of *P. petiti*; these are the only species in the area which together form an obvious mimicry-group. Of the endemic species, *P. petiti* and *P. lycaon* are found also further south but with restricted distributions. Among the non-endemic species in the lygarochromic area, both of the above themes are followed by *P. assimilis* Banks, with normally entirely black wings in both sexes; here the wings of females develop variably-sized amber patches, while the male wings acquire white tips. The white apex of the hind-wing in both sexes of *P. cyanescens* Lepeletier (another species of the *lampas*-group) also becomes more distinct and extensive in this area.

Of the non-endemic species which follow the second theme, one of the most notable is *Pepsis grossa* (Fabricius) which (like many species of the genus) normally occurs in two forms with a few intermediates: these are an entirely black form (save

for the white wing tips, constant in all forms) which is widespread in the USA, West Indies, Central America and north-western South America; and a pale form of a kind normal for the genus (i.e. wings entirely amber-orange except for basal and apical infuscation), found in parts of the USA and Mexico. However, the form occurring in the lygarochromic area has a very distinctive pattern of extensive pale brown and buff markings and a metallic, sandy sheen. The most remarkable colour change in the lygarochromic area, and surely the most beautiful, is that of *P. terminata* Dahlbom; this species already exhibits a greater than usual range of light–dark colour variation (see above) in its extremely extensive range, but here it excels, even outdoing the endemics: the female wings take on the most brilliant silver or golden metallic colour (in one female (BMNH) the opposite wings are of different colours), while the normally entirely black-winged males exhibit a white hindwing apex (the lygarochromic phenomenon, like other colour changes in the genus, usually affects females more than males).

The mystery deepens further when we consider *Pepsis montezuma* Smith, which is abundant on all high ground in the northern and western Neotropics (although absent from the West Indies) and also inhabits the western desert coast of South America. In the latter area, the usual montane form with orange-amber wings and black antennae undergoes a complete colour reversal with black wings and orange antennae. Although the western Andean watershed adjacent to the desert coast has not been well collected, a complete range of forms between the two colour extremes occurs in the Chiclayo area of the north Peruvian coastal plain (within the lygarochromic area). These specimens appear to be perfectly normal transitionals, unaffected by the lygarochromy phenomenon, yet strangely-coloured specimens do exist: they display an odd silver-grey sheen, which at first sight appears to be an artefact (such as dusting with pale powder might produce). One such specimen, a female, (UNLAMB) bears the locality Bagua (this seems unlikely, and needs confirmation - see following records) near the upper limit of the lygarochromic area. Further specimens (of both sexes) have been seen from the Ayacucho–Huancavelica area (2,700–3,400m, south east of Lima) (MHNLIM); a female from Matucana (at 2,400m, east of Lima) (MCZ); and a single male with only “Peru” as locality (UNALM). Whether the occurrence of this colour form of *P. montezuma* in apparently very few, restricted areas is connected with the lygarochromy phenomenon is questionable. Two further species occurring in the lygarochromic area but apparently unaffected by it are *P. chiliensis* Lepeletier and *P. tolteca* Lucas. The former is black with orange antennae, the latter has the wings amber with whitish apex and black antennae; both are more or less at the northern limit of their ranges, which include most of the Peruvian Andes.

Other phenomena exist which may have a bearing on the lygarochromy question; for example, several specimens of *Pepsis grossa* (Fabricius), from a small area at the eastern end of the U.S.A./Mexico border, which coincides with the transition zone between pale and dark forms of this species, have a silvery, transverse, basal band on the forewing strongly reminiscent of the normal patterns of *P. albocincta*, *P. caridei* and *P. foxi* in Argentina. Throughout most of its range, i.e. east of the Rocky mountains, the wings of the Nearctic species *P. pallidolimbata* Lucas are more or less covered with pale yellowish-metallic coloured hairs, imparting an almost sandy appearance. A *Pepsis rubra* male from the Dominican Republic has on the forewing an extensive patch of dull orange-metallic coloured hairs.

How is this odd situation to be explained? Maclean et al. (1978: 106) state “the degree of melanism has been correlated with humidity for a number of insect groups”; it appears that humidity is more important than temperature in influencing this phenomenon. The species may indeed be reacting to the semi-arid conditions which prevail for much of the year in the lygarochromic area; but this cannot be the whole answer because the phenomenon does not occur in other arid areas. In the case of those few species which are sufficiently widely distributed to include more than one hot, arid area in their ranges, a distinct kind of pale form occurs in each such area. Presumably remoteness, causing attenuated gene flow, and the rather different conditions prevailing in each area combine to produce these effects. It may be significant that all the species which are affected are on the edge of their range in the lygarochromic area (or are endemic); species at the edge of their range (or living in otherwise extreme conditions) are also, of course, at the extremes of their survival capacity, and this is known to increase the likelihood of their being unusual in some way. This can manifest in changes in colour, structure, or other aspects. Examples of divergent colours are *Pepsis grossa* (Fabricius) in north-eastern Mexico/south-eastern USA (forms with mainly amber wings); *P. montezuma* (dark-winged in highland Ecuador, very pale-winged in Argentina, black-winged on the Peruvian desert coast) and most species, including *P. grossa* (Fabricius), in the lygarochromic area. Each area produces its own kind of unusual colour variation in susceptible species. Further, Lawson (1994: 43), referring to Phasmidae (stick insects), states that “Parthenogenesis tends to occur in species on the edge of their ranges, where environmental conditions may not be favourable.” Furthermore, the area itself is highly unusual; it is the only extensive coastal transition zone between rainforest and desert in tropical South America, usually receiving rain for 3 months or more a year, beginning about Christmas. This is due to a southward shift of the warm Equatorial current which for that period supersedes the cold Humboldt current (in 1998 this phenomenon, called El Niño, occurred in the most extreme form ever recorded). Whether all these facts taken together can provide an answer is questionable. Perhaps only extensive field investigations will fully elucidate this striking phenomenon.

Anomalous colour resemblances.— Within the genus *Pepsis* there are several instances of very close resemblance in colour patterns which are not easily explained by invoking mimicry groups, for example, *P. decorata* Perty (fig. 76), found principally in the Amazon basin, and *P. roigi* spec. nov. (fig. 77), whose centre of distribution is east of the Argentine precordillera. These species have almost identical, very unusual and quite complicated silvery patterns on the wings in both sexes. However, since their ranges are barely sympatric, they are hardly likely to constitute a Müllerian mimicry group. Nor are they particularly closely related within the *P. rubra*-group, so that very recent common ancestry cannot be invoked as an explanation. Again, in both sexes of *P. equestris* Erichson (a member of the *P. rubra*-group) the forewing has a silvery sub-basal band and a white apex. So also does the female (only) of the totally allopatric *P. lycaon* Banks (in the *P. elevata*-group). It is even less feasible to explain this case by mimicry. Perfectly recognizable mimicry groups do exist in the genus, but each comprises several sympatric species, and these groups are thus in complete contrast to the phenomenon we are considering here. What about convergent evolution? Here again, the almost precise replication of detail in the different forms renders

this explanation scarcely plausible. It seems more likely that these patterns were developed in ancestral taxa, then ceased to be expressed or remained latent, later becoming (re)expressed in certain cases. It may be that the phenomenon is governed in some way so that the incidence and expression are in proportion to the degree of relationship between the forms concerned.

### Biology

Mimicry.— As might be expected in the case of wasps which are frequently large and dangerous if provoked, there exists a large number of mimics in several orders of insects. Examples include *Pepsis vitripennis* Smith, mimicked by the reduviid bug *Zelurus ater* Lepeletier in Colombia; *Pepsis basalis* Mocsáry mimicked by an ichneumonid *Cryptopyge* sp. in Costa Rica, Ecuador and Colombia. The bush-cricket *Scaphura nigra* (Thunberg) (Tettigoniidae) in Brazil is a generalized but excellent mimic of dark-winged *Pepsis* species walking on the ground (*teste* Dr L. Otero, MNRJ). The mimicry phenomenon is so powerful in *Pepsis* that even a humming-bird, *Discosura longicauda* (Gmelin) (Trochilidae) is a generalized but excellent in-flight mimic of dark-winged *Pepsis*, *teste* Dr E. O. Willis (Zoology Dept., UNESP, Rio Claro SP) (pers. comm.), who has observed it in tropical lowland forest in Brazil, at Monte Pascoal near the southern coast of Bahia.

Nocturnal activity.— Hurd (1952: 287) records specimens of *Pepsis grossa* (as *P. pattoni* Banks, 1944) being taken at light, the first evidence of nocturnal activity for the genus.

Economic importance.— Certain species of the genus are of some economic importance; for example, at least 2 species (*P. pallidolimbata* Lucas, 1895 and *P. thisbe* Lucas, 1895) have been recorded attacking grapes in California (McKenzie, 1933: 159). Furthermore, species of *Pepsis* are especially attracted to the flowers of *Asclepias* species (Asclepiadaceae) and probably form the largest group of pollinators (see Hurd, 1952: 269). Some *Asclepias* are important pest species in the Americas, where they are known as milkweeds (not to be confused with the plants of the same vernacular name in Europe belonging to the family Euphorbiaceae). It is difficult to assess what "economic" effect the wasps' predation on spiders has, since in most cases the economic significance of the spiders themselves is unknown. The female wasps can sting excruciatingly if they are handled, but they are not known to attack humans without being so provoked. According to Schmidt (in Tiesheng & Schmidt, 1992: 6), although the sting of *Pepsis grossa* (as *P. formosa* (Say, 1823)) is more painful than that of any other insect known to those authors, the venom is pharmacologically essentially inactive in mammals.

Flowers visited.— Apart from *Asclepias* species (see above), *Pepsis* species frequently show a predilection for visiting flowers of certain other plants, with a distinct hierarchy of preferences in any given area. For example, in north-central Perú there co-exist five very closely related species of *Acacia* (Mimosaceae) but *Pepsis* visits only one, *A. riparia* Bert. ex Spreng. In parts of that area where it is absent, *Serjania peruviana* Radlk. (Sapindaceae) is visited. M. Cooper, who collected these plants together with the wasps visiting them, says that where both plant genera occurred together, the *Acacia* was preferred by the *Pepsis*. *Cuscuta odorata* Poepp. ex Choisy (Convolvu-

laceae) is a climbing plant whose flowers are very attractive to these wasps in the Andes above Lima.

Physiology.— Punzo (1990, 1991) has investigated haemolymph composition and neurochemistry in *Pepsis grossa* (as *P. formosa* (Say)) in the USA; its tarantula host is given as *Rhechostica echina* (Simon).

Kairomones are probably used by female wasps to immobilize their hosts temporarily; Petrunkevitch (1926) noticed “a pungent odor” emitted if the wasp was “angered” or endangered. Hurd (1952, citing Lincecum, 1867) states “an odor is produced by the wasp which in some instances attracts other tarantula hawks. On these occasions a fight ensues between the wasps, which may end with both succumbing, or one is driven off while the other takes possession of the prey.”

Territorial and hunting behaviour.— Punzo (1994a: 239) states “The males [of *Pepsis thisbe*] are strongly territorial and will aggressively defend perch sites on mesquite (*Prosopis glandulosa* Torr.) and ocotillo (*Fouquieria splendens* J. Lodé) and various trees by aerial combative contests with conspecific males that stray too close.” He also states (p.238), “Although male and female *Pepsis* wasps frequently engage in inter- and intraspecific territorial displays (Williams, 1956; Alcock, 1983; Field, 1992), these displays are rarely fatal.” However, I have not succeeded in finding mention of such displays in this genus in any of the three references he gives, and I know of no such observations on any *Pepsis* species except the above-mentioned ones by Punzo himself.

Punzo & Garman (1989) and Punzo (1991) have investigated neurochemistry and hunting behaviour in *Pepsis grossa* (as *P. formosa* (Say)) in the USA; Punzo (1994b) studied the natural history of *Pepsis thisbe* and its tarantula prey, *Aphonopelma echina* Chamberlin in the USA (Texas, Transpecos). He concluded (p. 253) that “those specific behavioral components that improve with experience ... are precisely those that are most closely related with potentially unpredictable behavioral acts of the host.” However, especially if a female is old and worn, the tarantula is sometimes able to kill it; instances are given by Hurd (1952) and Williams (1956).

Host records.— As far as is known, all species of the genus are parasitoids of spiders belonging to Mygalomorpha. Of these, most are Theraphosidae; but it is uncommon to see a wasp with its captured host. The data given by Hurd (1952: 266), as well as subsequent records, suggest that *Pepsis* species are fairly specific to particular genera, and sometimes species, of spider. For example, Petrunkevitch (1926: 390) found that *Pepsis marginata* Beauvois preyed exclusively on *Cyrtopholis portoricae* Chamberlin, both in the field and in the laboratory. Punzo & Garman (1989: 513) found that *P. grossa* (as *P. formosa*) usually preyed on *Rhechostica echina* Simon; but (Punzo, 1994a, b) could use *Aphonopelma echina* Chamberlin. Punzo (1994b: 244) found that in his area of study in the USA (Texas, Transpecos) *P. thisbe* always used *Aphonopelma echina* Chamberlin. Furthermore, since all Pompilidae provision each cell with a single host only, the size of the wasp must be in approximate proportion to the size of host it can use (given that on average, male-producing eggs must be laid on smaller hosts, and female on larger).

In the present work, host records subsequent to Hurd (1952: 268) are noted under the individual species concerned. Hurd warned that many old records are unreliable because the name *Mygale hentzii* was applied to almost any tarantula in the USA, while *Pepsis formosa* (= *P. grossa*) was applied to almost any *Pepsis* there. Passmore

(1936) gives an interesting account in which the wasp is named as *P. formosa*, while the spider is unnamed. However, in one of the photographs, a large pinhole visible in the spider's thorax casts doubt on the accuracy of the report. Hurd also gives a Darwin's (1875) record of a "*Lucosa*" species taken by a *Pepsis* species; this is surely a misspelling of *Lycosa*, which is not a mygalomorph spider; furthermore, according to Smith (1987: 56) the wasp is likely to be a species of *Trypoxylon* (Sphecidae). Nevertheless, some of Hurd's records are especially interesting in that they pertain to mygalomorph spiders belonging to families other than Theraphosidae. These are as follows: the Poulton (1918) record of *Idiops* spec. (Idispidae, formerly Ctenizidae) (taken by *Pepsis* spec.) in southeast Brazil is substantiated by a record of the same genus being taken by *Pepsis smaragdina*, Dahlbom, 1844, a species very common in that area (specimens in MLU); unfortunately Poulton's material has not been located. A further record of an idispid spider is the genus *Bothriocyrtum* (given for *Pepsis mildei* Stål, 1857) while *Brachythele* (for *Pepsis* sp.) belongs to the Dipleuridae.

Immature stages.— Hurd (1952) gives several records of immature stages, and Williams (1956) has added further descriptions.

Parasites.— No insects are known to parasitize *Pepsis* species.

Predators.— Hurd (1952: 269) referred to some apparently rare instances of predation on species of this genus by "kingbirds", a reduviid bug and an asilid fly. Punzo (1994a: 237) gives details of how on two occasions he observed a roadrunner (*Geococcyx californianus* Lesson) attacking a wasp on the ground: "The bird grasped the wasp in its beak and beat it against the substrate prior to ingestion."

Mites.— Mites (in the deutonymph stage) are frequently found in the genital capsules of male *Pepsis*, sometimes under the edges of the gastral segments and less commonly on other body parts, in males and occasionally also in females. Samples were taken from six species of *Pepsis*, selected from the widest possible range of species-groups to be as representative of the genus as possible. Altogether, mites were noticed on 15 species of *Pepsis* (where their large numbers made them conspicuous) but more would surely have been found had closer search been made.

The mites proved to belong to the families Anoetidae (3 species) and Acaridae (4 species); both families belong to the Order Astigmata. In one case, one species from each family were found together on a single wasp, but in no case were two species from the same family found together. All of the species were using the wasps solely as a means of transport (phoresy). Species of the family Anoetidae (other than in the deutonymph stage) live in water films where they appear to filter-feed on bacteria; members of the Acaridae are very variable in habits.

Sleeping aggregations.— Williams (1928: 143) reported an observation of communal "roosting" behaviour in a species of this genus; from his description, and the fact that the observation was made near Guayaquil, the record may pertain to the lygarochromic form of *P. grossa* (Fabricius). The phenomenon is well known in other groups of aculeate wasps. (See also under *P. rubra* and *P. sericans* below; and under *P. ruficornis* (Fabricius, 1775) in a later part of this work.)

### General notes

Common names.— These large wasps have attracted public attention and thus

been given vernacular names. In the USA they are called "tarantula-hawks" (Hurd, 1952: 265); in Bolivia, "amigo del hombre" ["friend of man" - the reason for this name is not clear] (M. Cooper, pers. comm.). In Argentina, "San Jorge" [St. George] is the usual common name for species of *Pepsis* and other very large wasps in the east, around Buenos Aires; the derivation of this name is unknown. The derivation of the common name in the west of the country "mata-caballos" [horse-killer], is self-evident, albeit unlikely to reflect the truth; it is often applied to *P. albocincta* Smith, 1855. The term "marabunta" ("marimondo" in Brazil) is used throughout South America for almost any large or aggressive wasp-like creature.

Type material examined.— In specifying the type-material seen, two different ways of referring to single specimens are employed. The expression "a single syntype specimen" (or the equivalent) implies that there is evidence in the original description that the author had multiple specimens before him, but that I have only seen one of them. The expression "a single type-material specimen" means that, although there is no definite evidence that the original description applies to more than one specimen, the possibility of further type-material being recognized later cannot be excluded; and that therefore, in accordance with the International Code of Zoological Nomenclature Recommendation 73 F, a lectotype is here designated.

Dahlbom's type material.— In 1843 Dahlbom published on a number of specimens of *Pepsis*; some were described as new species and some were referred to existing ones. In 1845, however, in several cases he used the same name for a different specimen and sometimes described the earlier specimen as a new species. There is no clear indication in the text that he did this. One example is the specimen referred to as *P. heros* Fabricius in 1843; this is a specimen of *P. marginata* Beauvois, 1809. In 1845 this specimen was described as *P. reaumuri* spec. nov., whereas this time the name *P. heros* was applied to a specimen of *P. frivaldszkyi* Mocsáry, 1885. The true *P. heros* is, in fact, a large species in the *P. rubra*-group, treated in the present work.

Although most of Dahlbom's type-material is found in MZEL, I have seen a female specimen identified (correctly) as *P. thoreyi* Dahlbom in MNHU; it bears a label handwritten in German, "Probably type of *thoreyi*", and may be an original syntype. The specimen stood under *P. nigrocincta* Lucas, 1895 [= *P. menechma* Lepeletier, 1845], but has no apparent connection with that name.

Fabrician type depositories.— Most of Fabricius' type-material is found in two separate collections in the University Zoological Museum in Copenhagen; the original one is the Sehestedt & Tonder Lund collection, while the Kiel collection was acquired later and appears likely to remain there (teste Zimsen, 1964: 7). These are accordingly here designated UZMC and UZMC(K).

Types of Lucas, 1897.— Although the type-material of the species described by Lucas in 1897 (collected by H.H. Smith in Chapada [dos Guimarães], Mato Grosso; see Notes on localities below) is in the CMNH, conspecific material with similar collecting data is also present in the ANSP.

Types of Lucas, 1919.— It is likely that further type-material of Lucas, 1919 will be discovered, probably in European museums; the entire collection on which that paper was based was almost certainly sold by auction by Bang-Haas & Staudinger, the entomological dealers whose property it was at the time the descriptions were made. The few specimens I have seen bear inconspicuous hand-written labels and had not previ-

ously been recognized as type-material (for types still missing see note under "Unplaced names" in a later part of this work).

Species descriptions.— The species descriptions include those characters which appear to be most helpful in identification; to include all of those to which phylogenetic importance is attached would mean an unjustifiable increase in the length of the descriptions. The latter characters are of course given with the diagrams of proposed phylogenetic groupings.

The terminology used here mainly follows Hurd, 1952; a few terms are new (see Abbreviations above).

Material examined.— Material of newly described species is listed in detail; for all species, the numbers of specimens seen is stated, distributional range summarized and maps given. Although Hurd (1952) treated in detail the species of *Pepsis* which occur in the Nearctic region, he did not cater for specimens from south of the USA which often display hitherto undocumented variation. They are therefore treated fully here except for their nearctic distribution (see Notes on the distribution maps below).

Notes on the distribution maps.— ? = doubtful or unlikely record, needs confirmation; symbol plus an arrow pointing towards a country = no minor localities known or traceable; symbol inside a circle surrounding islands = found in all or most islands within the circle.

The Nearctic distribution of species common in that region is given in outline only, after Hurd (1952); collection localities of species rare there are shown in the same way as for Neotropical specimens.

Notes on localities.— The term "America meridionale" (often abbreviated to "Amer. merid." or just "Am. mer.") as used by Fabricius, Dahlbom and their contemporaries included the West Indies, the Caribbean coast of South America, occasionally the Amazon delta, and even (in at least one case) the eastern Brazilian state of Bahia. Both *Pepsis reaumurii* Dahlbom (= *P. marginata* Beauvois, 1809) and *P. ruficornis* (Fabricius, 1775) were described from "America meridionale" and are endemic West Indian species; yet, in the former case, from the first time the name was used after the description (Taschenberg, 1869 and all subsequent authors) it was misapplied to a common Argentine species (*P. caridei* Brèthes, 1908). In the latter case, Banks (1946: 315) arbitrarily restricted the provenance by declaring that "*P. ruficornis* was described from South America". Both misconceptions have caused much confusion.

The location of two place-names in the Mato Grosso, Brazil has also caused problems. They are "Nivac", now Nioaque; and "Chapada": there are several places with this name (meaning "plateau") in the area. The one where H.H. Smith collected is now called Chapada dos Guimarães; Papavero (1973: 379) refers to it as Santa Anna La Chapada, but the location is the same. Two topographical terms which proved very difficult to trace are gato (in Argentina), from the Quichua cato, a small open-air market; and ható (in Colombia, Venezuela and Cuba), a smallholding where cattle are bred.

Sex associations.— In the great majority of *Pepsis* species, the sexes have never been associated. This has to be done primarily on the basis of their distribution (which necessitates abundant material), after the difficult task of distinguishing the females from each other has been accomplished. Other features helpful in associating

the sexes are average size of the species; small, variable structural characters such as strength of MT, sculpture of MPN and propodeum; and venation details (especially SMC3 shape). Considerable experience is required to apply most of these criteria successfully. Occasionally, obvious colour characters exist to link the sexes, but most often the latter are strongly dimorphic. Associating the sexes is a process vital to classification within the genus because each sex displays its own unique set of characters important for assessing the inter-relationships of the species; the two sets of characters must be considered together.

### The *Pepsis rubra*-group

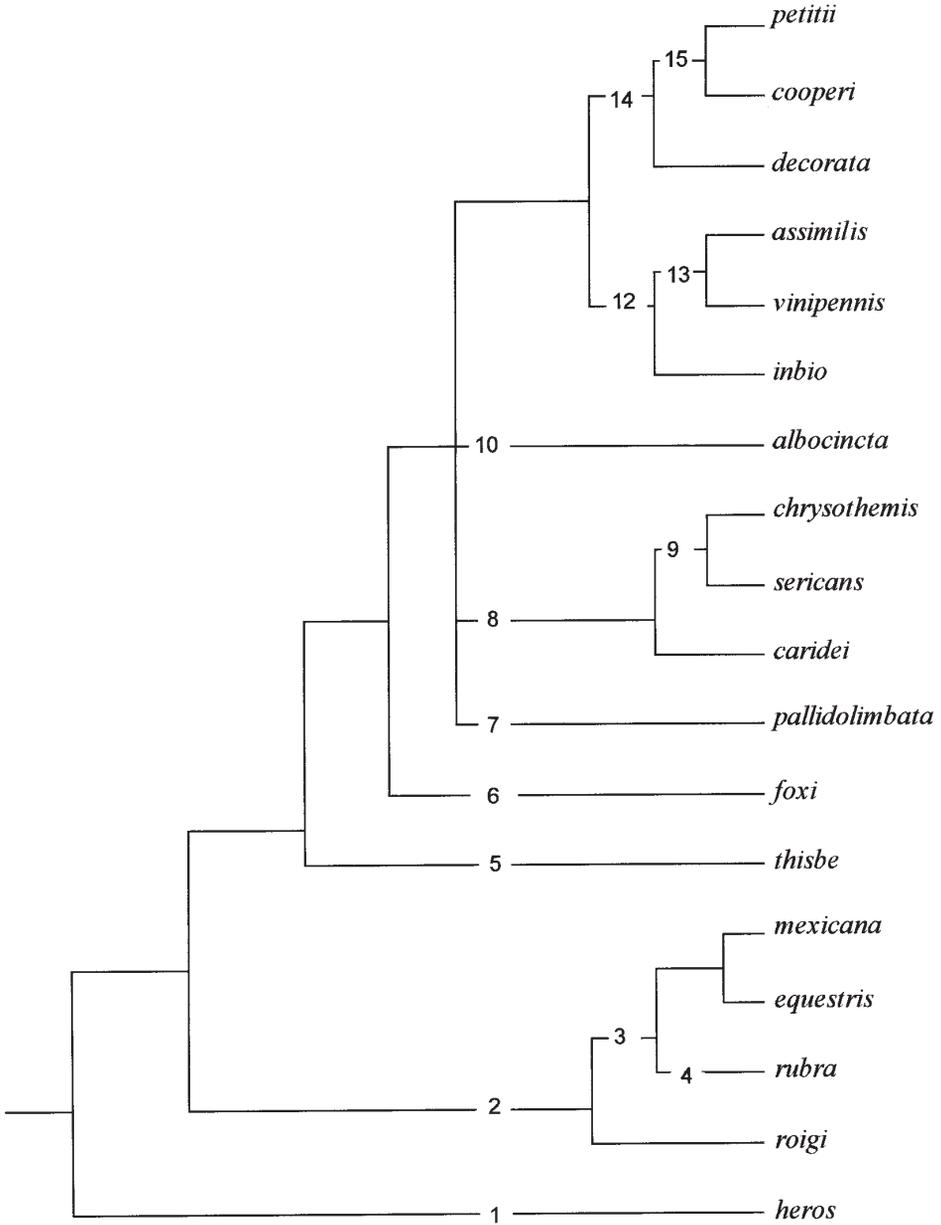
Definition.— No group-characters common to both sexes are known. Male sternites without strongly modified hairs. SGP always very strongly modified, with pre-apical carina, very variable but always with transverse or at least oblique component, never longitudinal alone (figs 7-45; 47-48). Females usually with apex of radial vein meeting costa at a very shallow angle (figs 70, 76-79; contrast fig. 80). Lateral extension of S.2 groove well developed.

Description.— Size variable; the majority are small to medium species. BL males 12-37, females 14-62. Body hair dark, rather long, sometimes dense. Antennae usually black, sometimes some apical segments orange. Wing colour variable, a few species sexually dimorphic; black, usually with a white or pale apex (often more extensive in males) and/or silvery markings; or orange (rarely pale amber with a yellowish sheen), usually with a dark apical border, which is often succeeded by a white or pale extreme apex; occasionally also with a dark or black base. Occasionally, wings silver-sandy colour with black base and pale apex. MT usually weak; strong in a few species and sexes. MPN with extremely variable sculpture. Propodeum with MG absent to fairly strong, APT fairly strong, PPT and PTC almost always strong, DTC variable, most often rather weak.

Discussion.— This group includes the type-species of the genus and is named after it. With 18 known species, it is the largest group in which the male SGP is strongly modified; its range includes the southern USA and the entire neotropical region south to Patagonia. Its species together display the greatest range of wing colour in the genus, although no colour is unique to this group. Female wing colour varies more than that of males, usually on a geographical basis. 5,937 specimens of the *rubra*-group from the neotropical region, and many from the Nearctic, have been examined in the course of this work.

This group is most closely related to the *P. grossa*- and *elevata*-groups by its general habitus, colour patterns and lack of modified hair on the gastral sternites, but the formation of the male SGP is distinct from that of all other groups and the unusual female venation character is shared only with the two species of the *grossa*-group. In fact Haupt (1952: 383 & fig. 44) noticed this character in *P. thisbe*, but failed to realize its importance as a group-character. The *P. rubra*-group is structurally the most specialized in *Pepsis*: the male SGP is the most complicated in the genus, and the *P. rubra*- and *grossa*-groups (the latter comprising only 2 species) are the only groups in which the females exhibit a venation character unique to their sex.

Cladogram for the *P. rubra*-group:



Legenda of cladogram for the *P. rubra*-group:

1. Body size very large; PAC including strongly oblique carinae; MPN & anterior propodeum matt.
2. SGP narrow; wings mainly black with white or silvery markings.
3. SGP very narrow, thick, its median keel strong; body size small.
4. Apical hair-tuft of digitus very sparse; wings with orange-red colour [a reversal].
5. SGP median carina partly lost; apex V-shaped, strongly projecting.
6. SGP thin; apex with sharp, strongly projecting lateral angles.
7. SGP median carina totally lost.
8. Apical hairs of digitus not dense, distributed over large area. SGP narrow, carinae elongate.
9. MPN furrow and MG broad, shining; DTC coarse.
10. Body size large; SGP with apex and PAC elongate.
11. Wings black with white or silvery markings; MPN furrow broad; propodeum long.
12. PAC narrow.
13. Digitus with apical hair-tuft very narrow; MPN furrow narrow [a reversal]; SGP with apex & PAC elongate, rather distant; SMC3 narrow anteriorly; female often with red wings [a reversal].
14. PAC broad.
15. Main plate of SGP projecting beyond base of apex; apex broad, centrally emarginate; propodeum very long and densely hairy; antennae orange; wings with pale, metallic pubescence.

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Phylogenetics.— The cladogram presented here is tentative, because of the extreme lability of the characters (especially those of the SGP) and the evident presence of reversals, producing multiple, self-contradictory cross-correspondences between species. Even within a single species, e.g. *P. albocincta*, the variation can be such as to suggest the presence of two distinct species (see discussion under that species). Furthermore, variation can be in different directions so that it is not comparable between species. Altogether, these facts render coding the characters for any computerized treatment both extremely difficult and largely meaningless: a computer is no more able to distinguish between ancestral and reversed characters than is an alpha-taxonomist. Indeed, the solution of this problem may not lie within the powers of alpha taxonomy. Analogies with the biogeography of other groups, to be treated later, may prove helpful; perhaps the best way of solving the problem will eventually prove to be the analysis of the relative proportions of nucleotide bases between species (see e.g. Maddison, 1994: 270).

Characters used.— Size and colour of insect; shape, dimensions, sculpture and pubescence of MPN (including its median furrow) and propodeum; SGP: thickness, degree of curvature, shapes and distance apart of apex and PAC and width of the latter; paramere: overall shape, ridges, indentations of inner edge; digitus: shape, especially width just before apex; density and distribution of strong hairs thereon, size and shape of inner, basal spine.

Biogeography.— The species most distant from each other taxonomically (*P. heros*, *P. thisbe*, *P. foxi*, *P. pallidolimbata*, *P. chrysothemis*, *P. caridei*, *P. albocincta*) are medium to large (on average, markedly larger than the remainder of the group); they are also the most geographically distant from the western Amazon basin (the putative centre of origin of this species-group) with the exception of *P. heros*, which is found in the Guianas and (apparently more rarely) north-western Amazon basin; however, it is also exceptional in being easily the largest species of the *P. rubra*-group as well as the oldest. In summary, the older species tend to be the largest, more peripheral to the range of the group and the wings are more often orange-amber than black.

Within each of the terminal cladogram clusters referred to above, all the species are allopatric; the result is that most regions contain several species from different subgroups. This situation can be explained by multiple radiations having taken place during the glacial/interglacial periods. Except for *P. rubra* and *P. sericans*, today isolated in the West Indies, all species of the group occur on the American mainland. The distributional ranges of all these latter at some point closely approach the virtually continuous western mountain spine running throughout the Americas; there is no species whose range is exclusively eastern. Furthermore, the greatest concentration of mainland, "restricted-distribution" species is in the region of the northern Andes. These facts together suggest that the group originated in north-western South America, probably western Amazonia.

Structure and ecology.— One of the most interesting ecological-biogeographical situations in this group is the existence of apparently analogous species-complements in two of the main arid areas of the Americas: south-western USA and western Argentina. In each region there are large, medium and small species, respectively *P. thisbe*, *P. chrysothemis* and *P. pallidolimbata* in the north, and *P. albocincta*, *P. caridei* and *P. foxi* in the south. Of these, one species in each region has the head strongly constricted behind the eyes, one has it strongly swollen; one has a particularly long AS3, another a particularly short one; one species has the fore wing with a distinct, pale apex - the detailed parallels are many. Furthermore, the northern species *P. grossa* has its counterpart in its southern sister-species *P. chacoana* Brèthes, 1908 (together they form the *P. grossa*-group). Similar species-complements may well exist elsewhere, but in view of the smaller numbers of species in this genus inhabiting desert areas, such situations are easier to discern there. Although the two allopatric sister-species of the *P. grossa*-group are structural counterparts, in the *P. rubra*-group the phenomenon does not have the same origin since the two complements do not consist of pairs of very closely related sister-species, and the structural characters enumerated above are found in different combinations, e.g. the smallest species in the Argentine complex is the one with the most strongly swollen back of head and the shortest AS3, whereas in the USA the smallest species has the most transverse head and the longest AS3. Inasmuch as the species of each complementary set are not particularly closely related within the group, they presumably evolved allopatrically and arrived singly in their current distributional ranges (the alternative being the postulation of multiple centres of spread, a less likely situation), then perhaps undergoing a further period of co-evolution to arrive at compatibility. Is the current situation really a reflection of comparable niche-complements in the two arid areas? The existence of such similar character-sets, distributed between the same small number of species in each case, seems more likely to have resulted from gravitation towards a common pattern than to have occurred by sheer chance. But why do the characters not occur in the same combinations in each case? It is as though the characters are distributed in a particular kind of habitat rather than in the species, the latter acting only as vehicles for the characters, and that three species is the optimum number to carry this particular character-suite. The situation appears to be complex; evidence forthcoming from the study of other species-groups may shed further light on the phenomenon.

Mimicry-groups and ancestral characters.— In the region of the Mato Grosso in Brazil, both sexes of *P. albocincta* and *P. foxi* assume a peculiar dark, infuscate-green-

ish tint. Together with a few species belonging to other groups, notably *P. discolor* Taschenberg, 1869 and *P. defecta* Taschenberg, 1869, which also occur in that area, they apparently form a Müllerian mimicry group. However, this explanation of similarity cannot hold good for *P. decorata* (fig. 68) and *P. roigi* (fig. 67) which, although only marginally sympatric (and not particularly closely related within the *P. rubra*-group), share virtually the same intricate colour pattern (silver-white on black) in both sexes. These would appear to be fortuitous manifestations of an ancestral character. The same probably holds good in the case of *P. equestris* Erichson, 1848 (*P. rubra*-group) and *P. lycaon* (*P. elevata*-group), again almost identical in colour but only marginally sympatric; however, here the phenomenon concerns both sexes of the former but only the female of the latter species; this may be connected with the fact that the species are more distantly related, and possibly also that females in general are more variable in colour than males.

Problems.— (1) The identity of a single female from the Mato Grosso, Nivac [now called Nioaque] is doubtful; it is placed as *P. roigi* rather than *P. decorata*. However, two other females from the same locality are identified as the latter species. Unfortunately, no males of either species are known from there.

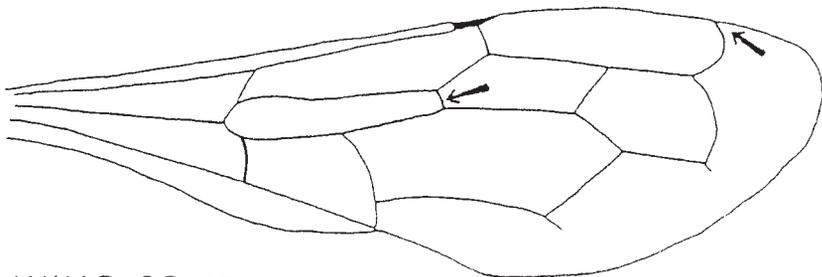
(2) See discussion under Phylogenetics.

**Key to males of the *Pepsis rubra*-group**

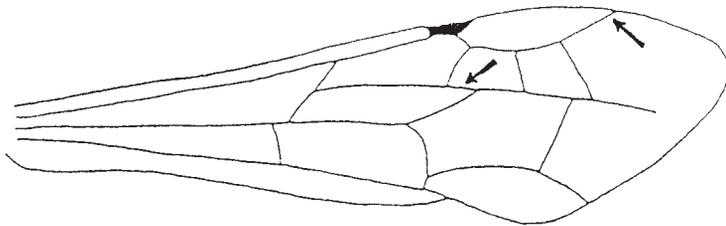
- 1. SGP: as well as the carina formed by the more or less upturned apex, there is a distinctly pre-apical one, which is usually transverse, but often at least partly oblique; (*P. rubra*-group) ..... 2
- SGP either not modified, or with various modifications (e.g. carinae, ridges or tubercles) which are usually median longitudinal (if transverse, then basal and usually weak); if the SGP has a longitudinal carina incorporating an oblique element (figs 3-6) then the body has long, dense, black hair, and the species inhabits moderate to high altitudes in the Peruvian Andes (occasionally the coast) [*P. tolteca* Lucas, figs 3-6 ] ..... (other groups, part 2 of this revision)
- 2. PAC more or less V-shaped, often with short, median keel extending apicad ..... 3
- PAC transverse, sometimes curved but not V-shaped ..... 11
- 3. Wings rather heavily infusate, virtually unicolorous; MPN matt, without carinae. SGP and genitalia figs 13-14, 55. Large species of east Andean foothills (BL 27-38) .  
..... *P. heros* p. 59
- At least forewing with obviously more than one colour ..... 4
- 4. Forewing with white apex, and/or silvery or silver-buff markings. Without amber, orange or red tones ..... 5
- Forewing partly amber, orange or red ..... 8
- 5. Forewing entirely black except for a white apex. SGP and genitalia figs 39-40, 50. South-western USA to Costa Rica ..... *P. mexicana* p. 65
- Forewing with silver or silver-buff marking near base ..... 6
- 6. Forewing with sub-basal silvery band and white apex. SGP and genitalia figs 41-42, 51. Northern South America ..... *P. equestris* p. 66
- Forewing without pale apex, but silvery sub-basal band extending distad, especially along costal cell ..... 7

7. Wings almost black, markings silver (fig. 67); SGP and genitalia figs 47-48, 66. Argentina, Bolivia, southern Brazil, Paraguay ..... *P. roigi* p. 67
- Wings dark brown, markings silver-buff; SGP and genitalia figs 43-46. Central Brazil ..... *P. foxi* p. 61
8. Forewing amber-orange with dark border extending right to apex. SGP and genitalia figs 43-46. Brazil and Argentina ..... *P. foxi* p. 61
- Forewing always with extreme apex white or pale ..... 9
9. Forewing broadly infuscate basally and apically, hind wing mostly infuscate. SGP and genitalia figs 37-38, 49. Small species (BL 12-23). West Indies ..... *P. rubra* p. 63
- Infuscation of both wings more or less confined to pre-apical dark border. Medium to large species, not in West Indies ..... 10
10. SGP as in figs 13-14. Large species (BL 27-38). Genitalia fig. 55. Guianas, northern and western Amazon basin ..... *P. heros* p. 59
- SGP as in figs 15-18. Medium species (BL 22-27). Genitalia fig. 56. USA to southern Mexico. .... *P. thisbe* p. 60
11. Forewing with silvery or silver-buff metallic markings at least about the middle; often with a white apex ..... 12
- Forewing without pale metallic colours, except occasionally narrowly near base ...  
..... 14
12. Forewing entirely silver-buff except narrow dark base and white apical border; antenna orange. SGP & genitalia figs 29-30, 62. Coastal Ecuador and Perú .....  
..... *P. petittii* p. 75
- Forewing with less extensive pale markings ..... 13
13. Forewing with broad, silvery, central band and rather broad white apex; antenna orange. SGP and genitalia figs 31-32, 63. North-central Perú. .... *P. cooperi* p. 76
- Forewing with sub-basal silvery band and smaller, more distal markings (fig. 68). SGP and genitalia figs 33-34, 64. French Guiana to Bolivia and Paraguay .....  
..... *P. decorata* p. 77
14. Forewing black with broad, white apex; hind wing entirely black; SMC3 very short (fig. 69). Antenna with orange apex. SGP and genitalia figs 21-22, 58. Middle and western Amazon basin ..... *P. vinipennis* p. 70
- If forewing is similarly coloured, the white apex is narrower, and the hindwing also has a white apex; the SMC3 is of normal length and the antenna is entirely black ..... 15
15. Wings entirely black. SGP and genitalia figs 19-20, 57. North-western South America and Panama. .... *P. assimilis* p. 69
- Wings not entirely black ..... 16
16. Wings black; at least hind wing with white apex ..... 17
- Wings otherwise coloured ..... 18
17. PAC scarcely narrower than narrowest part of SGP (figs 7-10); both wings with white apex. Genitalia fig 53. Amazon southwards ..... *P. albocincta* p. 80
- PAC only slightly broader than half narrowest part of SGP. Found elsewhere ... 22
18. PAC very long and narrow; only about one-third the width of the SGP apex (figs 11-12); wings orange with broad, dark apical border, without paler apex (except in very worn specimens). Genitalia fig. 54. Argentina, Bolivia and Chile .....  
..... *P. caridei* p. 63

- PAC shorter and broader, at least half width of SGP apex; wings often with pale apex ..... 19
- 19. PAC rather narrow, little more than half the SGP apical width ..... 20
- PAC as broad as SGP apex or almost so; forewing with at least the extreme apex clear or white ..... 21
- 20. SGP apex more or less expanded, and emarginate between projecting lateral angles (figs 23-24). Forewing usually with extreme apex whitish. Genitalia fig. 59. USA to southern Mexico ..... *P. chrysothemis* p. 74
- SGP apex slightly narrowed, without strong lateral angles (figs 25-26). Forewing apex usually entirely dark. Genitalia fig. 61. Cuba ..... *P. sericans* p. 71
- 21. Smaller species, BL 16-23. Only extreme apex of forewing whitish. SGP and genitalia figs 35-36, 65. USA to central Mexico ..... *P. pallidolimbata* p. 77
- Larger species, BL 25-39. White apex of forewing broader, covering about half the area beyond the cells, also extending around edge of hindwing. SGP and genitalia figs 7-10, 53. Amazon southwards ..... *P. albocincta* p. 80
- 22. Only hindwing with white apex; SGP rounded apically, PAC expanded apically, about half as high as broad. Figs 27-28; genitalia fig. 60. Honduras to Costa Rica ...  
..... *P. inbio* p.73
- Both wings with white apex; SGP emarginate apically, PAC parallel-sided, about as high as broad. Figs 19-20; genitalia fig. 57. North-western South America and Panama ..... *P. assimilis* p. 69



WING OF PEPSIS

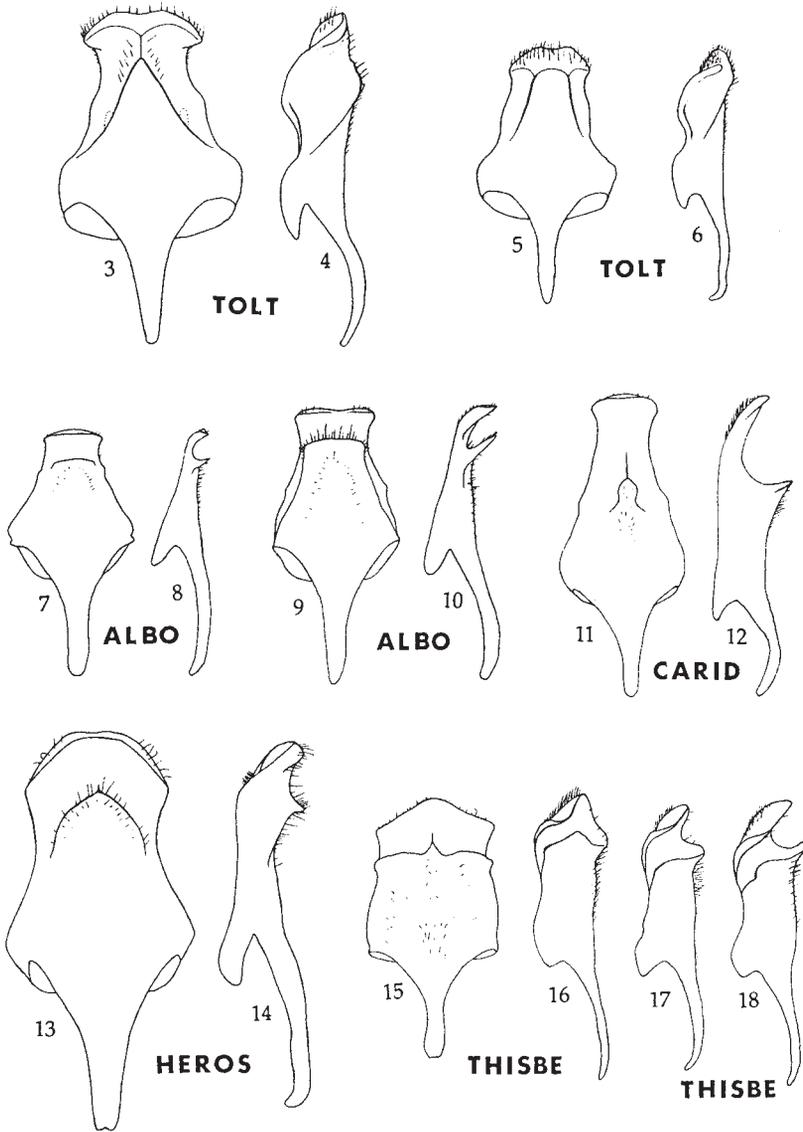


WING OF OTHER POMPILID

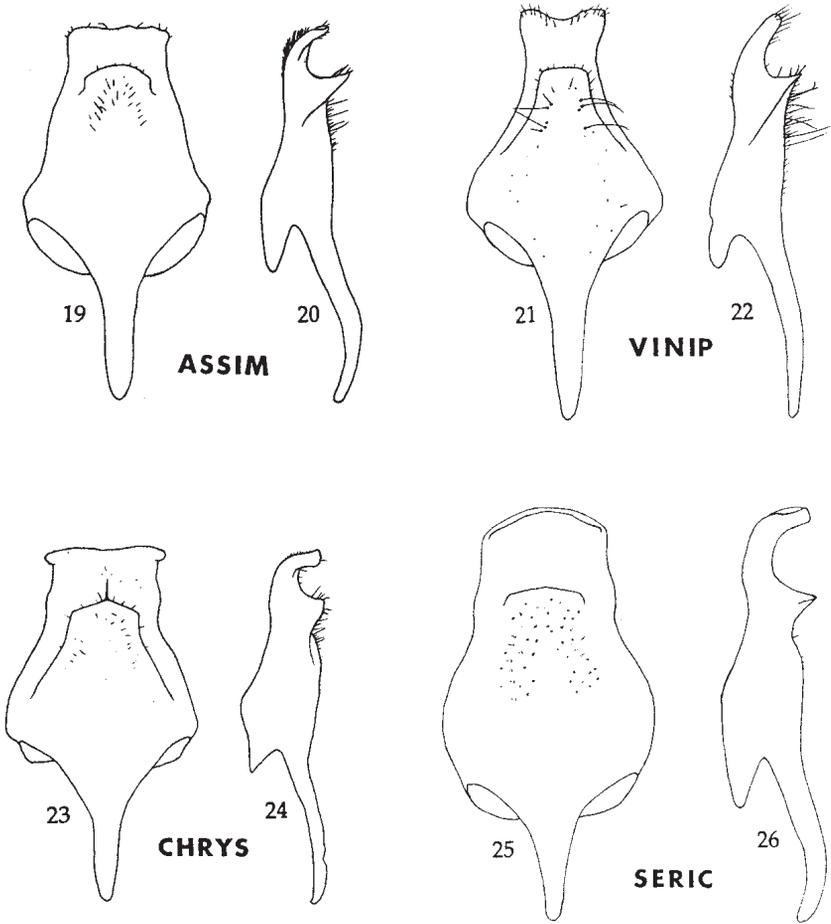
Fig. 1. Pompilidae: fore-wings, right side. Proximal arrow indicates postero-proximal vein of SMC2 ("PPV" in *Pepsis*); distal arrow indicates junction of radial vein with costa.



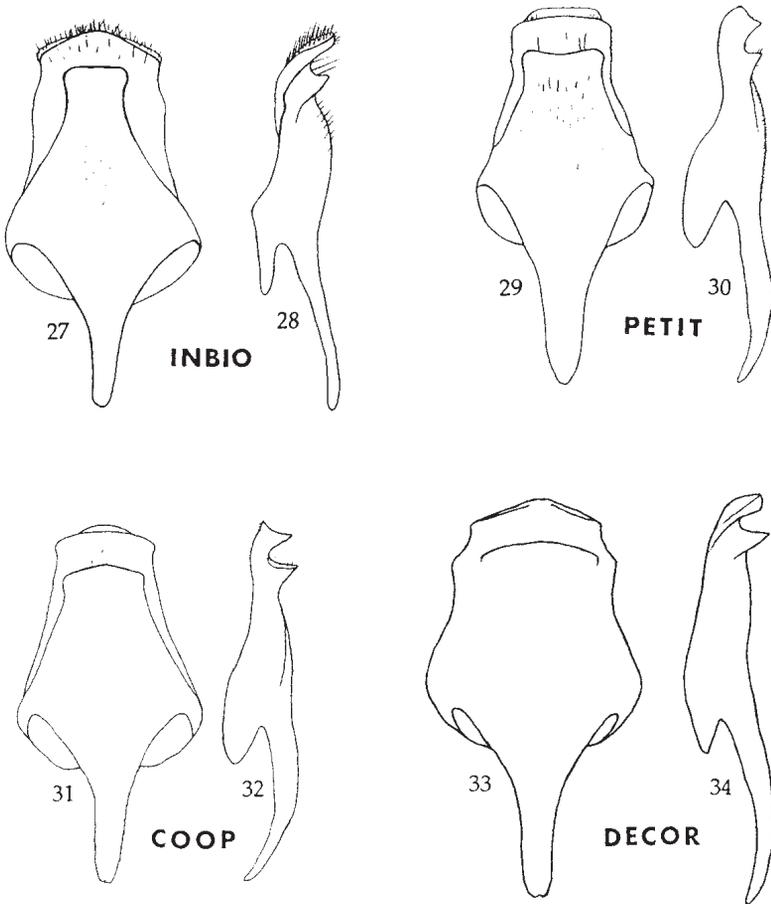
Fig. 2. South America, showing the lygarochromy hot-spot.



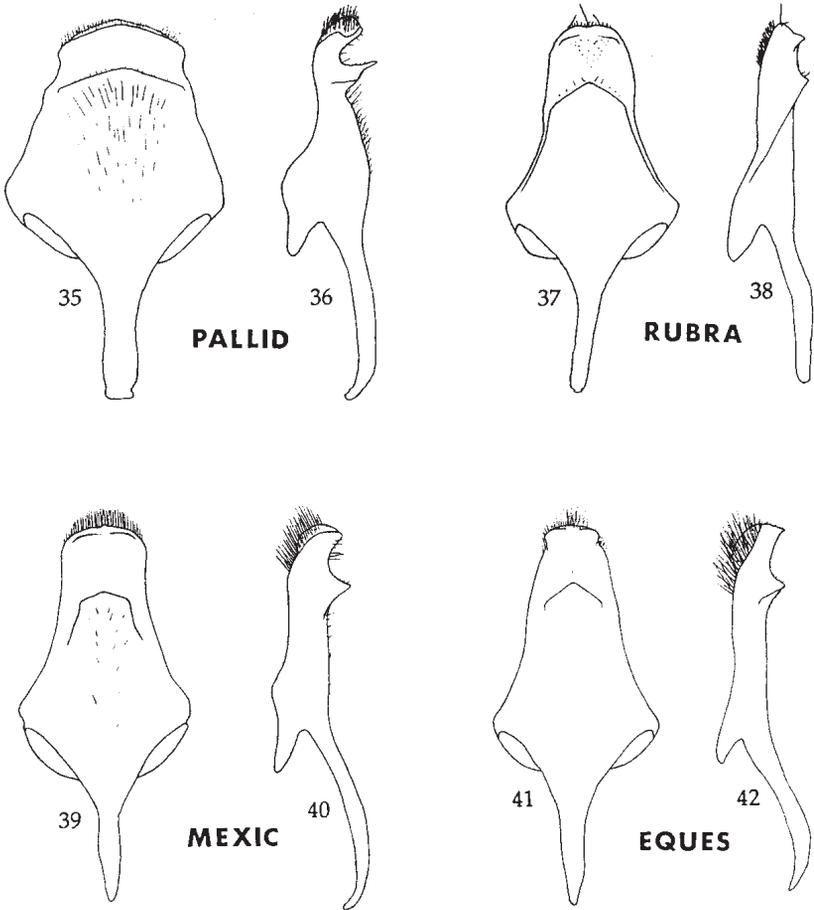
Figs 3-6, *Pepsis tolteca* Lucas; figs 7-10, *P. albocincta* Smith; figs 11-12, *P. caridei* Brèthes; figs 13-14, *P. heros* (Fabricius); figs 15-18, *P. thisbe* Lucas. 3-18, ♂ subgenital plates, ventral & left lateral aspect. Magnification × 25.



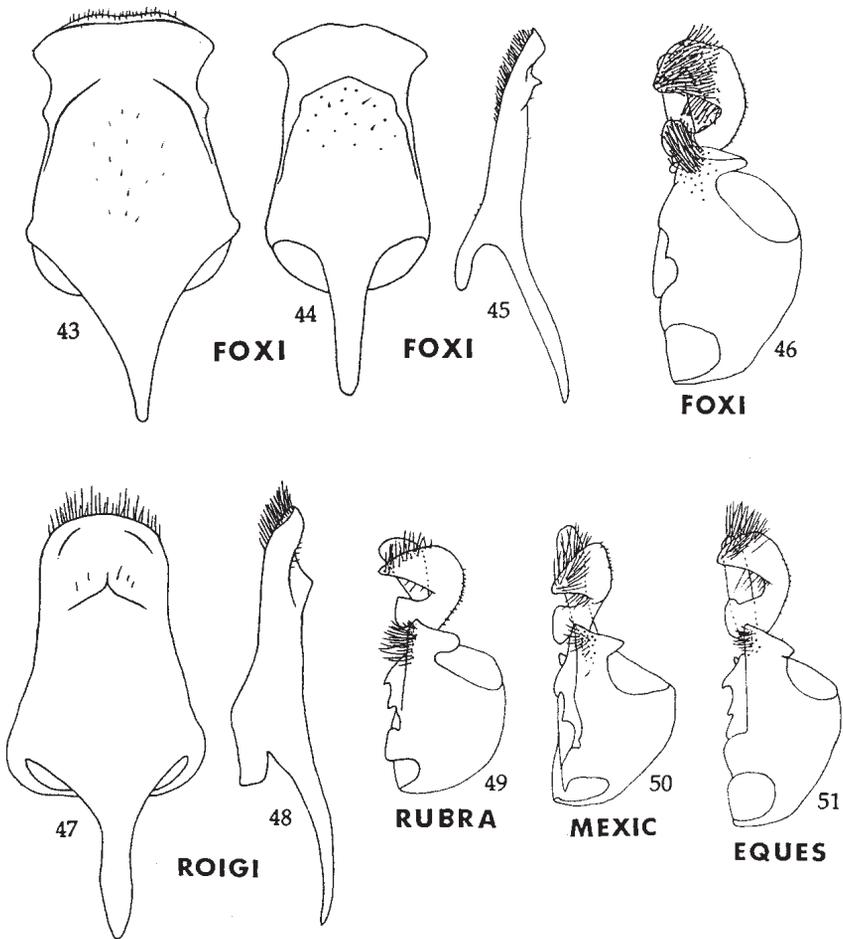
Figs 19-20, *Pepsis assimilis* Banks; figs 21-22, *P. vinipennis* Packard; figs 23-24, *P. chrysothemis* Lucas; figs 25-26, *P. sericans* Lepeletier. 19-26, ♂ subgenital plates, ventral & left lateral aspect. Magnification × 50.



Figs 27-28, *Pepsis inbio* spec. nov.; figs 29-30, *P. petitii* Guérion; figs 31-32, *P. cooperi* spec. nov.; figs 33-34, *P. decorata* Perty. 27-34, ♂ subgenital plates, ventral & left lateral aspect. Magnification × 50.



Figs 35-36, *Pepsis pallidolimbata* Lucas; figs 37-38, *P. rubra* (Drury); figs 39-40, *P. mexicana* Lucas; figs 41-42, *P. equestris* Erichson. 35-42, ♂ subgenital plates, ventral & left lateral aspect. Magnification × 50.



Figs 43-46, *Pepsis foxi* Lucas; figs 47-48, *P. roigi* spec. nov.; fig. 49, *P. rubra* (Drury); fig. 50, *P. mexicana* (Lucas); fig. 51, *P. equestris* Erichson. 43-45, 47-48, ♂ subgenital plates, ventral & left lateral aspect; 46, 49-51 ♂ genitalia, right half, ventral aspect. Magnification × 50.

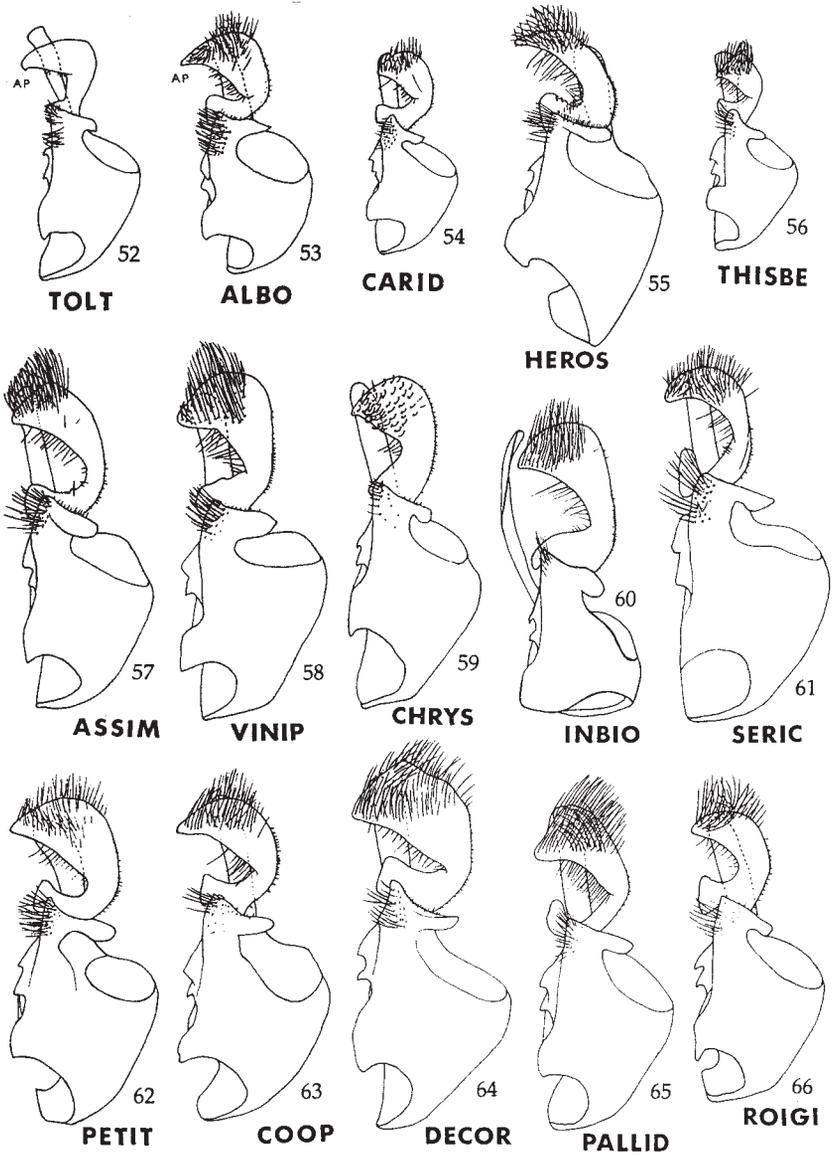


Fig. 52, *Pepsis tolteca* Lucas; fig. 53, *P. albocincta* Smith; fig. 54, *P. caridei* Brèthes; fig. 55, *P. heros*; (Fabricius); fig. 56, *P. thisbe* Lucas; fig. 57, *P. assimilis* Banks; fig. 58, *P. vinipennis* Packard; fig. 59, *P. chrysothemis* Lucas; fig. 60, *P. inbio* spec. nov.; fig. 61, *P. sericans* Lepeletier; fig. 62, *P. petitii* Guérin; fig. 63, *P. cooperi* spec. nov.; fig. 64, *P. decorata* Perty; fig. 65, *P. pallidolimbata* Lucas; fig. 66, *P. roigi* spec. nov. 52-66, ♂ genitalia, right half, ventral aspect. Magnification 52-56, × 25; 57-66, × 50. AP = apical projection of digitus.

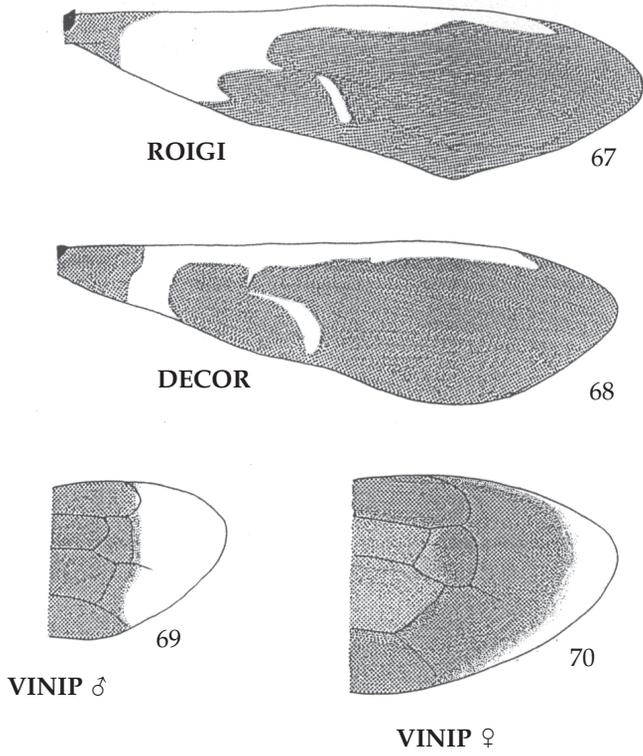
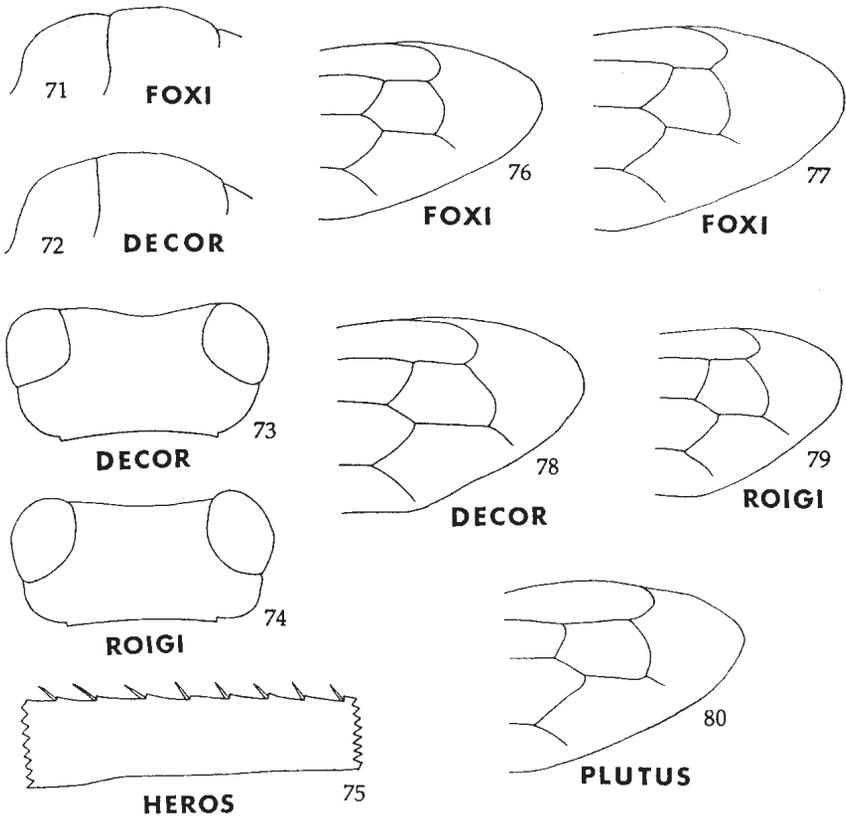
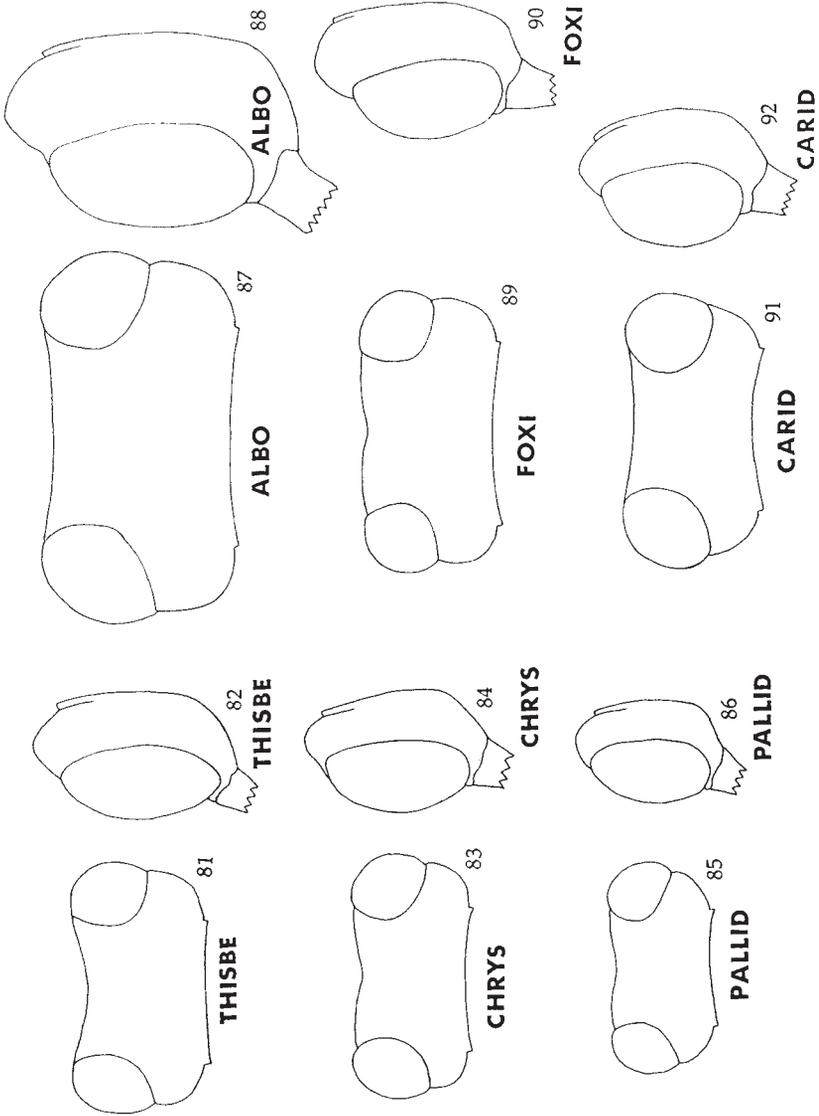


Fig. 67, *Pepsis roigi* spec. nov.; fig. 68, *P. decorata* Perty; fig. 69, *P. vinipennis* Packard, ♂; 70, id., ♀. 67-70, right forewings. Magnification × 6.



Figs 71, 76-77, *Pepsis foxi* Lucas; figs 72, 73, 78 *P. decorata* Perty; figs 74, 79, *P. roigi*; spec. nov.; fig. 75, *P. heros* (Fabricius); 80, *P. plutus* Erichson. 71-72, ♀ gastral tergites 1-2, dorsolateral aspect, from left; 73-74 ♀ head, dorsal aspect; 75 ♀ left hind tibia, apical half from inner side; 76-80 ♀ right forewing: Magnification 71-72, × 6; 73-75, × 12; 76-80, × 6.



Figs 81-82, *Pepsis thisbe* Lucas; figs 83-84, *P. chrysothemis* Lucas; figs 85-86, *P. pallidolimbata* Lucas; figs 87-88, *P. albocincta* Smith; figs 89-90, *P. foxi* Lucas; figs 91-92, *P. caridei* Brèthes. 81-92, ♀, head, dorsal and left lateral aspect. Magnification × 12.

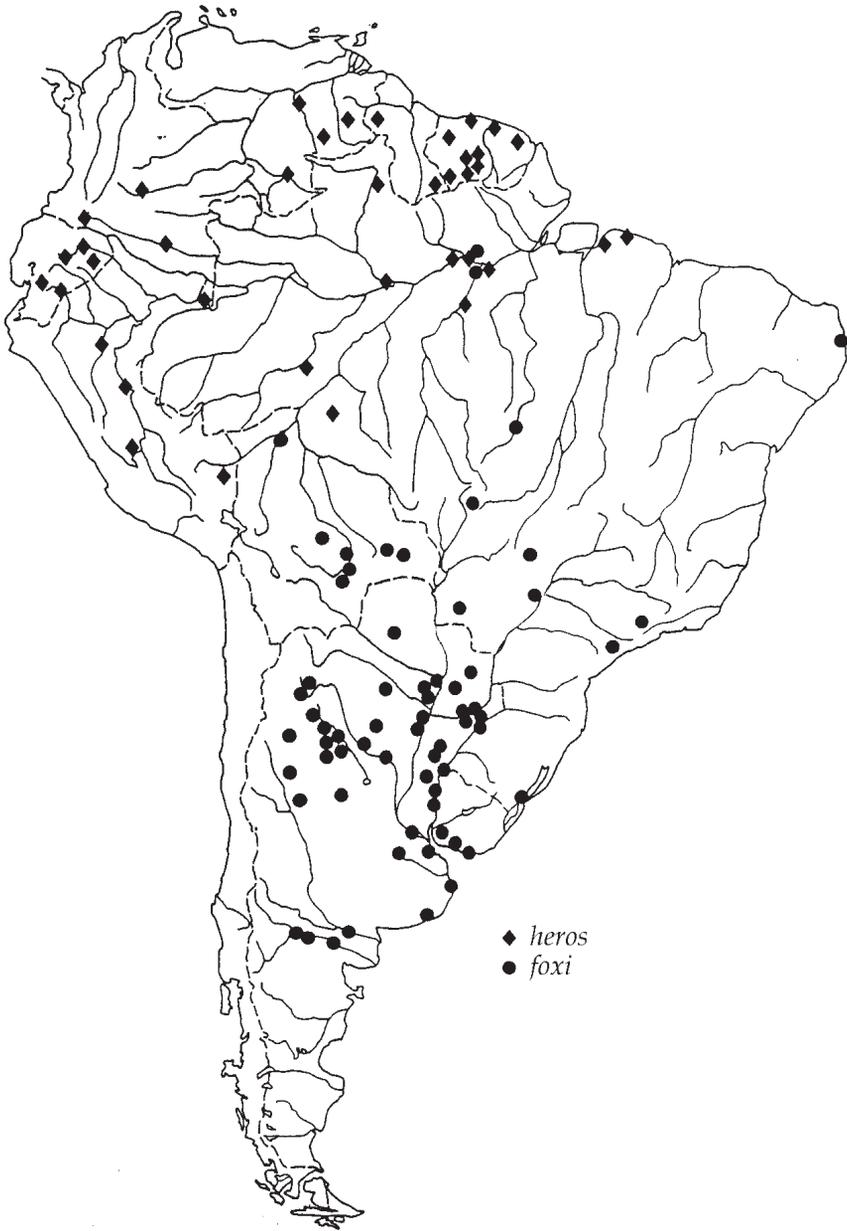


Fig. 93. Collection localities of *Pepsis heros* (Fabricius) and *P. foxi* Lucas.

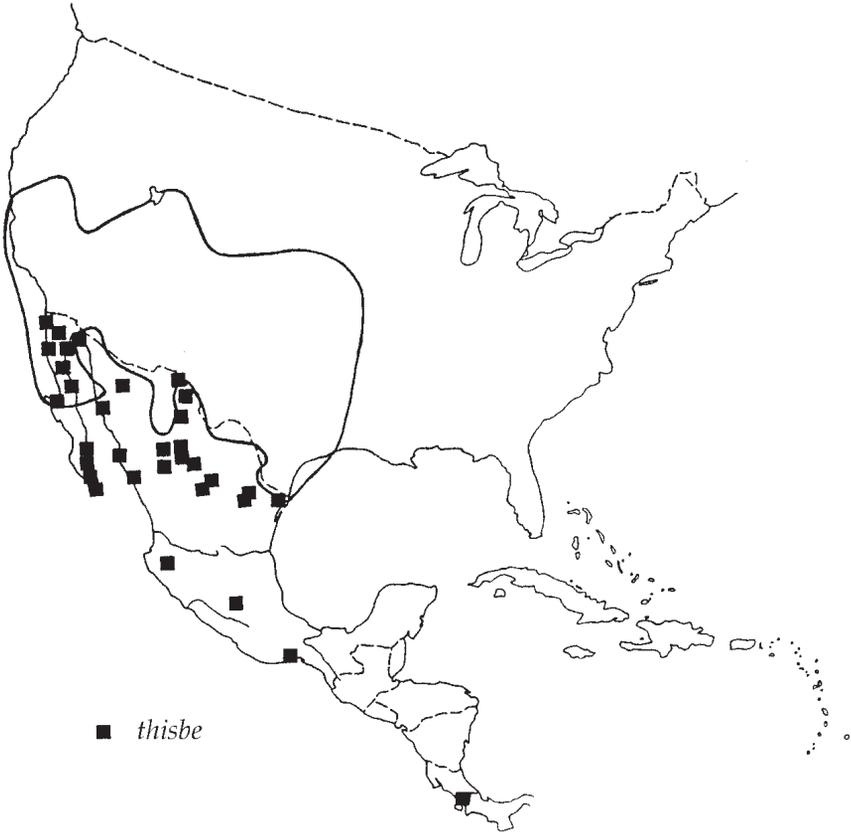


Fig. 94. Collection localities of *Pepsis thisbe* Lucas.

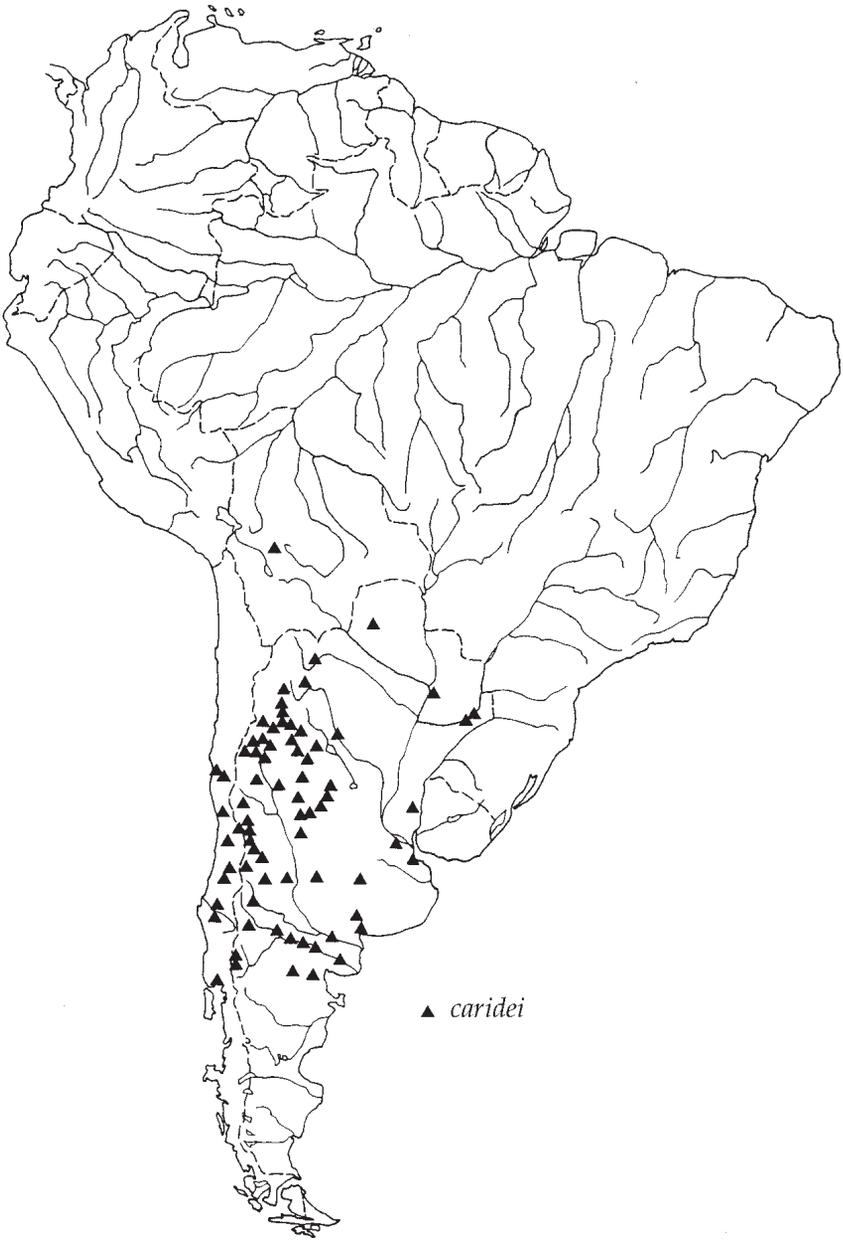


Fig. 95. Collection localities of *Pepsis caridei* Brèthes.

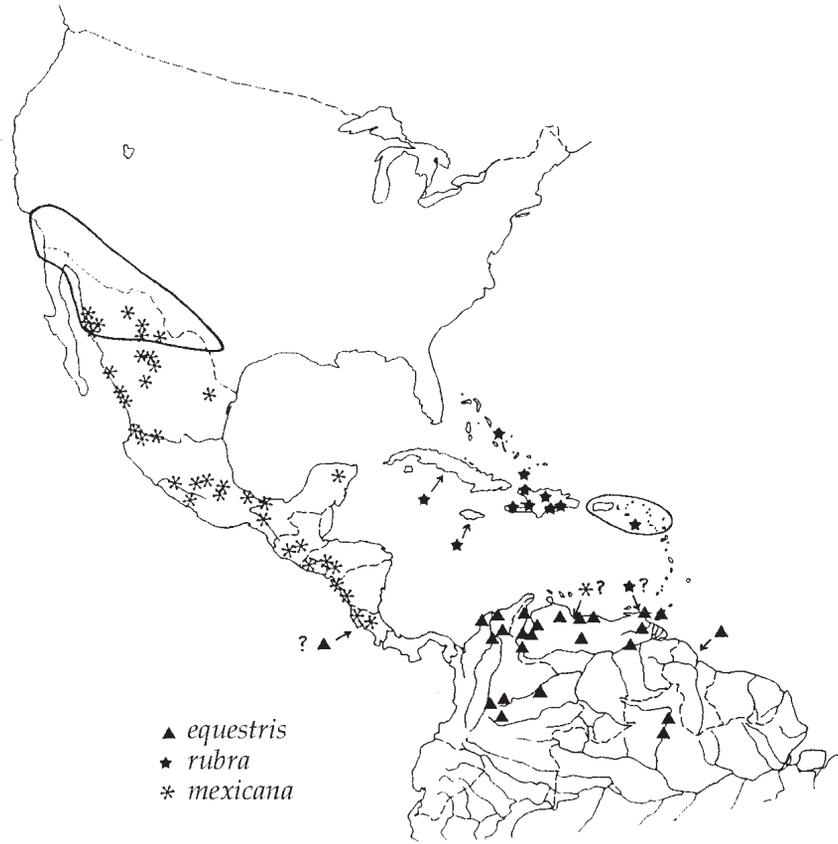


Fig. 96. Collection localities of *Pepsis equestris* Erichson, *P. rubra* (Drury) and *P. mexicana* Lucas.

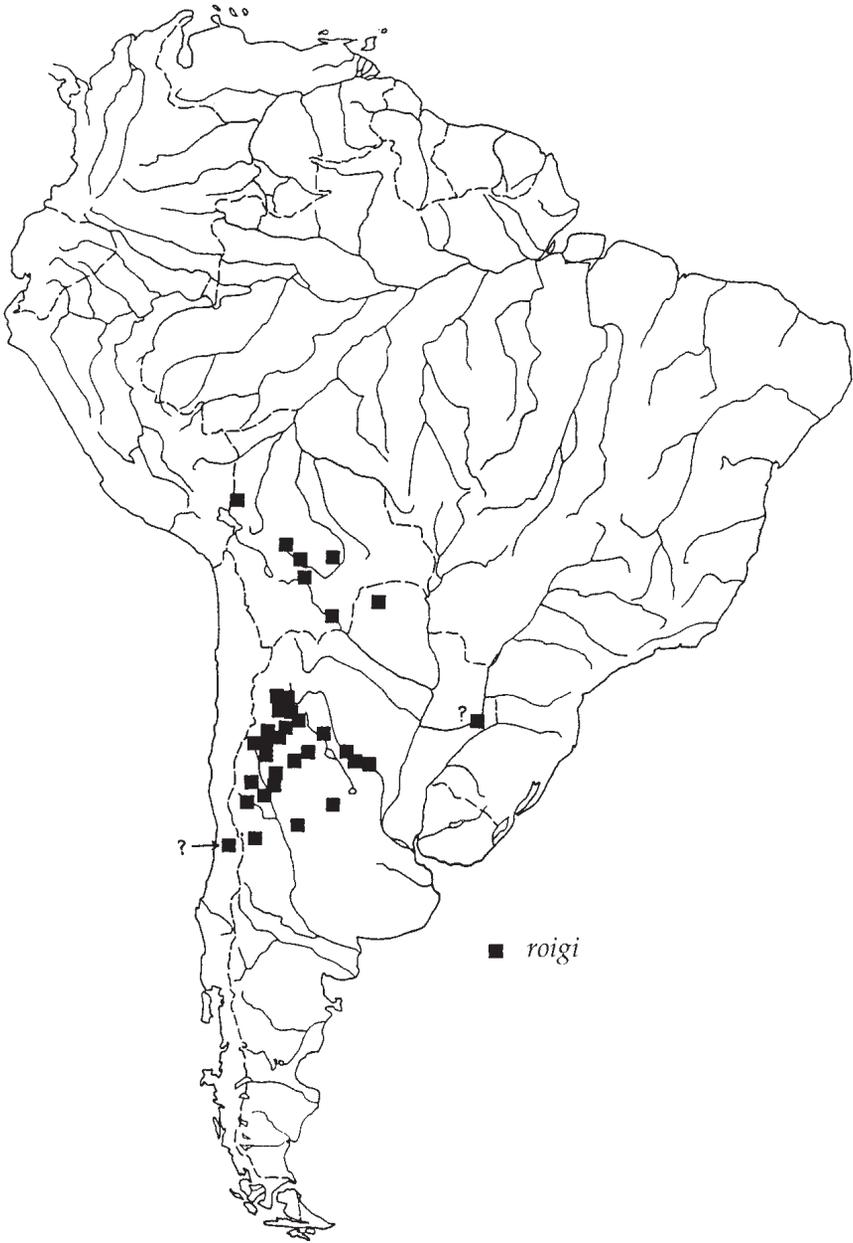


Fig. 97. Collection localities of *Pepsis roigi* spec. nov.



Fig. 98. Collection localities of *Pepsis vinipennis* Packard, *P. assimilis* Banks and *P. albocincta* Smith.



Fig. 99. Collection localities of *Pepsis sericans* Lepeletier and *P. inbio* spec. nov.

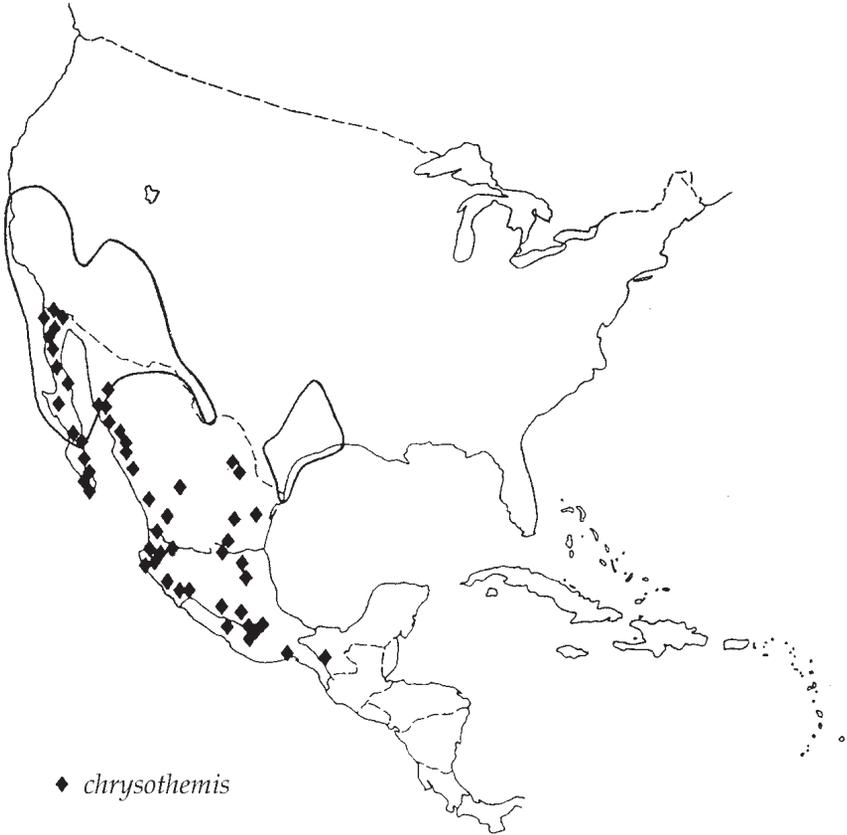


Fig. 100. Collection localities of *Pepsis chrysothemis* Lucas.

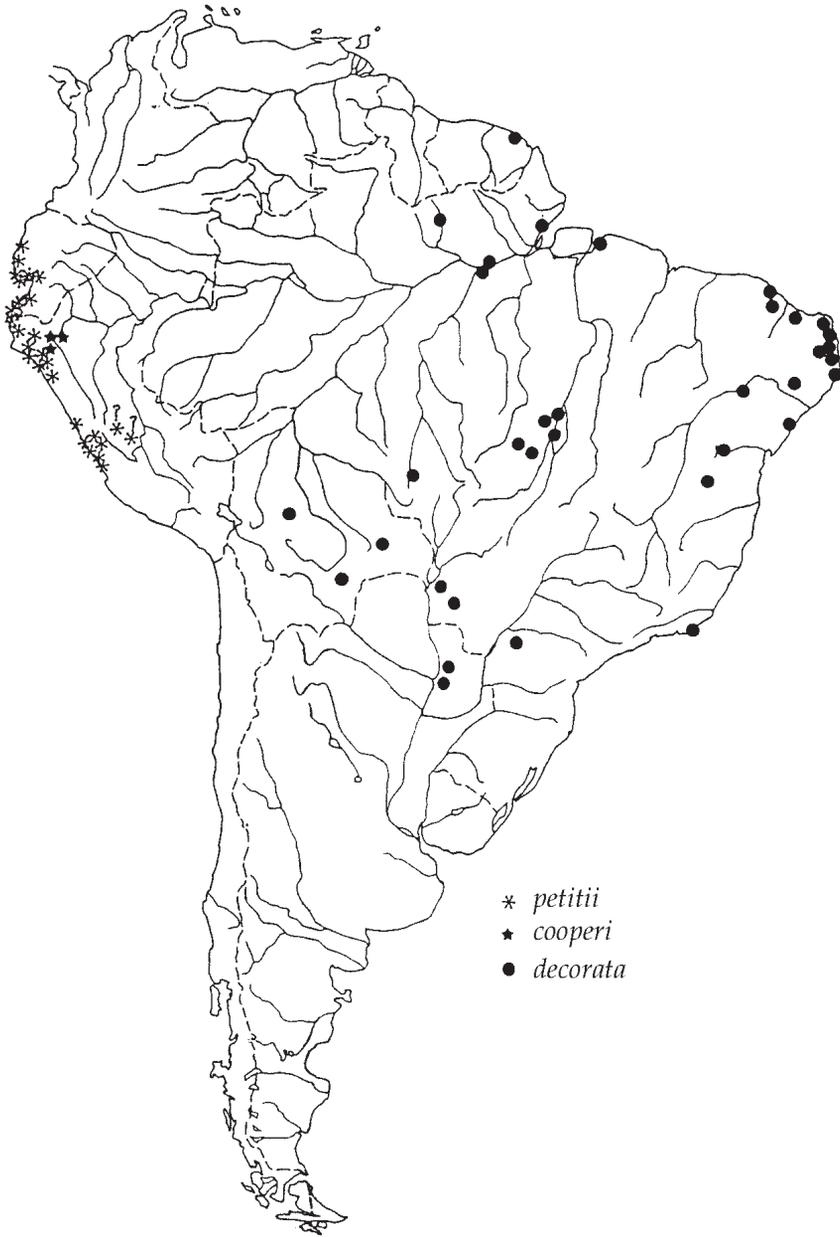


Fig. 101. Collection localities of *Pepsis petiti* Guérin, *P. cooperi* spec. nov. and *P. decorata* Perty.

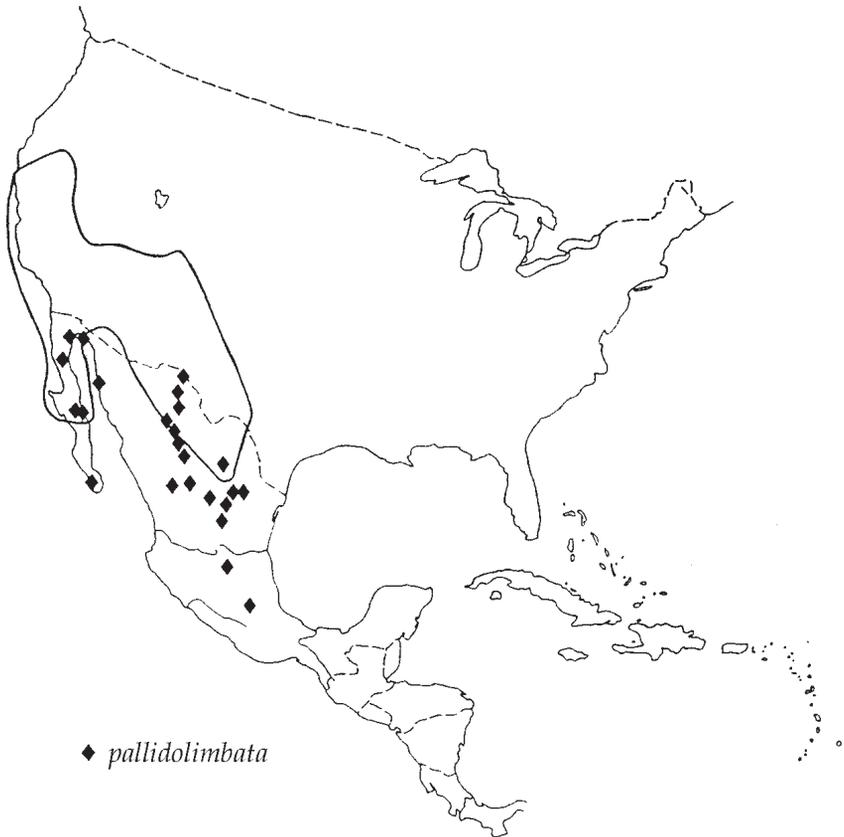


Fig. 102. Collection localities of *Pepsis pallidolimbata* Lucas.

**Key to females of the *Pepsis rubra*-group**

Notes.— The group-character which characterizes the females (radius joining costa at a very shallow angle) is very variable, but nothing better has been found. The character occurs fortuitously but rarely elsewhere in the genus; for example, the female of *P. limbata* Guérin, 1831), found in Argentina and Chile, often has the forewing venation similar to that of the *P. rubra*-group; it is distinguished from those of the latter in that immediately beyond the radial cell there is a small, strongly infuscate area along the forewing costa, and (in fresh specimens) some coarse hair below the anterior femur. Also the female of *P. taschenbergi* Lucas, 1895, often has forewing venation like that in the *P. rubra* group; it occurs in south-east Brazil where the only *P. rubra*-group species to occur, *P. albocincta*, is distinguished by its forewing having a pale tip. See also supplementary regional keys to females of USA and Argentine species at the end of these keys.

- 1. Radius meets costa at a very shallow angle (figs 70, 76-79); front femur without coarse hair below; lateral extension of S.2 groove always well developed; PTC usually very strong (*P. rubra*-group) ..... 2
- Radius usually meets costa at a broader angle e.g. fig. 80 (sometimes almost a right angle); if at a very shallow angle, then the front femur has more or less abundant coarse hair below ..... (other groups, part 2 of this revision)
- 2. Forewing entirely metallic silvery-brown except narrow, dark base and pale apical margin. Coastal Ecuador and Perú ..... *P. petittii* p. 75
- Forewing otherwise coloured ..... 3
- 3. Forewing with SMC3 very short (fig. 70); dark red with broad, dark border and poorly defined pale apex. Rather large species (BL 30-37) of middle and western Amazon basin ..... *P. vinipennis* p. 70
- If SMC3 very short, other characters not coinciding ..... 4
- 4. MPN and adjacent part of propodeum with only extremely fine, transverse carinae, matt apart from sutures. Very large species (BL 35-63) of Guianas and central & western Amazon basin; antenna black; forewing usually deep orange with broad, poorly defined dark apical border, but in eastern Andes of Colombia and Ecuador unicolorous dark brown; both forms with poorly defined, pale extreme apex. Hind tibial teeth small (fig. 75) ..... *P. heros* p. 59
- MPN and adjacent part of propodeum with at least some of the transverse carinae coarser, and at least slightly shining. Species usually smaller, colour forms and localities not coinciding as above ..... 5
- 5. Forewing black with bright silver markings ..... 6
- If forewing black or dark brown, it lacks bright silver markings ..... 9
- 6. Forewing black with broad silver band occupying about the middle third; apex broadly white, antenna mostly orange. North-central Perú ..... *P. cooperi* p. 76
- Forewing with silver markings mainly near base ..... 7
- 7. Forewing with sharply defined, rather narrow, sub-basal silver band and a white apex. Northern South America ..... *P. equestris* p. 66
- Silver markings not as above ..... 8
- 8. Silver markings as in fig. 68; head in dorsal view moderately swollen behind eyes

- (fig. 73); SMC3 elongate (fig. 78); larger species (BL 27- 44). French Guiana to Bolivia and Paraguay ..... *P. decorata* p. 77
- Silver markings as in fig. 67; head in dorsal view strongly swollen behind eyes (fig. 74); SMC3 moderately long (fig. 79); smaller species (BL 26-31). Argentina, Bolivia and Paraguay ..... *P. roigi* p. 67
9. Forewing mainly black, or at least quite strongly infuscate ..... 10
- Forewing mainly clear bright amber, orange or red; infuscation only at extreme base, usually an apical border, and sometimes slightly in the outermost cells .... 14
10. Forewing with apex pale ..... 11
- Forewing with apex dark ..... 12
11. Forewing black with narrow but distinct white apex. Antenna black. MPN usually with entirely fine transverse carinae. Small to medium species (BL 16-31). South-western USA to Costa Rica ..... *P. mexicana* p. 65
- Forewing strongly infuscate-orange to black, with poorly defined pale apex. Antenna usually becoming dull orange apicad. Large species (BL 30-55). Brazil and Paraguay ..... *P. albocincta* p. 80
12. Forewing entirely black, at most with small, pale marks near middle ..... 22
- Forewing with pale markings at least near base ..... 13
13. Forewing mainly dark orange-infuscate, with narrow, sub-basal paler patch and fairly distinct dark apical border. Hindwing with similar pattern. Chile ..... *P. caridei* p. 63
- Forewing entirely dark, with indistinct paler marks, mainly near base. Hindwing similar but paler markings often more extensive. Brazil ..... *P. foxi* p. 61
14. Forewing with narrow, very indistinct greyish border around apex, without darker patch by costa; border continued on apical and posterior edges of hindwing. Small species (BL 17-31) USA to central Mexico ..... *P. pallidolimbata* p. 77
- If dark border of fore wing is indistinct, it becomes markedly darker by costa ... 15
15. Forewing with extreme apex pale beyond a dark border ..... 16
- Forewing with more or less distinct dark border extending right to apex ..... 18
16. Apex of forewing milky white, sharply defined, confined to distal part of apex. Small species (BL 13-29). West Indies ..... *P. rubra* p. 63
- Apex of forewing merely pale, poorly defined, pale area extending posterad .... 17
17. Dark border of forewing narrow, less than width of SMC3. AE index 81-93. Medium species (BL 25-42). USA to southern Mexico ..... *P. thisbe* p. 60
- Dark border of forewing about as broad as SMC3. AE index 91-104. Large species (BL 30-55). Amazon southwards ..... *P. albocincta* p. 80
18. AS3 very short (AE index 67-84) ..... 19
- AS3 longer (AE index 80-108) ..... 20
19. Robust species with quadrate head, vertex and genae strongly swollen in dorsal view (figs 89-90); dark border almost equally wide on fore- and hindwings. Southern South America ..... *P. foxi* p. 61
- More slender species, head constricted behind eyes in dorsal view; dark border narrower on hindwing than on forewing. Cuba ..... *P. sericans* p. 71
20. Dark border of forewing distinct, at least as broad as SMC3 ..... 21
- Dark border of forewing indistinct, narrower than SMC3. USA to southern Mexico ..... *P. chrysothemis* p. 74

- 21. Dark border of forewing with inner edge irregular, usually invading outermost cells, especially the discoidal; with pale silver-golden, sub-basal metallic patch, often spreading along veins. AE index 80-91. Argentina, Bolivia and Chile ..... *P. caridei* p. 63
- Dark border of forewing regular; without pale patch near base. AE index 97-108. Northern Colombia and Panamá ..... *P. assimilis* p. 69
- 22. Hindwing entirely black, forewing sometimes with a few pale marks near middle. North-western South America and Panama ..... *P. assimilis* p. 69
- Hindwing with pale, whitish apex, forewing entirely black. Honduras to Costa Rica ..... *P. inbio* p. 73

Regional keys.— The three orange-winged species in Argentina, and three in the USA, are sometimes very difficult to separate from each other. In the latter case, Hurd’s (1952: 281) keys sometimes break down at couplet 26 due to variation, especially in Mexican specimens. The following regional keys will assist in distinguishing them.

**Key to orange-winged *Pepsis rubra*-group females in Argentina**

Note.— See *P. albocincta* distinctions from *P. chacoana* Brèthes (p. 82).

- 1. Head strongly quadrate (figs 89-90); AS3 very short (AE index 67-84). Dark border of forewing rather narrow, with inner margin well defined and even, not usually entering cells. Smaller species, BL 25-37 ..... *P. foxi* p. 61
- If head somewhat quadrate, then AS3 is longer (AE index at least 91). Dark border of forewing broad, with inner margin irregular, often diffuse, usually entering cells. Species often larger, BL 30-55 ..... 2
- 2. Head usually more or less quadrate (figs 87-88); AS3 longer (AE index (82-91-104). Border of forewing moderately infusate, extreme apex pale. Hind tibial spines about three times height of teeth. Foreleg with inner spur reaching to about 1/4 length of basitarsus. MPN often strongly concave behind .. *P. albocincta* p. 80
- Head usually strongly constricted behind eyes (figs 91-92); AS3 shorter (AE index 80-91). Border of forewing strongly infusate, usually including apex. Hind tibial spines about twice height of teeth. Foreleg with inner spur reaching to about 1/3 length of basitarsus. MPN almost straight posteriorly ..... *P. caridei* p. 63

**Key to orange-winged *Pepsis rubra*-group females in the USA**

Note.— The similar and sympatric *P. grossa* (Fabricius) has coarse hairs below the front femur.

- 1. Head with vertex and temples scarcely swollen (figs 85-86). Forewing with apex paler, virtually without infuscation immediately proximal to it. Antenna slender, AE index 92-109. Smaller species (BL 17-31), usually with pale, more or less metallic, sandy-coloured wings ..... *P. pallidolimbata* p. 77
- Head with vertex and temples at least moderately swollen (figs 81-84). Forewing with infuscation at or near apex. Antenna usually more robust, AE index 81-100.

- Often larger species (BL 20-42), usually with bright orange-red wings ..... 2
2. Infuscation of forewing extending right to apex (extreme apex sometimes slightly paler in Mexican specimens). Vertex usually only moderately swollen (figs 83-84). Occipital carina obsolescent as it approaches preular suture. Carinae of posterior face of propodeum more or less strongly obsolescent in central area. Smaller species (BL 20-30) ..... *P. chrysothemis* p. 74
- Infuscation of forewing leaving extreme apex pale. Vertex usually strongly swollen (figs 81-82). Occipital carina reaching preular suture unattenuated. Carinae of posterior face of propodeum at most slightly obsolescent in central area. Larger species (BL 25-42) ..... *P. thisbe* p. 60

### Descriptions of species

*Pepsis heros* (Fabricius, 1798)

(figs 13, 14, 55, 75, 93)

*Sphex heros* Fabricius, 1798: 245, no. 88-9. Lectotype, ♀, Cayenne (MNHNPS), here designated [examined].

*Pepsis heros*; Fabricius, 1804: 213, no. 29.

*Pepsis atrata* Lepeletier, 1845: 470, no. 1, ♀, Cayenne (lost). **Syn. nov.**

*Pepsis magnifica* Montet, 1921: 212. Lectotype, ♀ (MHNGV), here designated [examined]. **Syn. nov.**

N.B. See also *Pompilus heros* in "List of species excluded from *Pepsis*" in a later part of this revision.

Type material.— *P. heros*: two conspecific females bearing "Bosc collection" labels stand under *P. heros* in MNHNPS. I regard both as syntypes, although Zimsen (1964: 390, no. 614) lists only one specimen. The one in better condition bears an old label "Cayenne" (thus not disagreeing with the locality given by Fabricius "America meridionali" - see Notes on localities in Introduction) and also a more recent label "*Pepsis heros* Fabr.". I have selected and labelled as lectotype this latter specimen; the other is a paralectotype. *P. atrata*: the combination of colour and size of specimen, together with the locality given in the original description combine to make the identity of this species reasonably certain. *P. magnifica*: I have seen both of the ♀ syntypes; one bears original labels, and I have labelled it lectotype. The other bears no labels; it is conspecific with the lectotype, and I have labelled it paralectotype.

Description.— ♂. BL 26-38. Body and legs black with a blue-green sheen. Antenna black. Wings usually dark amber to orange-red with a more or less dark border which often enters the cells; forewing with the extreme apex narrowly pale (but see Variation). Occiput quite strongly swollen. MT weak. MPN furrow usually very broad and deep, but ending abruptly just before anterior margin of MPN; sometimes expanded posteriorly. Carinae extremely fine (only visible under high magnification); surface appears matt. Propodeum: MG sometimes weakly indicated anteriorly and posteriorly. APT fairly strong, PPT and PTC very strong. DTC rather weak anteriorly, as on MPN, but increasingly coarse posterad. SGP & genitalia figs 13-14, 55.

♀. BL 35-63. AE index 90-104. Otherwise as ♂ except: occiput very strongly swollen. Wing apex never more than slightly pale. Anterior femur often with a few short hairs below. MG usually in the form of a sharp incision near MPN. DTC anteriorly similar to those of MPN. PTC sometimes only moderately strong, especially in smaller specimens. Hind tibial teeth small (fig. 75).

Variation.— Specimens of both sexes with the wings dark brown (but the borders

darker still) occur in the western part of the species' range, near the Andean foothills (Colombia: Mocoa and La Macarena; Ecuador: Tena). A ♀ from the Rio Tapajos, c. 300k south-west of Santarém, has the wings including the border very dark but with the veins weakly outlined paler. These colour changes are probably due to the more humid conditions prevailing in those localities (which are also near the edge of the species' range).

Distinctions.— The ♂ has a highly distinctive SGP; females can be distinguished by their *P. rubra*-group venation, and both sexes by their wing colour (even the dark, western forms are not nearly as dark as *P. grossa*, and the ♀ never has such numerous and coarse subfemoral hairs as in that species). A further good character in both sexes is the exceptionally fine sculpture of MPN and anterior propodeum, appearing smooth but matt. Once recognized as members of the *P. rubra*-group, the identity of specimens of this species can often be guessed by their size alone, since it is the only really large species of the group in northern South America.

Biology.— A ♀ of this species is preserved in BMNH with its putative prey, a ♂ *Theraphosa leblondi* (Latreille) (det. A. Smith) from Guyana, Kutari river, 16.ii.1936. The distributional range of this tarantula spider is similar to that of *Pepsis heros*; it is likewise a giant of its group.

Distribution.— The Guianas and Amazon basin (sparse in the south); up to 750m in Colombia and 1,100m in Venezuela. A single ♀ (of the more usual red-winged form) was evidently collected at a locality in Arizona (CAS) but this must represent a chance introduction (fig. 93).

Material depositories.— 9 ♂♂, 141 ♀♀; AMNH, BMNH, CAS, CMNH, CUNY, FDAG, INPA, LACM, MCZ, MEM, MHNGV, MHNLM, MHNNEU, MIZAM, MNHNPS, MNRJ, MZUSP, NHMBAS, NMV, NRS, RMNH, RSM, TMB, UCALB, UMOX, UNPBOG, USNM, USU, UZMC, WAHIS, WILLIAMS, ZMPUCEQ, ZSM.

*Pepsis thisbe* Lucas, 1895

(figs 15-18, 56, 81, 82, 94)

*Pepsis thisbe* Lucas, 1895: 744, no. 142. Lectotype, ♂ (NMV), here designated [examined].

*Pepsis sayi* Banks, 1926: 202. Lectotype, ♂ (MCZ), here designated [examined]. **Syn. nov.**

*Pepsis chrysothemis*; McKenzie, 1933: 159. Misidentification.

*Pepsis sherillae* Hurd, 1948: 146. Holotype ♂ (UCALR) [not examined]. [Synonymized by Hurd, 1952: 303].

Type material.— *P. thisbe*: I have seen a single ♂ syntype labelled "Cornuvacca" ("Cuernavaca" in Lucas) and labelled it lectotype. *P. sayi*: I have seen both of the two syntypes, ♂ and ♀, and have labelled the ♂ as lectotype. The paralectotype ♀ is a specimen of *P. basifusca* Lucas.

Description.— ♂. BL 18-27. Body and legs black with blue-green sheen. Antenna black. Wings amber to orange with variably weak, narrow dark apical border, usually entirely outside the cells, the extreme apex of the forewing narrowly white (very rarely, wings entirely heavily infuscate except for white forewing apices). MT very weak or absent. MPN furrow rather broad, sometimes deep; posterior margin of MPN polished near furrow. Carinae usually rather fine, often one much stronger than the others. Propodeum: MG broad, shallow. APT very weak, PPT weak, PTC moderate, DTC moderate to weak. SGP & genitalia figs 15-18, 56.

♀. BL 25-42. AE index 81-93. Head with vertex strongly, and temples moderately swollen, in dorsal view more or less quadrate (figs 81-82); occipital carina reaching preregular suture. Otherwise as ♂, except: white wing apex usually less distinct (but melanistic forms not known to occur). MPN furrow often very broad and deep. All propodeal tubercles and carinae stronger, especially PTC.

Variation.— I have seen three melanistic males: from Nevada, Baker (CAS); Baja California, San Felipe (AMNH); and Baja California Sur, 34 mi nw La Paz (MEM).

Distinctions.— The ♂ is distinguished from those of other species by its SGP structure and white wing border; the ♀ from those of other similarly coloured sympatric species of the *P. rubra*-group as follows: from *P. chrysothemis* and *P. pallidolimbata* by its head shape, greater size, very weak MT (usually, but some specimens of *P. chrysothemis* and *P. pallidolimbata* are similar in this respect), and wing colour; from *P. pallidolimbata* also by its lower AE index.

Biology.— This species has been recorded (as *P. chrysothemis*) as attacking grapes in California, leaving only the skins and seeds (McKenzie, 1933: 159). Williams (1956: 452-457) gives details of life history; prey (*Aphonopelma* spec.); egg and larva. Evans (1959: 431) also gives details of the larva. [See also Host records and hunting behaviour in main Introduction].

Distribution.— USA to Central America, ascending to altitudes of nearly 2,000m in Mexico (Durango) (fig. 94).

Material depositories.— Mesoamerica only: 116 ♂♂, 140 ♀♀. Isolated records from southern Costa Rica; Panama, "Vadona" [locality not traced] and Trinidad, BWI all need confirmation; AMNH, ANSP, BMNH, BPBM, BRIO, CAS, CMNH, CSU, CUNY, EMMSU, FDAG, LACM, MCZ, MEM, MHNNEU, MLU, MNHNPS, NMV, OSUC, PORTER, RMNH, SEMKU, TMB, UCALD, USNM, USU, UZMC, WAHIS, WASBAUER, ZMMICH.

*Pepsis foxi* Lucas, 1897  
(figs 43-46, 71, 76, 77, 89, 90, 93)

*Pepsis foxi* Lucas, 1897: 291, no. 1. Lectotype, ♂ (CMNH), here designated [examined].

*Pepsis flaminia* Brèthes, 1914: 332, no. 122. Lectotype, ♂ (MACN), here designated [examined]. **Syn. nov.**

*Pepsis prixi* [= *prixii*] *gemella* Banks, 1946: 398. Lectotype, ♂ (CUNY), here designated [examined]. **Syn. nov.**

Type material.— *P. foxi*: I have seen two conspecific syntypes, ♂ and ♀, and have labelled the ♂ as lectotype. The ♀ is a paralectotype. *P. flaminia*: I have seen a single type-material ♂ and labelled it lectotype. *P. gemella*: I have seen a single type-material ♂ and labelled it lectotype.

Description.— ♂. BL 15-30. Body and legs black with blue-green to blue-violet sheen. Antenna black. Wings narrowly black at base; with fairly broad, dark apical band with a usually well defined inner edge; forewing usually with silver-golden sub-basal patch, extending along costal cell and very narrowly along rear edge. Rest of wings orange, amber or infuscate (see Variation below). MT moderately strong to weak. MPN furrow narrow, more or less expanded posterad, or rather broad throughout; often obsolescent into a polished triangular area anteriorly; carinae usu-

ally fine, occasionally a few stronger; those of opposite sides forming a more or less strong angle between them. Propodeum: MG more or less distinct anteriorly; all tubercles and carinae moderate to weak, occasionally PTC a little stronger. SGP & genitalia figs 43-46.

♀. BL (21-)25-37. Antenna short, AE index 67-84. Head in dorsal view more or less quadrate, occiput moderately strongly swollen (figs 89, 90). Otherwise as ♂, except: MT weaker, propodeal tubercles and PTC often stronger.

General variation.— In some specimens of both sexes from Bolivia, the sub-basal metallic patch of the forewing is weak or lacking. The general wing colour of specimens from Bolivia, Argentina, Paraguay and south Brazil is orange to amber; in some specimens from Paraguay and eastern Brazil the apical infuscation extends weakly into the cells, while in both sexes from the Mato Grosso, and in a ♀ from Paraguay, Cororo, Rio Ypané, the wings are entirely infusate except for the metallic patch which often spreads distally on the forewing (mostly along the costa) and also on to the hindwing base. Specimens of both sexes from the Lower Amazon have the wings varying from orange with a lightly infusate border (not well defined proximally as in Argentine specimens, but extending weakly into the cells; also lacking the silvery base), to heavily infusate with variable orange-red patches concentrated on the basal halves. Propodeal tubercles and carinae are rather stronger in Mato Grosso specimens, while strong MPN carinae are commoner in Bolivian specimens.

Particular variation.— A ♀ from Bolivia: Ivon Beni (USNM) has the short pubescence of the body and legs a dull yellow-silver; there are several normal ♀♀ from the same locality.

Distinctions.— The ♂ SGP is distinctive but subject to some variation as shown in the above-mentioned figures. Both dark- and orange-winged forms of the ♀ resemble their sympatric counterparts of *P. albocincta*, which see for differences. The dark-winged ♀ resembles that of the larger species *P. defecta* Taschenberg, 1869 (*P. sumptuosa*-group) (sympatric in the Mato Grosso), but lacks the latter's strong group characters (*viz.* short, thick hind tibial spurs; strongly curved hind claw joint; tooth beyond middle of hind claw); it resembles that of *P. roigi*, but the latter is distinguished by its higher AE index (90-97); the two species are also allopatric (see also the table under *P. decorata*). The orange-winged ♀ resembles those of *P. chacoana* and *P. caridei*. *P. chacoana* has the occiput much more strongly swollen, coarse hair below femur I, and the teeth and spines of tibia III about equal (spines distinctly longer than teeth in *P. foxi*). *P. caridei* has a less quadrate head shape (*cf.* figs 91 and 92), longer AS3 (AE index 80-91), and apical wing border generally broader but less well defined.

Distribution.— Widespread in Argentina south to Patagonia; in Bolivia, Paraguay, Uruguay and southern Brazil, apparently occurring only sparsely northwards to the Lower Amazon; ascending to 1,200m in Argentina (Salta) (fig. 93)

Material depositories.— 360 ♂♂, 317 ♀♀; AEIG, AMNH, ANSP, BMNH, CMNH, COOPER, CUNY, EMMSU, FRITZ, IMLT, MACN, MCZ, MLP, MLU, MNHNPS, MNHNPG, MNHNSA, MNRJ, MNS, MZUSP, NRS, OSUC, RMNH, SEMKU, TMB, UCALB, UMOX, USNM, UZMC, WAHIS, ZMMICH.

*Pepsis caridei* Brèthes, 1908  
(figs 11, 12, 54, 91, 92, 95)

*Pepsis reaumuri*; Taschenberg, 1869: 29 and all subsequent authors. Misidentification.

*Pepsis caridei* Brèthes, 1908: 240. Lectotype, ♂ (MACN), here designated [examined].

*Pepsis pampeana* Brèthes, 1908: 240. Lectotype, ♂ (MACN), here designated [examined]. **Syn. nov.**

Type material.— *P. caridei*: I have seen a single type-material ♂ and labelled it lectotype. *P. pampeana*: I have seen two syntypes, ♂ and ♀, in MACN, and have labelled the ♂ as lectotype. The ♀, a paralectotype, is a specimen of *P. nitida* Lepeletier, 1845.

Description.— ♂. BL 16-31. Body and legs black, with blue-green to violet sheen. Antenna black. Wings orange to amber; forewing with narrowly black base and an adjacent, silver-golden patch, usually extending along the entire costa and often along some veins; both wings with broad, dark apical border, diffusely but more or less evenly entering the outer cells. MT moderate to fairly strong. MPN furrow narrow, often expanded posteriorly, somewhat obsolescent anteriorly; carinae fine. Propodeum: MG rather weak, strongest anteriorly, APT moderate to weak, PPT & PTC strong, DTC moderate to rather fine. SGP & genitalia figs 11-12, 54.

♀. BL 33-43. AE index 80-91. Head in dorsal view strongly constricted behind eyes, occiput slightly swollen (figs 91, 92). Hind tibial spines about twice height of teeth. Foreleg with inner spur reaching to about 1/3 length of basitarsus. Otherwise as ♂, except: apical wing infuscation invading the cells more irregularly; PPT and PTC broader.

Variation.— Badly abraded specimens lose the silver-golden and orange pubescence from the wings, leaving them a dirty amber.

Distinctions.— The ♂ SGP is unlike that of any other ♂; the ♀ is distinguished from that of *P. chacoana* Brèthes, 1908 (*P. grossa*-group) in that its hind tibial spines are distinctly longer than the teeth they subtend (about equal in *P. chacoana*) and its lack of that species' very strongly swollen occiput and coarse hair below femur 1. It also resembles *P. albocincta* and *P. foxi*: see under the former species for distinctions between them.

Distribution.— Bolivia, the whole of Argentina south to Patagonia, central Chile; ascending to 3,000m in Argentina (Mendoza). It is interesting that the range of this species extends southwards equally on both sides of the Andes (fig. 95).

Material depositories.— 345 ♂♂, 618 ♀♀; AEIG, AMNH, BMNH, CAS, CUNY, EMMSU, FDAG, FRITZ, IMLT, MACN, MCZ, MLP, MLU, MNCN, MNHNPS, MNHNSA, MNS, NMV, OSUC, PAGLIANO, PORTER, RMNH, SEMKU, TMB, UCALB, UCALD, UCMB, UMCE, UMOX, USNM, USU, UZMC, WASBAUER, WAHIS, ZSM.

*Pepsis rubra* (Drury, 1773)  
(figs 37, 38, 49, 96)

*Sphex rubra* Drury, 1773: 75, pl. 39, f. 6, ♀, Antigua (lost).

*Sphex rubripennis* Christ, 1791: 264. [Unnecessary replacement name for *S. rubra*.]

*Sphex sanguigutta* Christ, 1791: 293, pl. 29, f. 3, ♂ [no locality] (lost). [Synonymized by Schulz, 1904: 466].

*Sphex papiliopennis* Christ, 1791: 297, pl. 29, f. 7, ♂ [no locality] (lost). **Syn. nov.**

*Sphex speciosa* Fabricius, 1793: 217, no. 83 [no locality] (not Smith, 1855). Lectotype, ♀ (UZMC(K)), here designated [examined]. [Synonymized by Smith, 1855: 190].

*Sphex stellata* Fabricius, 1793: 219, no. 91, "America meridionali". Lectotype, ♂ (UZMC(K)), here designated [examined]. **Syn. nov.**

*Pepsis stellata*; Fabricius, 1804: 214, no. 34.

*Pepsis speciosa*; Fabricius, 1804: 216, no. 45.

*Pepsis quadrata* Lapeletier, 1845: 478, ♂, Saint Domingue (lost). [Synonymized by Schulz, 1904: 466].

Type material.— *P. rubra*: Drury's excellent illustration of this species, together with its provenance, leave no doubt as to its identity. *P. sanguigutta* and *P. papiliopennis*: Christ's illustrations of these both show obvious pale wing tips, which indicate that they are conspecific with *P. rubra* rather than with *P. sericans* Lapeletier, whose wing colour is otherwise similar. *P. speciosa*: type-material in BMNH (Banks coll.) is lost; but Petersen (pers. comm.) notes two ♀♀ in UZMC(K), one of which has an original Fabrician label "*speciosa*". I have seen this latter specimen (which lacks the head) and labelled it lectotype. *P. stellata*: Petersen (pers. comm.) notes two ♂♂ in UZMC(K) of which one has an original Fabrician label "*stellata*". I have seen this specimen and labelled it lectotype.

Description.— ♂. BL 12-23. Body and legs black with blue-green sheen. Antenna black. Wings dark; forewing with distinct white apical border covering about half the area beyond the cells, and with a variable orange central patch; hindwing usually also with a smaller orange patch than in the fore wing. MT moderately strong to weak. MPN furrow variably wide, usually abruptly expanded posteriorly; carinae many, fine but distinct, those on opposite sides of the furrow at a strong angle to each other. Propodeum: MG shallow, deeper anteriorly. APT weak, PPT and PTC fairly strong. DTC fairly strong. SGP & genitalia figs 37-38, 49.

♀. BL 13-29. AE index 68-93. Otherwise as ♂ except: both wings entirely orange with only narrow, dark apical and posterior borders; the forewing also with a white apex.

Variation.— The only colour variations exhibited by the ♀ are changes in the shade of the orange in the wings, but the ♂♂ vary more: the patch in the forewing varies from pale amber through orange to smoky brown; it also varies greatly in size, from covering most of the wing area to a rather small patch in the centre. In the latter case the orange patch in the hindwing can be completely absent. In a ♂ from the Dominican Republic (TEXAM) the forewing has an extensive, dull orange patch covered by metallic hairs. As in other widely distributed West Indian species, e.g. *P. ruficornis* (Fabricius), the sculpture of the MPN tends to gravitate towards a particular pattern in each group of islands, but individual variation is such as to render it of little use in ascertaining the origin of any given individual; nor is any clinal pattern obvious.

Distinctions.— The ♂ is distinguished from those of all other species by its SGP structure, and from most others by its white wing tips (although the forewing of the sympatric *P. sericans* Lapeletier, 1845, sometimes has the extreme apex obscurely whitish). The ♀ is distinguished from most others by its wing colour, especially the white tips; *terminata* Dahlbom, 1844, usually has black wings where it is parapatric with *P. rubra* (i.e. in the West Indies); however, there is a single record of a ♀ with red wings from Guadeloupe (possibly mislabelled) (BMNH), which island lies within the range of *P. rubra*. This record clearly needs confirming. Whatever its colour, *P. termi-*

*nata* is always distinguishable since it has a more bulbous T1, lacks the lateral extensions of the S.2 groove, and the junction of the radius with the costa is much closer to perpendicular.

Biology.— The following information is based on observations in the British Virgin Islands by R.R. Snelling (pers. comm.). The species frequents open ground (contrasting with *P. ruficornis*, treated in a later part of this work). The ♀♀ avoided tarantula burrows; possibly they prey only on smaller individuals. They hold their wings flat, back over the body, constantly flicking them up and down. They searched an area of perhaps 6-8 m square very thoroughly, diving into masses of leaves and investigating “every nook and cranny” over periods ranging up to 10-12 min. In the late afternoon, ♂♂ form sleeping clusters at the ends of leafy branches on shrubs with fairly large leaves. Such clusters may consist of 2-25 individuals and it is not unusual to see several such groupings on one plant or on adjacent plants. Although the same branch is not necessarily used on succeeding nights, the same ♂♂ definitely roost in the same general area night after night.

Distribution.— West Indies, including the Bahamas, Cuba and Jamaica south to the Guadeloupe Passage only (there is a single unconfirmed record from Trinidad); ascends to 1,385 m in Haiti (fig. 96).

Material depositories.— 269 ♂♂, 202 ♀♀; AFZD, AMNH, ANSP, BMNH, BRIO, CAS, CMNH, CUNY, FDAG, LACM, MCZ, MEM, MHNNEU, MNCN, MNHNPS, MZEL, NMV, NRS, RSM, TEXAM, TMB, UMOX, USNM, UZMC, WAHIS, ZMMICH, ZMMOSC, ZSM.

*Pepsis mexicana* Lucas, 1895  
(figs 39, 40, 50, 96)

*Pepsis mexicana* Lucas, 1895: 566, no. 46. Lectotype, ♂ (MNHU), here designated [examined].

*Pepsis messerschmidti* Lucas, 1895: 558, no. 43. Lectotype, ♀ (NMV), here designated [examined]. **Syn. nov.**

Type material.— *P. mexicana*: I have seen two syntypes: a ♂ (labelled “Mexico. Deppe”) in MNHU, which I have labelled lectotype; and a ♀ (labelled “Mexico, Cornuavacca” [“Cuernavacca” in Lucas]. Bilimek) in NMV, which is a paralectotype and conspecific with the ♂. *P. messerschmidti*: I have seen a single ♀ syntype and labelled it lectotype.

Description.— ♂. BL 13-21. Body and legs black with blue-green-violet sheen. Antenna black. Wings black with blue-violet reflections and usually a narrow, white apical border (often broader in hindwing than in forewing). MT usually strong. MPN furrow broad, deep; carinae fine, sometimes a few are slightly stronger. Propodeum: MG narrow, more or less distinct; all tubercles and carinae fairly strong. SGP & genitalia figs 39-40, 50.

♀. BL 16-34. AE index 68-71. Otherwise as ♂, except: MT less strong; MPN furrow usually very broad; MG generally stronger.

Variation.— A ♀ from Costa Rica, San José, San Pedro (INBIO) has much of the body and legs dull reddish and the normally black parts of the wings weakly infuscate. The specimen is almost intact structurally (only the tips of the antennae are missing); see discussion Fading, in the Introduction.

Distinctions.— The ♂ is distinguished by its SGP structure and wing colour; the white border is narrower than in other similar species. The ♀ can be distinguished by its white wing borders, *P. rubra*-group venation (cf. fig. 76), and very low AE index. Locality and details of sculpture are also useful, particularly where the white wing borders are completely abraded.

Biology.— Williams (1956: 456, 458) gives details of life history and prey (*Aphonopelma* spec.). Evans (1959: 431, 432) gives details of the larva.

Distribution.— South-western USA to Costa Rica, ascending to 2,500m in Mexico (Chiapas) (fig. 96).

Material depositories.— Mexico and Central America only: 291 ♂♂, 204 ♀♀; AMNH, BMNH, BRIO, CAS, CUNY, EMMSU, INBIO, LACM, MCZ, MHNGV, MICR, MNHNPS, MNHU, NMV, NRS, OSUC, RMNH, SEMKU, TEXAM, TMB, UCALB, UCALD, UMOX, UNAN, USNM, UZMC, WASBAUER.

*Pepsis equestris* Erichson, 1848  
(figs 41, 42, 51, 96)

*Pepsis equestris* Erichson, 1848: 588. Lectotype, ♂ (MNHU), here designated [examined].

*Pepsis leucobasis* Smith, 1855: 193. Lectotype, ♂ (BMNH), here designated [examined]. [Synonymized by Mocsáry, 1887: 18].

Type material.— *P. equestris*: in MNHU are two syntype ♂♂; one of them is smaller, and lacks the left antenna, foreleg, and wings; the larger one lacks only some tarsal segments. Both bear labels: "Britisch Guyana, Schomburgk". I have labelled the larger specimen as lectotype; the smaller is a conspecific paralectotype. *P. leucobasis*: in BMNH are 1 ♂ and 2 ♀ syntypes, all conspecific. I have labelled the ♂ as lectotype; the ♀♀ are paralectotypes. 2 ♂♂ and 2 ♀♀ in UMOX are also conspecific but without type-status.

Description.— ♂. BL 13-25. Body and legs black with blue, green, violet or copper-coloured sheen. Antenna black. Forewing with rather broad, transverse, silver to golden (discoloured?) band near base, reaching fully to costa; both wings with rather narrow, white apical border. MT extremely strong and sharp. MPN furrow broad, deep, often obsolescent anteriorly, slightly expanded posteriorly. Propodeum: MG present anteriorly, weak. APT rather weak, PPT and PTC moderately to very strong. DTC fairly strong. SGP & genitalia figs 41-42, 51.

♀. BL 19-36. AE index 67-81. Otherwise as ♂, except: MT sometimes only moderately strong, some MPN carinae often stronger, APT often quite strong.

Variation.— Only as noted above.

Distinctions.— The ♂ is distinct from all others in its SGP structure and colour; the silver forewing band is much narrower and closer to the base than in *P. cooperi*. The ♀ is almost identical in colour to that of *P. lycaon* Banks, 1945, but that species has a much higher AE index (86-92), the lateral extensions of the S.2 groove are vestigial, and its forewing radius meets the costa at a much greater angle (cf. figs 78 and 80). The two species are also almost entirely allopatric (there is a single, authentic record of *P. lycaon* from north Perú: Cajamarca, Jaen).

Note.— A specimen from Colombia: Lake Zapatoza [labelled "Sapatoza"] (BMNH) has most body parts ♀, but the antennae ♂.

Distribution.— Northern South America (excluding the west coast), mostly at low altitudes but recorded at 1,800m in Colombia (Cundinamarca); a single record from Costa Rica needs confirming (fig. 96).

Material depositories.— 157 ♂♂, 116 ♀♀, 1 gynandromorph; AEIG, AMNH, ANSP, BMNH, CMNH, CUNY, FDAG, FRITZ, LACM, MACN, MHNGV, MHNNEU, MNHNPS, MNHU, MNRJ, MZEL, NHMBAS, NRS, RMNH, UCALD, UMOX, UNCSG, USNM, USPRIB, USU, UZMC, WASBAUER, ZSM.

*Pepsis roigi* spec. nov.  
(figs 47, 48, 66, 67, 74, 79, 97)

Type material\*.— Holotype ♂, **Argentina**: Mendoza, Chacras de Coria [near Mendoza city], ii.[19]74 (Roig) (MACN). Paratypes. **Argentina**: Catamarca: Ampajango: 1♂, 1♀, 7.iv.1968 (Willink, Terán) (BL, GL) (IMLT); Andalgalá: 1♀, 4-6.ii.1972 (Duckworth) (USNM); 1♂, 20.xii.73, 82678 (Neff) (GL) (IMLT); 1♂, 75877, IBP Programme, Desert Scrub Site, # refers to host and date (Neff) (GL) (IMLT); 15k e Andalgalá: 25.x.[19]72 (Bohart), 2♂ (1 without head) (USU); Andalgalá-Belén: 1♀, 6.ii.[19]66 (Porter) (MCZ); 1♂, 7.ii.1968 (Willink) (BL, GL) (BMNH); Andalgalá, 30k hacia Belén: 2♂, 11.x.1968, *Prosopis alba*, 13-15 hrs. (Willink, Stange) (BL) (IMLT); 6k n Belém, 1240m: 1♀, 16-28.ii.1969, Malaise (Willink, Terán, Stange) (BMNH); 3♂, 1♀, 7.ii.[19]66 (Porter) (MCZ); 2♂ (BL, GL) (IMLT); 1♂, 1-15.xi.1969 (Malaise) (Willink, Terán, Stange) (BL, GL) (BMNH); 2♂, 16-28.ii.1969 (Malaise) (Willink, Terán, Stange) (BL, GL) (IMLT); 3♂, 5.xii.1970 (Porter, Stange) (GL) (IMLT); Andaluca (Ruta Aimogasta-Tinogasta): 5♀, 23.iii.1973 (Terán, Willink) (GL) (IMLT); Belén-Andalgalá: 3♂, 12.x.[19]68 (Porter) (MCZ); Belén, Barranca Larga: 1♂, ii.[19]37 (GL) (IMLT); Belén-Los Nacimientos: 1♀, 14.iii.1969 (Porter) (MCZ); Dto. Belén: 1♂, 7.ii.[1]966 (Hayward, Willink, Stange) (GL) (IMLT); Dpto. El Alto: 1♀, i.1950 (Argañaraz) (GL) (IMLT); El Molino (Campo del Arenal), 2,700m: 1♂, 9.i.1969 (Terán, Willink) (GL) (IMLT); Quebrada de Belén: 2♂, 7.ii.[19]66 (Willink, Stange) (GL) (IMLT); Belén, Quelo Belén: 1♂, 7.ii.1966 (Willink, Stange) (GL) (IMLT); Concepción: 1♂, 1♀, 9.ii.[19]68 (Willink) (BL, GL) (IMLT); Pirquitas: 1♂, 3♀, 13.ii.1958 (Golbach) (GL) (IMLT); Pomancillo: 1♀, xi.1944 (Remes) (INTAC); Quebrada La Cebila, km.30: 2♂, 16.i.[1]960 (Willink) (GL) (IMLT); Santa María: 1♂, 10-16.ii.1972 (Matthews) (MCZ); 10km Tinogasta: 1♀, 9.ii.[19]66 (Willink, Terán) (BL, GL) (IMLT); [no further locality]: 1♀, *P. decorata* (ZSM); 1♂, 5♀, *P. decorata* (MLP); 1♀, xii.[1]952 (GL) (IMLT); La Rioja: Camino de Vinchina Jagtue: 1♀, 26.ii.1971 (Terán, Willink) (GL) (IMLT); Chilecito, 1,000m: 1♂, 2♀ (1 on *Baccharis* fls.), 23.ii.1978 (van der Vecht) (RMNH); 1♀, 29.ii.1920 (Harris) *Pepsis decorata* Perty det. Babiý 1928, *Pepsis decorata* Perty det. Banks (CUNY); 3♂, xii.1951 (Kormilev) (MACN); 1♂, i.[1]947 (Monros) (BL, GL) (IMLT); 1♂, 20.i.1960 (Willink) (GL) (IMLT); Chilecito, Samay Huasi (2k e Chilecito): 1♂, 21.i.1969 (Terán, Willink) (BMNH); 1♂, 25.i.1969 (Terán, Willink) (BL, GL) (IMLT); 4♂, 25.i.1969 (Brito) (GL) (IMLT); 1♂, 2♀, same data but with (BL); 1♂, 21.i.1969 (Terán, Willink) (GL) (IMLT); Cuesta de la Aguadita, 9k s Angulos: 2♂, 1♀, 25.ii.1978 (Willink, Dominguez) (GL) (IMLT); 2♂, 26.i.1969 (Terán, Willink) (GL) (IMLT); Famatina, 1580m: 1♂, 2♀, 11.ii.[19]66 (Porter) (MCZ); 4♂, 10.ii.1966 (Willink, Weyrauch, Stante [= Stange]) (BL, GL) (IMLT); 3♂, 3♀, 11.ii.1966 (Willink, Stange) (GL) (IMLT); 4♂, 30.xi.1977 (Willink, Fidalgo) (GL) (IMLT); Molanzara: 1♀, 10.i.1923 (MACN); Piedra Pintada (Cam[ino] V[illa] Unión-Nonogasta): 1♂, 12.ii.1966 (Stange, Willink) (GL) (IMLT); Quebrada La Aguadita (Entre Famatina, Angulos): 2♂, 10.ii.1966 (Weyrauch, Willink, Stange) (GL) (IMLT); Tinogasta-Chilecito: 1♂, 10.ii.[19]66 (Porter) (MCZ); Villa Castelli: 1♀, 12.i.[19]48 (Foerster) (ZSM); Villa Mazan: 2♂, 2♀, 19.xii.[19]75 (R.M. Bohart) (UCALD); [no further locality]: 2♂, both 46946; 1♀, (Giacomelli) (MCZ); 2♀ (MACN); Mendoza: Chacras de Coria: 2♀, 18-21.ii.[19]66 (Porter) (MCZ); 1♂, 12-20.iii.1980 (Porter) (FDAG); 1♂, 11.ii.[1]908 (MLP); 1♂, 18.i.[1]908 (MLP); 1♂, 3.i.[1]946 (Willink) (GL) (IMLT); Cerro Bodeguita [12k nw Mendoza city]: 2♂, xi.[19]72, en vuelo, *Zucognia punctata*, 447 & 448 (Roig) (ROIG); Las Heras, Puerto "La Obligación", 1,800m: 1♂, 15.i.1977 (Willink) (GL) (IMLT); Papagallos: 1♀, xi.74; 1♀, iii.[19]75 (Roig) (MACN); Pie del Cerro de la Gloria: 2♂, 14-20.i.1977 Willink) (GL) (IMLT); Potrerillos, 1,700m: 1♂, 16-20.iii.1920 (Harris) (MCZ); 1♂, 20.i.1907 (Joergensen)

(UZMC); 2♂, i.[19]56 (Fritz) (FRITZ); 1♂, 23.ii.[1]908 (MLP); 1♂, 23.ii.[1]908, 2728, 33 (MLP); 1♂, 8.i.1980 (Willink, Fidalgo, Claps, Dominguez) (GL) (IMLT); Quebrada de la Pe[laeo?][Pelada?] 1,200m; 1♂, i.[19]07 (Schiller) (MLP); Reboredo CI: 1♀, i.[19]28 (GL) (IMLT); [no further locality]: 1♂, (Reed) (AMNH); 1♂ (Jensen-Haarup) (UZMC); 1♀, "10231; *Brethesia decorata*"; Cornell U. Lot 709, Sub. 19; *Pepsis decorata* Perty det. Banks"; 1♂, as ♀ but lacking 5-fig. code (CUNY); 5♂, 15, 74, 112, 731 & 795 (Roig) (ROIG); 2♀, 434 & 793 (Roig) (ROIG); 1♂, 62 (Reed) (MLP); 1♂, (Reed) (CAS); Misiones: [all from this province may be mislabelled]: San Ignacio: 1♂, 5♀, 22.iii.[1]908, 2♀, 15.iii & 5.iv.[1]908 (MLP); 1♂, 54908, 3405, 33 (MLP); 1♀, 54908 (MLP); Salta: Alemania: 1♂, 9.ii.[1]948 (Willink, Monros) (GL) (IMLT); Cachi: 1♂, 20-22.i.[19]66 (Porter) (MCZ); Cafayate, 1980m: 2♀, ii.[1]948 (Hayward) (RMNH); 1♂, 20.i.1968 (Golbach, Terán, Willink) (BL, GL) (IMLT); 1♀, ii.1954 (Porter, Hayward) (GL) (IMLT); 1♀, 1-7.iii.1977 (Hayward) (GL) (IMLT); 1♀, ii.1954 (Hayward) (GL) (IMLT); Camino Colalao del Valle-Tolombón: 3♂, 12.i.[19]67 (Barrera, Paganini) (GL, 1 also BL) (IMLT); El Carmen: 1♀, i.[19]83 (Fritz) (FRITZ); Molinos: 1♂, 19.i.[1]950 (Monros, Willink) (RMNH); Tacuil, 2,400m: 1♂, 1♀, 22.ii.[19]77 (Willink) (GL) (IMLT); Yacochuya 9k ne Cafayate: 1♂, 2.ii.1972 (Duckworth) (USNM); 1♂, 26.iv.1970 (Stange, Porter) (BL, GL) (IMLT); San Juan: Angaco [5k e San Juan city]: 1♂, xii.[19]06 (Berg) (MACN); Caucete [20k se San Juan city]: 1♂, xii.[19]06 (Berg) (MACN); 7k n Huaco: 1♂, 12.ii.[19]77 (Willink, Stange) (GL) (IMLT); Valle Fertil: 1♂, 23.xi.1977 (Willink, Fidalgo) (GL) (IMLT); 20k s Valle Fertil, Ruta 510: 1♂, 1♀, 24.xi.1977 (Willink, Fidalgo) (GL) (IMLT); San Luis: F. de los Funes: 1♀, 28051 (MACN); San Francisco: 1♀, 22 1940 (Biraben) (MLP); [Santa Fé]: Gran Chaco: Rio Tapenago [= Tapenaga], 1♂, January [N F D] (MNRJ). Santiago del Estero: Añatuya: 1♀, iii.[19]79 (Fritz) (FRITZ); Chaco de Santiago del Estero, environs d'Icaño: Guarda Escolta: 3♂, 1909 (Wagner); bords du Rio Salado: 1♂, 1904 (Wagner); Místol Paso: 1♀, i.1912 (Wagner); Chaco de Santiago del Estero: Rio Salado: 1♀ (Wagner); 1♀, "*Brethesia decorata* Perty" (Wagner) (MACN); 2♂, 2♀ (Wagner) (MLP); bords du Rio Salado: Paso de Don José 15k n Icaño, 1♀, 1909 (Wagner), La Palisa del Bracho 25k nno Icaño, Laguna Mamaíta, 1♀, 1904 (Wagner) (MNHNPA); 1♀, El Charco, iii.1956 (Walz) (AEIG); [no further locality]: 1♀, i.1950, *Pepsis equestris* Klug det. Dreisbach (EMMSU); 1♂ (Wagner) (MLP); 1♀, iv.[1]949 (GL) (IMLT); 1♀, i.1946 (Argañaraz) (GL) (IMLT); Tucumán: Amaicha del Valle, 1,900-2,000m: 1♂, 9.i.1970 (Vardy, Arguindeguy) (BMNH); 1♀, 13.iv.1946 (Vecht) (RMNH); 1♂, 12.xii.64 (MCZ); 3♂, 12.xii.64 (Porter) (PORTER); 2♂, 28.xii.[19]65 (Townes) (AEIG); 1♀, ii.1917 (MACN); 2♀, ii.1917 (IMLT); 1♀, 28.ii.1978 (Willink, Dominguez) (GL) (IMLT); 1♀, ii.1917, Green Hotel (IMLT); Dpto. Capital, Santa Barbara: 1♀, 7.ii.1957 (Singer) (GL) (IMLT); Presumed Argentine localities not traced: [Chacras de?] "Coria": 1♀, 16.i.1908, *Brethesia decorata* ♀ (MLP); "Pie de Palo, Gato": 2♂, 7626 & 7627 (MACN); "Rio San Gregorio, Corbado" [= Córdoba]: 1♂, 16.iii.1940 (Biraben) (MLP); "Salad.": 1♂, 9.i.[19]19 (Hubrich) (ZSM); "San Ignacio": 1♂, 22.iii.1908 (Joergensen) (UZMC).

**Bolivia:** La Paz, Corapori [= Corapara]: 1♂ (no head), 11.v.[19]66 (Ballard) (USU); Chuquisaca: Sucre, Chuqui Chuki: 1♀, 8.v.[19]66 (Ballard) (USU); Cochabamba: Cochabamba: 1♂, 1♀, 30.x.[19]66 (Ballard) (USU); Aiquile, Novillero: 2♂, 10.ii.[19]79 & 20.xi.[19]80, 2♀, 2.ii.[19]79 & 6.i.[19]81 (Bonelli) (BONELLI); Tarata, 1900: 1♀, (TMB); Santa Cruz: Santa Cruz: 1♂ (no head) 22.v.[19]66 (Ballard) (USU); Tarija: Aguile: 2♂, 17.xi.[19]66 (Ballard) (USU); Villa Montes: 1♀, 20.ix.[19]67 (Ballard) (USU); 1♀, v.[19]26 (Lind. D. Chaco-Exped.) (MNS). **Chile:** Santiago: (Faz) 1♀ (BMNH). **Paraguay:** Chaco: Cerro Leon: 1♂, x.[19]79 (Fritz) (FRITZ). No locality: 1♂, (Jensen-Haarup) (UZMC); 1♂, "Coll. Antigua"; 2♀, 23.396 and 23751; 2♀ "Coll. Antigua" (MACN); 1♂, "11 *Brethesia decorata* (Perty), ♀" (MLP); 1♂♀, "*Pepsis decorata*" (MLP); 1♀, "*Pepsis decorata* Perty" (MLP); 1♂, ii.[19]74 (Zota) (MACN).

\* The data from many specimens in IMLT include the abbreviations "(BL)" and "(GL)". These signify a blue label bearing the words "Entomofauna Subandina" and a green label with "Colección Fundación M. Lillo, 4000 S.M.Tucumán, TUCUMAN-ARGENTINA" respectively.

**Etymology.**— This species is named after Dr Arturo Roig Alsina of the Museo Argentino de Ciencias Naturales.

**Description.**— ♂. BL 17-24. Body and legs black with blue-green-violet sheen. Antenna black. Forewing dark brown with a black base and silvery pattern (fig. 67). Hindwing with a narrow white border (soon abraded). MT fairly strong, to very

strong and sharp. MPN furrow fairly broad, usually weakly expanded posteriorly. Carinae fine. Propodeum: MG usually present anteriorly, moderately strong to weak. Both tubercles fairly strong. PTC moderately to very strong. DTC fairly strong, partly obscured by long, dark hair. Usually with a shallow, longitudinal median groove, strongest anteriorly. SGP & genitalia figs 47-48, 66.

♀. BL 26-31. AE index 90-97. Otherwise as ♂ except: MG usually shallow, but over whole length of dorsum. APT, PPT and PTC stronger, lateral ridge between APT and PPT strong.

Variation.— Only as already noted.

Distinctions.— Both sexes have a distinctive colour pattern which strongly resembles that of *P. decorata*, also that of *P. foxi* in certain localities; the ♂♂ are easily distinguished by their SGP structure, but see the table given under *decorata* for distinguishing the ♀♀.

Distribution.— Bolivia, north-western Paraguay and western Argentina, ascending to 2,800m in Argentina (Salta); the record from Argentina, Misiones needs confirming, while that from Chile probably represents a labelling error (fig. 97).

Material depositories.— 156 ♂♂, 101 ♀♀; AEIG, AMNH, BMNH, BONELLI, CAS, CUNY, EMMSU, FDAG, FRITZ, IMLT, INTAC, MACN, MCZ, MLP, MNS, MNHNPS, MNRJ, PORTER, RMNH, ROIG, TMB, UCALD, USNM, USU, UZMC, ZSM.

*Pepsis assimilis* Banks, 1946

(figs 19, 20, 57, 98)

*Pepsis assimilis* Banks, 1946: 343. Holotype ♀ (MCZ) [examined].

Description.— ♂. BL 17-29. Body and legs black with blue-green sheen. Antenna black, sometimes partly orange (see Variation). Wings black with strong blue reflections, or strongly infusate and with a narrow, white apical border. MT quite strong. MPN furrow broad, often very broad, especially posteriorly, usually narrower anteriorly. Carinae mostly fine, often a few slightly coarser. Propodeum: MG variable (see below); APT, PPT and PTC very strong, the two latter sometimes connected. DTC moderate to strong. SGP & genitalia figs 19-20, 57.

♀. BL 24-38. AE index 87-108. Otherwise as ♂ except: wings entirely more or less heavily infusate, or orange with a dark border.

Variation.— The principal pattern of colour variation in this species is unusual, and evidently more strongly connected with geographical distribution than is the case with most species. Both sexes are entirely black in Venezuela; while the ♂♂ remain so in Colombia, the ♀ wing colour becomes orange-amber with a dark border. In Panamá, however, the ♀ wings take on a most unusual, bright orange-pink hue ("salmon"), while in both sexes the antennae become mostly orange. The colour variation found in Ecuador (part of the "lygarochromic" area - see Introduction), however, does not form part of the graduated variation. Here, the ♂ wings develop a more or less distinct white apical border, while those of the ♀ usually show a few, small pale marks; the ♂ antenna is orange to a very variable extent, that of the ♀ usually has an orange tip. The only material of this species seen from west coastal Colombia

(Valle, Buenaventura; in MCZ) is a ♀; this has orange wings like those from the north coast.

Structural variation is most obvious in the MG, which varies with size of insect: in smaller ♂♂ it is usually absent or weakly indicated anteriorly, in large ones it is stronger or more extensive. In ♀♀ it is weakly indicated anteriorly and posteriorly.

Distinctions.— The ♂ is distinguished by its SGP structure; however, the ♀ is easily confused with those of various other dark-winged species, especially those of the *P. ruficornis*-group. It can be separated from them by its *P. rubra*-group venation (cf. figs 76 and 80), strong MT, MPN sculpture and distributional area (see also *P. inbio* p. 72); however, great care is needed to distinguish it from worn specimens of the sympatric *P. grossa* in which only the hair pits remain below the front femur.

Distribution.— This species is known only from Panamá and the Pacific and Caribbean coasts of north-western South America, except for a few records from inland Colombia and Venezuela. It reaches altitudes of about 1,000m. The single record from Ecuador: Mera [25k east of Baños] needs confirming (fig. 98).

Material depositories.— 38 ♂♂, 42 ♀♀; AEIG, AMNH, ANSP, BMNH, CMNH, COOPER, CUNY, FDAG, FRITZ, MACN, MCZ, MIZAM, MNHNPS, NMV, OSUC, PMA, RMNH, RSM, SEMKU, TMB, UNCSBOG, UNPBOG, USNM.

*Pepsis vinipennis* Packard, 1869

(figs 21, 22, 58, 69, 70, 98)

*Pepsis vinipennis* Packard, 1869: 61. Lectotype, ♀ (MCZ), here designated [examined].

*Pepsis insignis* Mocsáry, 1885: 248, no. 14. Lectotype, ♂ (TMB), here designated [examined]. **Syn. nov.**

*Pepsis erythroptera* Mocsáry, 1885: 244, no. 9. Lectotype, ♀ (TMB), here designated [examined]. [Synonymized by Banks, 1946: 345].

Type material.— *P. vinipennis*: I have seen a single type-material ♀ and labelled it lectotype. *P. insignis*: I have seen a single type-material ♂ and labelled it lectotype. *P. erythroptera*: I have seen 2 ♀ syntypes, and have labelled as lectotype the one which has "Mocs." handwritten on the original identification label. The other is a conspecific paralectotype.

Description.— ♂. BL 17-25. Body and legs black with weak blue-green sheen. Antenna black with up to 4 apical segments orange. Wings black with bluish reflections. Forewing with a sharply defined white apex, which includes almost all the area beyond the cells and often just enters the apex of the radial cell. Gaster often with red-brown patches in the basal half. Pronotal shoulders strongly swollen. MT rather weak. SMC3 extremely short (fig. 69). MPN furrow rather narrow, often obsolescent anteriorly, carinae fine, those of opposite sides often forming a strong angle with each other. Propodeum: MG often weakly indicated anteriorly. All tubercles and carinae strong, weaker in small specimens. SGP & genitalia figs 21-22, 58.

♀. BL 30-38. AE index 103-113. Otherwise as ♂ except: up to 3 apical antennal segments orange. Wings dark smoky-red with dark brown border beyond cells and a rather narrowly whitish-translucent apex, the junction blurred. MT strong. SMC3 not quite so short (fig. 70).

Variation.— Especially in the ♂♂, there is variation in the length of SMC3, which is always short in any case. In one extreme specimen from Ecuador, Pastaza, Sarayacu

(MNS) the anterior veinlet of this cell is scarcely longer than the antennal thickness.

Distinctions.— Both sexes are strongly characterized by the short SMC3; the ♂ also by wing colour and SGP structure, the ♀ further by its colour. The *P. rubra*-group ♀ venation character is less clearly exhibited in this species than in most (cf. figs 70 and 78). It is most likely to be confused with ♀ *P. terminata* but unlike that species has the usual lateral extensions of the S.2 groove, and is markedly larger.

Distribution.— Found in the middle and western parts of the Amazon basin, usually reaching an altitude of only about 500m, but recorded from 1,270m in Colombia (Cundinamarca) (fig. 98).

Material depositories.— 67 ♂♂, 27 ♀♀; AMNH, ANSP, BMNH, CAS, CMNH, CUNY, INPA, MACN, MCZ, MEM, MHNNEU, MLU, MNHNPS, MNRJ, MNS, MZUSP, TMB, UNCBG, UNPBOG, WAHIS.

*Pepsis sericans* Lepeletier, 1845

(figs 25, 26, 61, 99)

*Pepsis sericans* Lepeletier, 1845: 473. Lectotype, ♀ (MIZSU), here designated [examined].

*Pepsis domingensis* Lepeletier, 1845: 477, ♂ (lost). **Syn. nov. & stat. rev.** [wrongly synonymized with *P. marginata* Pal. de Beauvois by Haupt, 1952: 366].

*Pepsis ignicornis* Cresson, 1865: 134. Lectotype, ♂ (ANSP), here designated [examined]. **Syn. nov.**

*Pepsis domingensis decepta* Banks, 1928: 4. Lectotype, ♂ (MCZ), here designated [examined]. **Syn. nov.**

Type material.— *P. sericans*: I have seen a single ♀ syntype and labelled it lectotype. *P. domingensis*: although the type of this name is lost (a specimen standing under the name "*dominicensis*" [sic] in MIZSU disagrees with the original description), the usual interpretation of this name is in accord with *P. sericans*. *P. ignicornis*: I have seen a single type-material ♂ and labelled it lectotype. *P. decepta*: I have seen a single type-material ♂ and labelled it lectotype.

Description.— ♂. BL 17-30. Body and legs black with blue-violet sheen. Antenna usually entirely black, but sometimes partly orange (see Variation). Wings dark brown with violet reflections; forewing with variable, central orange patch (sometimes absent), hindwing with small, antero-central orange spot. MT weak. MPN furrow broad, deep, expanded posteriorly; carinae numerous, weak, increasingly obsolescent posterad. Propodeum: MG usually narrow but distinct over most of dorsum; APT and PPT fairly strong; PTC strong. DTC moderately strong. SGP & genitalia figs 25-26, 61.

♀. BL 18-34. AE index 70-77. Otherwise as ♂ except: antenna always black; most of wings deep orange-red, strong infuscation confined to base and a broad apical band; cells sometimes slightly infusate. PPT stronger, PTC strong and broad.

Variation.— The ♂ antenna is usually entirely black, occasionally bright orange from segment 3 onwards. The size of the irregularly shaped orange patch in the forewing varies from a scarcely visible central spot to so large that only the wing base (narrowly) and apex (rather broadly) remain infusate. Where the forewing patch is small, the hindwing patch is very small, otherwise it is more in proportion to that of the forewing. Sometimes the extreme apex of the forewing is pale. There is much less variation in the wing colour in ♀♀: it concerns the width of the dark apical border and the sharpness of its junction with the orange colour; also the orange itself varies somewhat in tone.

Particular variation.— A remarkable ♂ labelled “Haiti: Ibo Lele, Detionville” (AMNH) is tentatively assigned to this species. It has the PAC of the SGP very narrow, high and far from the AC - similar to that of *P. caridei* (found in Argentina) but without the median keel. Its wings are pale orange with a dark border; the forewing has a sharply defined white apex occupying half the width outside the closed cells, as in *P. rubra*. The specimen is normal in genital structure, sculpture and venation. It may be a hybrid between *P. sericans* and *P. rubra* (the most likely of the sympatric species); the bilateral symmetry of the SGP and lack of obvious deformity suggest it is a hybrid, rather than a malformed specimen.

Distinctions.— ♂♂ are well characterized by their wing colour and SGP structure; ♀♀ lack the white wing tips of *P. rubra* and *P. terminata*, but are very similar to ♀♀ of *P. marginata* Beauvois (*P. elevata*-group); see the accompanying table for distinguishing between them.

Biology.— Starr & Hernández (1995) observed a sleeping aggregation of ♂♂ of this species in Cuba.

Distribution.— West Indies, known only from Cuba, apparently always at low altitudes; the single record from Jamaica needs confirming (fig. 99).

Material depositories.— 75 ♂♂, 42 ♀♀; AMNH, ANSP, BMNH, BRIO, CUNY, EMMSU, FDAG, MCZ, MHNNEU, MIZSU, MLU, MNHNPS, TMB, UCALB, USNM, UZMC, WAHIS, ZMMOSC.

Table for distinguishing between ♀♀ of *P. sericans* and *P. marginata*.

<i>P. sericans</i>	<i>P. marginata</i>
- Antennal segment 3 distinctly shorter than upper interocular distance (AE index 70-77)	- Antennal segment 3 approximately equal to upper interocular distance (AE index 100-112).
- S.2 groove with distinct, clearly-incised, longitudinal, lateral extensions.	- S.2 groove with lateral extensions almost obsolete.
- Propodeum: ridges on posterior face distinct throughout (sometimes weaker above).	- Propodeum: ridges on posterior face obsolete centrally.
- Metapostnotum: central groove broadens markedly posterad; highly polished. Transverse carinae very weak (one in middle slightly stronger); increasingly polished posterad.	- Metapostnotum: central groove of even width, only a very narrow central line polished. Transverse carinae strong, matt except a posterior, transverse, polished line no wider than a carina.
- Radial vein: distal part curving almost in a semicircle to join costa.	- Radial vein: distal part slightly angulate before junction with costa.
- Forewing infuscation forming a poorly defined apical band entering radial cell; other cells only slightly paler.	- Forewing infuscation forming a usually distinct band around apex, not or scarcely entering any closed cells and in marked contrast to their paler colour.
- Beyond the junction of radius and costa, edge of wing behind continuation of costa with very narrow, pale line.	- Beyond the junction of radius and costa, edge of wing is at least as dark as general infuscation of apex, often darker.
- Smaller species, BL 18-34.	- Larger species, BL 30-55.

*Pepsis inbio* spec. nov.  
(figs 27, 28, 60, 99)

Material.— Holotype ♂, **Costa Rica**: Guanacaste: Fca. Jenny 31k n Liberia, 85.34.27.W., 10.51.55.N., 300m, GNP Biodiversity Survey: x.1988 (INBIO). Paratypes. Data as holotype: 19♂, 22♀ (AEIG, BMNH, CAS, CMNH, INBIO, MACN, MZUSP, TMB, UMOX, USNM). 7♂, 8♀, same data but 316200, 364400; 2♂, iii-iv.1989, 1♀ x.1989 (Araya & Espinoza); 1♂, 9-26.vii.1993, #2239, (Araya); 1♂, 5-26.viii.1993, #2325 (INBIO, RMNH). **COSTA RICA**: Guanacaste: Los Almendros, P.N. Guanacaste: 1♂, 1-22.vii.1992, LN 334800-369800 (Lopez); same data but #2267: 1♂, 11-30.vi.1993; PN Barra Honda, 3k nw Nacaome, 100m, L-N 239000, 386000 (Reyes): 1♂, 2♀, 3-25.viii.1992, 1♀, 14.ix-5.x.1992, 1♀, iii.1993, (all INBIO). Bebedero: 3♂, 26.ii.1964, 6 m (Evans) (BMNH, MCZ); S. Cañas Exp. Sta.: 1♀, 8-18.iii.1988 (Parker) (WASBAUER); Liberia, 123 m: 2♂, 29.vii.1963 (Scullen, Bolinger) (MCZ); Estac. Pitilla, 9k s Santa Cecilia, 85.25.40.W., 10.59.26.N., 700m, GNP Biodiversity Survey: 1♀, xi.1988 (INBIO); Comelco Property: 1♂, 17.i.1976 (Reed) (TEXAM); El Coco: 1♂, 1♀, 30.viii.1965 (Naumann) (SEMKU); 1♂, 31.xii.1980 (Gomez) (MICR); Playa del Coco: 1♂, 20.vii.1962 (Truxal) (USU); Vicinity Estac. Murcielago, 8k sw Cuajiniquil, 100m, GNP Biodiversity Survey, W85°43'59", N10°54'08": 3♂, 2♀, ii.1989.; same data but LN 320300-347200, #2324: 2♂, 1♀, 11-29.viii.1993 (Quesada); same but #2351: 1♂, 10-18.ix.1993, 2♂, 11-20.xi.93 (all INBIO). PN Palo Verde, Est. Palo Verde, 10m, L-N 259000, 388400: 1♂, 25.iii-21.iv.1992 (Gutierrez) Ref[ugio] Nac. Fauna Silvestre Rafael Lucas Rodriguez, Palo Verde, 10m, L-N-259000, 388400: 1♂, iii.1991 (Acevedo) PN Guanacaste, Est. Santa Rosa, 300m, I Curso Microhym, L-N-313000, 359800: 1♂, i.1991 (all INBIO). Santa Rosa National Park [now called Guanacaste National Park], 300m: 1♂, 9-12.viii.1977 (Janzen) (BMNH); 1♂, 1-28.viii.1983 (Janzen, Hallwachs) (BMNH); PN Santa Rosa, Est. Santa Rosa, 300m, L-N 313000, 359800: 2♂, ii.& vii.1992, (Moraga); PN Santa Rosa, Playa Naranjo, L-N-309300-353300: 3♀, xii.1990 (Alcazar) (all INBIO). Alajuela: Orotina: 1♀, 6.v.1924 (Bradley) (CUNY); [NFL]: 1♀, 10.vi.1971 (Asotoa); Puntarenas: Tivives: 1♀, 2.x.1977 (Vedazma) (both INBIO). **Guatemala**: Amatitlan 4,000ft. [= 1,230m]: 1♂ ♀, 6.vii.1947 (Vaurie) (AMNH). **Honduras**: Amapala: 1♂, vii. (TMB); Choluteca, 1♀, 13.v.1989 (Lopez) (MEM); Fco. Morazan, 32k "E 7es" [illegible], El Zamorano, 1♂ ♀, 6.vi.[19]86, volando en cultivo de maiz [illegible word] (Nuñez) (MEM). **Nicaragua**: Leon, El Pochote: 1♂, 1♀, vi.[19]87 (Desmedt) (UNAN); Managua, 200ft.[= 61 m]: 1♂, 2.xi.1971 (Harding) (LACM); Polvon: 1♂ (McNeill) (MCZ); Rivas, Pica-Pica, 190ft. [= 58 m]: 2♂ ♀, 31.x.1971 (Harding) (BMNH, LACM); S. Antonio: 1♀, v.1899 (CAS).

Etymology.— This species is named after INBio, the Instituto Nacional de Biodiversidad de Costa Rica.

Description.— ♂. BL 18-28. Body and legs black with blue-green sheen. Antenna black. Wings black with fairly strong blue-violet reflections, hindwing with variably broad, poorly defined, pale apical band. MT weak to moderate. MPN furrow broad, deep, sometimes slightly expanded posterad; carinae fine, occasionally with a few slightly coarser ones. Propodeum: MG narrow but rather deep, obsolescent posterad; APT and PPT weak to moderate, PTC moderate to very strong, the two latter sometimes connected; DTC fine anteriorly, becoming much coarser posterad (less obvious near MG). SGP & genitalia figs 27-28, 60.

♀. BL 25-36. AE index 86-100. Otherwise as ♂ except: antennal segments weakly orange apically; head behind eyes rather strongly swollen dorsally and laterally (cf. figs. 83-84); MT weaker; MPN with 1-2 carinae markedly coarser than others. Propodeum with PPT occasionally strong, DTC moderately strong anteriorly (thus not contrasting so much with posterior ones as in ♂).

Variation.— Only as noted above.

Distinctions.— The most obvious difference between this and similar species

which are sympatric or almost so is that only the hindwing has a white apex in both sexes; in other species the wing apices are both the same colour (either dark or white). The ♂ SGP of *P. inbio* is distinctive; the ♀ is further distinguished from that of *P. grossa* by the latter's possession of coarse hairs below the front femur (caution with worn specimens!); it is also distinguished from the ♀ of the nearly-sympatric *P. assimilis* by the deeper MG, broader and less strong PTC; and by the hind tibial spines which are about 2.5 times as long as the teeth (about 1.5 times in *assimilis*).

Distribution.— Part of Central America only (Guatemala to Costa Rica), occurring up to altitude 1,230m in Guatemala (fig. 99).

Material depositories.— 66 ♂♂, 51 ♀♀; AEIG, AMNH, BMNH, CAS, CMNH, CUNY, INBIO, LACM, MACN, MCZ, MZUSP, MACN, MEM, SEMKU, TMB, UMOX, UNAN, USNM, USU, WASBAUER.

*Pepsis chrysothemis* Lucas, 1895  
(figs 23, 24, 59, 83, 84, 100)

*Pepsis chrysothemis* Lucas, 1895: 739, no. 139. Lectotype, ♂, (NMV), here designated [examined].

*Pepsis cinnabarina* Lucas, 1895: 804, no. 179. Lectotype, ♀, (MNHU), here designated [examined]. [Synonymized by Hurd, 1948: 136.]

*Pepsis circularis* Fox, 1898: 144. Holotype ♂ (ANSP) [examined]. [Synonymized by Hurd, 1952: 312 & 318.]

*Pepsis lucasii* Fox, 1898: 145. Holotype ♀ (ANSP) [examined]. **Syn. nov.**

Type material— *P. chrysothemis*: I have seen two ♂ syntypes and labelled the one (locality "Texas") in NMV as lectotype. It is in better condition than the conspecific paralectotype (locality "Mexico") in MNHU. *P. cinnabarina*: I have seen two conspecific ♀ syntypes, and have labelled as lectotype the one in MNHU. The other, a paralectotype, is in NMV; both are from Mexico.

Description.— ♂. BL 12-27. Body and legs black with blue-green-violet sheen. Antenna black. Wings amber to orange, with base and apex rather broadly infuscate; forewing with a narrow, sometimes indistinct, white apex. MT usually fairly strong (occasionally weak or even vestigial). MPN furrow usually rather broad and deep, sometimes posteriorly expanded; carinae fine, often slightly coarser anteriorly. Propodeum: MG narrow, usually rather deep. APT usually weak. PPT moderately strong to weak; PTC very strong to very weak; DTC only moderately strong. SGP & genitalia figs 23-24, 59.

♀. BL 20-30. AE index 81-100. Head with vertex and temples moderately swollen, in dorsal view more or less quadrate (figs 83, 84); extent of occipital carina variable, usually not reaching preular suture. Otherwise as ♂, except: dark border of forewing extends right to apex (extreme apex slightly paler in some Mexican specimens). All sculpture, tubercles and MT usually stronger, but DTC more variable.

Variation.— A single ♀ from Lower California, between San José del Cabo and Triunfo (AMNH) has the body covered with short, tawny hairs.

Distinctions.— The ♂ is easily distinguished by its SGP structure; the ♀ from those of other similarly coloured sympatric species of the *P. rubra*-group as follows: from *P. thisbe* and *P. pallidolimbata* by its head shape (cf. figs 81-86) and wing pattern; from *P. thisbe* also by its weaker occipital carina, smaller size and usually much stronger MT.

Biology.— Williams (1956: 456) gives details of life history and spider prey (*Aphonopelma* spec.)

Distribution.— USA to southern Mexico, ascending to 2,300m. The more southerly, the higher; the maximum altitude given pertains to the southernmost record: San Cristóbal de las Casas (Mexico, Chiapas). A single ♂ has been taken in England (Devon, N. Bovey, 24.vii.1921) (fig. 100).

Material depositories.— Mexico only: 227 ♂♂, 212 ♀♀; AMNH, ANSP, BMNH, BRIO, CAS, CMNH, CSU, CUNY, EMMSU, FDAG, LACM, MCZ, MEM, MNHU, NMV, NRS, OSUC, RMNH, SEMKU, TEXAM, UCALD, UMOX, USNM, USU, UZMC, WAHIS, WASBAUER, ZSM.

*Pepsis petittii* Guérin, 1831

(figs 29, 30, 62, 101)

*Pepsis petittii* Guérin, 1831: 255, ♀. Lectotype, ♀ (MCSNGO), here designated [examined].

*Pepsis tolteca*; Giner Mari, 1944: 360. Misidentification.

Type material.— *P. petittii*: The specimen I have seen bears two old labels: "*Pepsis petittii* Guer. ♀. Voy. Coquille. Perou" and "*Pepsis* .... Perou". It agrees with the original description except that it measures about 30mm long rather than 24. The last two gastral segments are missing. I have labelled the specimen lectotype.

Description.— ♂. BL 16-34. Body black with weak blue-green sheen, especially on gaster; with long, dense, black hair. Antenna orange from segment 3 onwards, slightly dark on inner side. A rather narrow band at base of forewing, and basal half of hindwing, infusate. A white band covers most of the area outside the cells in both wings. The remainder of the wings is a beautiful and unusual light brown or metallic silver-buff, depending on the viewing angle. MT sharp. MPN furrow deep, broad, obsolescent anteriorly, carinae fine to very fine, those of opposite sides often at a strong angle to each other. Propodeum: MG usually weakly indicated anteriorly. APT fairly strong, PPT and PTC very strong but obscured by hair. SGP & genitalia figs 29-30, 62.

♀. BL 22-35. AE index 100-104. Otherwise as ♂, except: antenna not dark on inner side. MT weak. MPN with 1-2 carinae stronger than others. MG often also indicated posteriorly. PPT and PTC moderate to very strong.

Normal variation.— Only as noted above.

Lygarochromic variation.— Although not itself varying, this species nevertheless forms the main "model" of the "lygarochromic" area, where it is endemic (see Introduction).

Distinctions.— Both sexes are distinguished by the highly unusual colour pattern of their wings, orange antennae and long, black body hair. However, care must be taken with worn specimens where most of the wing colour is abraded. Otherwise the species is only likely to be confused with an undescribed species of the *P. lampas*-group which is sympatric in the north of Peru and very similar in colour; however, that species is smaller, lacks the apical white wing bands and has strong group-characters which will at once separate it (very strong MT, ♂ SGP unmodified but with strongly modified S.4 hairs, ♀ gaster dorsally flattened and highly polished, pygidi-

um with polished, impunctate median line). Sympatric, lygarochromic ♀♀ of *P. terminata* somewhat resemble *P. petittii* in the main colour of the wings but have a very broad black, apical border; they also lack the strong lateral extensions of the S.2 groove found in *P. rubra*-group ♀♀.

Distribution.— Inhabits the western desert coast of South America from just north of Guayaquil to south of Lima; in the latter area it ascends to 1,500m in the Andes. A single ♂ labelled Peru: Tembladera (Valle Jequetepeque), 4,000m (MHNLM) may have been transported to that altitude by wind currents; a single record from Chile, Valparaiso also needs confirming (fig. 101).

Material depositories.— 172 ♂♂, 58 ♀♀; AMNH, BMNH, CARRASCO, CAS, FDAG, FRITZ, IMLT, LACM, MACN, MCSNGO, MCZ, MHNLM, MHNNEU, MNHNPS, NHMBAS, PORTER, RSM, SEMKU, TMB, UMOX, UNALM, UNLAMB, UNTRUJ, USNM, ZSM.

*Pepsis cooperi* spec. nov.  
(figs 31, 32, 63, 101)

Type material.— Holotype ♂, Peru: Cajamarca: Jaen, 900m, 12.iv.1984 (Cooper) (BMNH). Paratypes. Peru: Amazonas: Bagua Grande 500m: 1♂, 1♀, 3.vi.1982; 1♂, 4.vi.1982; 2♂, 6.iv.1984, 1♂, 1♀, 14.iv.1984; 2♂, 3.vi.1982; (all Cooper) (BMNH); Cajamarca: Jaen, 900m: 1♂, 2♀, 19.ii.66 (Carrasco) (FRITZ); 2♂, 2♀, 2.iv.66, vuelo (Carrasco) (CARRASCO); R. Lallanga, Vic. Llangue [42k se Pomahua-ca]: 2♂, 1♀, 12.vi.[19]36 (Woytkowski) (SEMKU); Lambayeque: 69k e Olmos: 1♂, 18.i.1955 (Schlinger, Ross) (CAS); [no further data]: 1♂ (UNALM).

Etymology.— This species is named after Martin Cooper, who made special efforts to establish the localities where this species occurs.

Description.— ♂. BL 17-26. Body and legs black with scarcely any metallic sheen. Antennal segments 1-2 and 3 partly, black; the rest orange. Forewing black with a broad, central band of silver pubescence, usually containing a small black dot in the middle; also a broad, white apical band including almost all the area outside the cells and just entering the radial cell anteriorly; hindwing with only a white apical band. MT strong, usually sharp. MPN furrow fairly broad, deep; carinae very fine but usually a few stronger ones anteriorly. Propodeum: MG narrow, often indicated only anteriorly, APT rather weak, PPT and PTC strong but obscured by hair. DTC rather weak. SGP & genitalia figs 31-32, 63.

♀. BL 24-34. AE index 103-108. Otherwise as ♂ except: MT weak or vestigial. MG generally weaker but sometimes evident along whole of dorsum. MPN often with a single, strong carina anteriorly. PTC sometimes very strong, DTC often strong, especially posteriorly.

Variation.— Only as noted above.

Distinctions.— Both sexes of this species are immediately distinguishable from all other species of the genus by wing pattern alone.

Distribution.— Known only from a short stretch of the upper Marañon and lower parts of the Chamaya and Utcubamba rivers in the Andes of north-central Peru at around 500-1,000m (fig. 101).

Material depositories.— 18 ♂♂, 8 ♀♀; BMNH, CARRASCO, CAS, COOPER, FRITZ, SEMKU, UNALM.

*Pepsis pallidolimbata* Lucas, 1895  
(figs 35, 36, 65, 85, 86, 102)

*Pepsis pallidolimbata* Lucas, 1895: 745, no. 143. Lectotype, ♀ (NMV), here designated [examined].  
*Pepsis bequaerti* Salman, 1928: 23. Holotype ♂ (MCZ) [examined]. [Synonymized by Hurd, 1948: 140.]  
*Pepsis cinnabarina*; McKenzie, 1933: 159. Misidentification.  
*Pepsis pallidolimbata smithi* Hurd, 1948: 142. Holotype ♂ (CAS) [not examined]. **Syn. nov.**

Type material.— *P. pallidolimbata*: I have seen a single type-material ♀ and labelled it lectotype.

Description.— ♂. BL 12-24. Body black with blue-green-violet (occasionally bronze) sheen. Legs usually black, but tarsi sometimes red-brown. Antenna black. Wings amber to orange (usually pale sandy-metallic) with a very weak, narrow dark border, the extreme apex of the forewing narrowly whitish. Base of wings dark, sometimes very narrowly. MT moderately strong. MPN furrow broad, often obsolescent anteriorly, somewhat expanded posteriorly; carinae rather fine. Propodeum: MG variable, usually distinct; all tubercles and carinae usually very weak, occasionally PPT and PTC fairly strong. DTC fine to moderately strong. SGP & genitalia figs 35-36, 65.

♀. BL 17-31. Antenna slender, AE index 92-109. Head with vertex and temples scarcely swollen, in dorsal view strongly constricted behind eyes (figs 85, 86); occipital carina reaching preular suture. Otherwise as ♂ except: dark border of wings virtually absent (but the whitish apex remains). PPT, PTC and DTC often stronger.

Variation.— This species usually has a pale, sandy-yellow wing colour: only in certain parts of California does this species exhibit the vivid orange-red common in *P. thisbe* and *P. chrysothemis*.

Distinctions.— The SGP structure is diagnostic for the ♂; the ♀ is distinguished from those of other similarly coloured sympatric species of the *P. rubra*-group as follows: from *P. thisbe* and *P. chrysothemis* by its head shape and much weaker apical wing-banding; from *P. thisbe* also by its stronger MT, higher AE index and smaller size.

Biology.— Williams (1956: 456) gives the prey of this species as *Aphonopelma* spec. MacKenzie (1933: 159) reported this species (as *P. cinnabarina*) as attacking previously undamaged grapes in California, leaving only the skin and pips.

Distribution.— USA to central Mexico, ascending to 1,750m in Mexico (San Luis Potosí). A single ♂ (UMOX) is labelled St. Lucia; the species is not known from the West Indies, but this may refer to the St. Lucia Mts. in Monterrey, Mexico, within the usual range of the species (fig. 102).

Material depositories.— Mexico only: 61 ♂♂, 54 ♀♀; AMNH, BMNH, BRIO, CMNH, CUNY, GILLASPY, LACM, MEM, OSUC, SEMKU, TEXAM, UMOX, WAHIS, WASBAUER, ZMMICH.

*Pepsis decorata* Perty, 1833  
(figs 33, 34, 64, 68, 72, 73, 78, 101)

*Pepsis decorata* Perty, 1833: 143, pl.28, f.2. Brasilia australi. Lectotype, ♂, (ZSM), designated by Diller (1990: 75) [examined].

*Pepsis dives* Lepeletier, 1845: 486, no.28, ♀, Cayenne (lost). [Synonymized by Smith, 1855: 190.]

*Pepsis praesidialis* Taschenberg, 1869: 27, no.1, ♀, Paraná (lost). [Synonymized by Lucas, 1895: 808.]  
*Pepsis incompleta* Brèthes, 1908: 234. Lectotype, ♂, (MACN), here designated [examined]. **Syn. nov.**  
*Pepsis decorata opposita* Banks, 1946: 382. Holotype, ♀, (MCZ) [examined]. **Syn. nov.**

Type material.— *P. decorata*: in addition to the lectotype, I have seen 9 ♀ paralectotypes in ZSM, all bearing labels: "Brasilien, Perty coll.; *Pepsis decorata* Pty., det Perty". Diller (loc. cit.) mentions only 8 of these latter, which are all conspecific with the lectotype; the ninth one is a specimen of *Pepsis varipennis* Lep. *P. incompleta*: I have seen a single type-material ♂ and labelled it lectotype (although much of the gaster, with its distinctive characters, was already missing at the time Brèthes described the specimen, the SMC3 shape places it decisively as this species, not *P. roigi*).

Description.— ♂. BL 20-32. Body and legs black with dull blue-green sheen. Antenna black. Forewing (fig. 68) with silver to silver-golden pattern, hindwing with white, apical band. MT fairly strong, especially in small specimens. MPN furrow broad, deep, sometimes expanded posterad or posteriorly; carinae very fine. Propodeum: APT fairly strong to weak, PPT strong, PTC very strong. DTC fairly strong to weak. MG narrow. SGP & genitalia figs 33-34, 64.

♀. BL 27-44. AE index 79-92. Otherwise as ♂ except: hindwing entirely black. Only PTC fairly strong.

Variation.— Very little (but see distinctions).

Distinctions.— ♂♂ are separable on details of the SGP (figs 33-34), and both sexes are well distinguished by their wing patterns; however, care must be taken in separating ♀♀ from those of the very similar *P. foxi* and *P. roigi* where they occur together (see table below). The present species has also been confused with *P. varipennis* and a sympatric colour form of *P. nitida*, but in those species the wing patterns are different, and their group-characters even more so (*P. varipennis* has a dorsoventrally flattened gaster and the pygidium a polished, impunctate median line; *P. nitida* has an almost conical, downward pointing last gastral segment and the hind coxa with a very sharply carinate upper, outer margin).

Distribution.— Found in French Guiana, Lower Amazon, central and eastern Brazil, Bolivia and Paraguay; at low altitudes, reaching only 700m in south-eastern Bolivia (fig. 101)

Material depositories.— 184 ♂♂, 227 ♀♀; AMNH, BMNH, CAS, CMNH, COOPER, CUNY, EMMSU, INPA, LACM, LEBRAS, MACN, MCSNGO, MCZ, MEM, MHNGV, MHNNEU, MLP, MNHNPS, MNRJ, MNS, MPEP, MZUSP, NMV, NRS, RMNH, RSM, UCALB, UFPCUR, UFVIC, UMOX, UNALM, USNM, USPRIB, UZMC, WAHIS, WASBAUER, WILLIAMS, ZMMICH, ZMMOSC, ZSM.

Table for distinguishing between females of *Pepsis decorata*, *P. foxi* and *P. roigi*. N.B. Since all the characters are variable, identifications must be based on a majority of "correct" characters.

<i>P. decorata</i>	<i>P. foxi</i>	<i>P. roigi</i>
- Head in dorsal view moderately swollen behind eyes (fig. 73).	- Head in dorsal view strongly swollen behind eyes (fig.89)	- Head in dorsal view moderately swollen behind eyes (fig. 74).
- Occipital carina reaching upper edge of pregular groove weakly.	- Occipital carina obsolete shortly before reaching pregular groove.	- Occipital carina obsolete shortly before reaching pregular groove.

<i>P. decorata</i>	<i>P. foxi</i>	<i>P. roigi</i>
- AE index higher, 79-92.	- AE index lower, 67-84.	- AE index higher, 90-97.
- MT merging evenly all round with surface of mesopleuron.	- MT more or less incised behind, thus directed slightly backwards.	- MT merging evenly all round with surface of mesopleuron.
- Infuscation of wings very heavy, almost black (not possible to read a label through it).	- Infuscation of wings moderately heavy, dark brown (possible to read a label through it).	- Infuscation of wings very heavy, almost black (not possible to read a label through it).
- Extreme apex of forewing slightly paler than rest of wing.	- Forewing apex usually unicolorous with rest of wing.	- Forewing apex usually unicolorous with rest of wing.
- Metallic colour of wings bright silvery.	- Metallic colour of wings silver-buff.	- Metallic colour of wings bright silvery.
- Distance between tegula and sub-basal metallic-coloured band of forewing greater than width of complete part of band (fig. 68).	- Distance between tegula and sub-basal metallic-coloured band of forewing less than width of complete part of band (cf. fig. 67).	- Distance between tegula and sub-basal metallic-coloured band of forewing less than width of complete part of band (fig. 67).
- Mark on 1m-cu strong and usually connected, or almost so, to rest of metallic markings (fig. 68).	- 1m-cu without metallic-coloured hairs in dark-winged forms.	- Mark on 1m-cu variable, often distant from rest of metallic markings (fig. 67).
- SMC3 elongate (fig. 78).	- SMC3 shorter (figs 76, 77).	- SMC3 shorter (fig. 79).
- Base of hindwing without metallic colour.	- Base of hindwing usually with more or less extensive metallic patch.	- Base of hindwing without metallic colour.
- MPN furrow rather broad but parallel-sided, with fine carinae.	- MPN furrow very broad, strongly expanded posterad, with one or more carinae much stronger than the others.	- MPN furrow broad, expanded posterad, with two or more carinae much stronger than the others.
- Propodeum more elongate, its dorsal face about as long as scutellum, postscutellum and MPN together.	- Propodeum more transverse, its dorsal face, only about as long as scutellum and postscutellum together.	- Propodeum more transverse, its dorsal face only about as long as scutellum and postscutellum together.
- DTC of propodeum complete on most of dorsum.	- DTC of propodeum extending little beyond ridges bordering MG.	- DTC of propodeum strong, covering whole of dorsum.
- APT weak, a shallow bulge.	- APT fairly strong, a prominent bulge, occasionally pointed.	- APT very strong, usually tooth-like.
- PTC quite strong, but not preceded by a strong depression.	- PTC very strong, preceded by a deep, shining depression, in front of which is a weak "reflection" of the PTC.	- PTC very strong, preceded by a deep, shining depression, in front of which is a weak "reflection" of the PTC.
- Propodeum with transverse carinae of posterior face closer together and weaker than those on dorsal face; obsolescent centrally.	- Propodeum with transverse carinae of posterior face closer together and usually much weaker than those of dorsal face; obsolescent on either side of the centre-line,	- Propodeum with transverse carinae of posterior face slightly irregular, but almost as strong as those of dorsal face, and covering whole of surface.

<i>P. decorata</i>	<i>P. foxi</i>	<i>P. roigi</i>
- Lateral groove of propodeum evenly curved throughout.	or over a larger area. - Lateral groove of propodeum often more or less sinuate anteriorly.	- Lateral groove of propodeum evenly curved throughout.
- T1 & T2 moderately swollen, so that they form an even outline (fig. 72).	- T1 & T2 usually quite strongly swollen, so that their junction is more or less constricted (fig. 71).	- T1 & T2 usually quite strongly swollen, so that their junction is more or less constricted (cf. fig. 71).
- Inner spur of hind tibia reaches 1/4-1/3 of basitarsus length.	- Inner spur of hind tibia reaches about 1/4 of basitarsus length.	- Inner spur of hind tibia reaches 1/5-1/4 of basitarsus length.

*Pepsis albocincta* Smith, 1855, **stat. rev.**  
(figs 7-10, 53, 87, 88, 98)

*Pepsis albocincta* Smith, 1855: 192. Lectotype, ♂ (BMNH), here designated [examined]. [Wrongly synonymized with *P. grossa* (Fabricius) by Haupt, 1952: 376.]

*Pepsis pertyi* Lucas, 1895: 572, no. 49; & p. 574, footnote. Lectotype, ♂ (MNHU), here designated [examined]. [Unnecessary replacement name for *P. elevata* Fabricius; Perty, 1833: 143. Lucas' own material is not conspecific and is here regarded as representing the name *P. pertyi*.] **Syn. nov.**

*Pepsis bicarinata* "Mocsáry"; Lucas, 1895: 572, no. 49 [MS name cited in synonymy].

*Pepsis rubescens* Lucas, 1895: 735, no. 136. Lectotype, ♀ (MNHU), here designated [examined]. **Syn. nov.**

*Pepsis pertyi* var. *ruficornis* Lucas, 1897: 293, no. 2; not Fabricius, 1781. Holotype ♂ (CMNH) [examined]. **Syn. nov.**

*Pepsis staudingeri* Enderlein, 1901: 145. Lectotype, ♂ (MNHU), here designated [examined]. **Syn. nov.**

*Pepsis chrysothorax* Brèthes, 1908: 233. Lectotype, ♀ (MACN), here designated [examined]. **Syn. nov.**

*Pepsis ichesi* Brèthes 1908: 235. One ♂, Rep. Argentina (lost). **Syn. nov.**

*Pepsis abrupta* Brèthes, 1908: 239. Lectotype, ♂ (MACN), here designated [examined]. **Syn. nov.**

*Pepsis ameghinoi* Brèthes, 1908: 240. Lectotype, ♀ (MACN), here designated [examined]. **Syn. nov.**

*Pepsis echeverriai* Brèthes, 1908: 240. Lectotype, ♂ (MACN), here designated [examined]. **Syn. nov.**

*Pepsis prixii* Brèthes, 1908: 240. Lectotype, ♂ (MACN), here designated [examined]. **Syn. nov.**

*Pepsis sulcata* Brèthes, 1908: 241. ♀, Paraguay (lost). **Syn. nov.**

*Pepsis erythrocerca* Brèthes, 1914: 244. [Replacement name for *P. ruficornis* Lucas, 1897, not Fabricius, 1781]. **Syn. nov.**

*Pepsis copelloi* Brèthes, 1914: 317, no. 98. Lectotype, ♀ (MACN), here designated [examined]. **Syn. nov.**

*Pepsis nutrix* Brèthes, 1914: 337, no. 130. Lectotype, ♀ (MACN), here designated [examined]. **Syn. nov.**

*Pepsis annaerdmuthae* Lucas, 1919: 118. ♂, Argentina, La Rioja (lost). **Syn. nov.**

*Pepsis lycaste* Banks, 1946: 341. Holotype ♀ (MCZ) [examined]. **Syn. nov.**

*Pepsis grossa*; Haupt, 1952: 376. Misidentification.

Type material.— *P. albocincta*: I have seen two syntypes, a ♂ in BMNH and a ♀ in UMOX, and have labelled the ♂ as lectotype. The ♀ paralectotype (and another ♂ without type-status) in UMOX are specimens of *P. grossa*. *P. pertyi*: I have seen four conspecific syntypes and labelled one of them, a ♂ in MNHU, as lectotype. A ♀ in NMV is a paralectotype, as also are a ♂ and ♀ in TMB. *P. rubescens*: I have seen a single syntype ♀ (from Pará) and labelled it lectotype. *P. staudingeri*: I have seen two of the three ♂ syntypes mentioned by Enderlein, and have labelled as lectotype the one complete with SGP and genitalia; the other specimen, a conspecific paralectotype, lacks them. *P. chrysothorax*: I have seen a single type-material ♀ and labelled it lectotype. *P. abrupta*: I have seen a single type-material ♂

and labelled it lectotype. *P. ameghinoi*: I have seen a single type-material ♀ and labelled it lectotype. *P. echeverriai*: I have seen a single type-material ♂ and labelled it lectotype. *P. praxii*: I have seen two conspecific ♂ syntypes (both in MACN) and labelled the one in better condition (bearing the locality "Andalgalá") as lectotype; the paralectotype is without locality. *P. copelloi*: I have seen a single type-material ♀ and labelled it lectotype. *P. nutrix*: I have seen six ♀ syntypes, one in MLP, the rest in MACN. I have labelled as lectotype the specimen with pale wing tips in MACN; this and the one in MLP are conspecific. The remaining four are specimens of *P. inclyta* Lepeletier.

Description.— ♂. BL 25-39. Body and legs black with weak blue-green-violet sheen. Antenna black with up to 3 apical segments (sometimes more) orange. Wings amber to deep orange with a dark subapical border, or entirely dark brown or black with weak blue-violet reflections; always with a rather broad apical white margin covering about half the area beyond the cells. MT weak to vestigial. MPN furrow narrow but usually deep, especially posteriorly, where it is often expanded. Carinae very fine, slightly curved; or few, rather strong and irregular, those of opposite sides usually forming a strong angle between them. Propodeum: MG narrow, often deep. APT variable, PPT and PTC moderate to strong, DTC weak to moderate. SGP & genitalia figs. 7-10, 53.

♀. BL 30-55. AE index (82-)91-104. Head in dorsal view more or less quadrate, occiput moderately strongly swollen (figs. 87, 88). Forewing with white apex less distinct (but always at least weakly present). Foreleg with inner spur reaching to about 1/4 length of basitarsus. Hind tibial spines about 3 times height of teeth. Otherwise as ♂, except: antennal segments 3 onwards with extreme apex orange, 6 onwards becoming entirely orange.

Variation.— There is considerable variation in the shape of both carinae of the SGP, especially in western Argentina. This is sometimes accompanied by small differences in the internal genitalia. However, these are considered insufficient to support distinct specific status, especially as intermediate specimens occur. There is a distinct geographical cline in MPN sculpture: in some Argentine specimens there is a tendency for the anterior carinae of the MPN to curve posterad near the central furrow. This tendency is stronger in specimens from Paraguay and Brazil (Minas Gerais) while in Amazon specimens the anterior carinae are usually very strong, and a polished, triangular area is left between them. In Argentine ♀♀ (especially very large ones), the propodeum often joins the MPN in a V-shape, so that the latter is shorter centrally than laterally. In Argentina and southern Brazil both sexes have amber to orange wings (except for a single ♀ from Argentina: San Luis with rather heavily infusate wings, comparable with western specimens of *heros*) and the antenna usually black except for orange apical rings on most segments and the apical half of the last segment. Further north the wing colour is commonly entirely black except for the constant white apex, but orange-winged forms also exist, as well as infusate-orange intermediates from Brazil: Mato Grosso; Bolivia and Paraguay. A ♀ from Pará is of an unusual intermediate colour form: in the basal two-thirds of the wings the veins are outlined in orange, broadly basally, more narrowly distally. The colours of wings and antennae appear usually to be correlated; some ♂♂ from Bolivia have heavily infusate wings, and some from Paraguay, black; they all have the antennae orange from segment 3 onwards. However, ♂♂ from the Amazon with black wings have only the last 2-3 antennal segments orange. Two ♂♂ are labelled "COLOMBIA: Meta, Guaya-

betal, La Virgin Monument" (BMNH, WASBAUER). There is some doubt about the authenticity of this locality (Wasbauer, pers. comm.), which is well outside the otherwise known range for the species. However, these two specimens do show an even more extreme development of those characters which are more pronounced in Lower Amazon individuals than in specimens from further south (viz. anteriorly short SMC3; MPN furrow rather strongly expanded posterad; strong propodeal DTC) which would not disagree with such a locality. Both specimens have orange-red wings, as do some other Amazon specimens.

Particular variation.— Several aberrant individuals have been seen: a ♀ (paralecotype of *P. nutrix*, MLP) has the extremely low AE index of 82. Another ♀ (lectotype of *P. chrysothorax*, MACN) has the entire head covered with very short, dense, adpressed, pale golden pubescence; the thoracic hair is similar, but slightly longer and tending to violaceous. The vertex is slightly more swollen than that of the largest of other Argentine specimens. Both ♀♀ are otherwise normal. A further ♀ from **Argentina**: San Juan (BMNH), although possessing the normal ♀ venation for the group, also has the apex of the forewing radial cell appendiculate, the extra vein rejoining the costa.

Distinctions.— The ♂ of this species is distinguishable from those of most others by its SGP structure, but its black-winged form resembles the ♂ of *P. assimilis* north of the Amazon, where the two approach sympatry; see under the latter species for distinctions. Both dark- and orange-winged ♀♀ of this species resemble sympatric, concolorous forms of *P. foxi*. They can be distinguished by the longer AS3 (AE index 91-104) of *P. albocincta* (in *P. foxi* AE index 67-84); *P. albocincta* also has a less quadrate head (cf. figs 87-88 and 89-90), its forewing has a pale apex, and the pre-apical dark border is broader but less well defined (see also special key). The dark-winged form also resembles those of *P. grossa* and *P. defecta*. It differs from both in unusual anterior MPN sculpture; further from *P. grossa* in lacking that species' coarse hair below femur I; and further from *P. defecta* in lacking that species' strong group-characters (short, thick hind tibial spurs; strongly curved hind claw joint; tooth beyond middle of hind claw). The orange-winged ♀ resembles those of *P. chacoana* and *P. caridei*. *P. chacoana* is distinguished by its very swollen occiput, coarse hair below femur I (caution with worn specimens!) and teeth and spines of tibia III about equal in length (spines distinctly longer than teeth in *P. albocincta*). *P. caridei* differs in its shorter AS3 (AE index 80-91), the dark forewing border extending right to the apex, and less swollen occiput (cf. figs 91, 92).

Distribution.— This species is found along the Lower Amazon (two specimens possibly from the Upper Amazon - see Variation) southwards through eastern Brazil and the Mato Grosso to Paraguay, Bolivia and Patagonian Argentina, reaching altitudes of 2,700m in Argentina (Salta and Catamarca) (fig. 98).

Material depositories.— 395 ♂♂, 341 ♀♀; AEIG, AMNH, BMNH, BONELLI, CMNH, CUNY, EMMSU, FRITZ, IMLT, LACM, LEBRAS, MACN, MCZ, MLP, MLU, MNHNPS, MNHU, MNRJ, MNS, MZUSP, NMV, NRS, RMNH, SEMKU, TMB, UCALB, UCALD, UCMB, UMB, UMOX, USNM, UZMC, WAHIS, WASBAUER, WILLIAMS, ZSM.

## References

- Notes on priority of publication.— 1845: Dahlbom, manuscript finished 12 June, probably published later than Lepeletier; Lepeletier, must have been published shortly before 12 July (teste Verhoeff, 1948: 183). The following dates are printed on the journal-part covers: 1894: Gribodo, 1 January; Mocsáry, 30 June. 1921: Montet, February; Banks, April. 1952: Hurd and Haupt (no clash of priorities, as no new species were described in the former).
- Alcock, J., 1983. Consistency in the relative attractiveness of a set of landmark territorial sites to two generations of male tarantula hawk wasps (Hymenoptera: Pompilidae).— *Anim. Behav.* 31: 74-80.
- Banks, N., 1921. New Nearctic fossorial Hymenoptera.— *Ann. ent. Soc. Am.* 14 (1): 16-26.
- Banks, N., 1926. Several new species of Psammocharidae (Hymenoptera).— *Can. Ent.* 58: 201-203.
- Banks, N., 1928. Studies on Cuban insects 1. Notes on Cuban and other West Indian Psammocharidae.— Harvard Biological Laboratory and Botanical Garden in Cuba 1: 3-10.
- Banks, N., 1945. The Psammocharidae of northern South America.— *Boln Ent. venez.* 4: 81-126.
- Banks, N., 1946. Studies of South American Psammocharidae. Part 1.— *Bull. Mus. comp. Zool. Harv.* 96: 311-525.
- Bohart, R.M. & A.S. Menke, 1963. A reclassification of the Sphecinae with a revision of the Nearctic species of the tribes Sceliphronini and Sphecini.— *Univ. Calif. Publ. Ent.* 30: 91-182.
- Brèthes, J., 1908. Contribución preliminar para el conocimiento de los *Pepsis*.— *An. Mus. nac. Hist. Nat. B. Aires Ser. 3*, 10: 233-243.
- Brèthes, J., 1914. Contribution a l'étude des *Pepsis*.— *An. Mus. nac. Hist. Nat. B. Aires* 26: 235-360.
- Brown, W.L. & E.O. Wilson, 1956. Character displacement.— *Syst. Zool.* 5: 49-64.
- Christ, J.L., 1791. Naturgeschichte, Klassifikation und Nomenclatur der Insekten vom Bienen-, Wespen-, und Ameisengeschlecht: 1-535.— Frankfurt-am-Main.
- Cresson, E.T., 1865. On the Hymenoptera of Cuba.— *Proc. ent. Soc. Philad.* 4: 1-200.
- Cresson, E.T., 1872. Hymenoptera Texana.— *Trans. Am. ent. Soc.* 4: 153-292.
- Dahlbom, A.G., 1843-1845. Hymenoptera Europeae praecipue borealia: 1: 119-123, 463-465.— Lund.
- Diller, E., 1990. Die von Spix und Martius 1817-1820 in Brasilien gesammelten und von J.A.M. Perty 1833 bearbeiteten Hymenopteren in der Zoologischen Staatssammlung München (Insecta, Hymenoptera).— *Spixiana* 13: 61-81.
- Drury, D., 1773. Illustrations of natural history, 2: i-vii+1-90.— London.
- Eberhard, W.G., 1985. Sexual selection and animal genitalia: i-x+1-244.— Cambridge, USA & London, England.
- Enderlein, G., 1901. Neue *Pepsis*-arten aus dem Königlichen Museum für Naturkunde zu Berlin.— *Stettiner ent. Ztg* 62: 145-150.
- Erichson, W. F., 1848. In: Schomburgk, M.R., Reisen in Britisch-Guiana in .... 1840-1844. 3: 1-1260.— Leipzig. [Klug is often wrongly quoted as the author of Erichson's new species; although his name is mentioned in the publication as author, there is no evidence that he actually wrote the descriptions.]
- Evans, H.E., 1959. The larvae of Pompilidae.— *Ann. ent. Soc. Am.* 52 (4): 430-444.
- Fabricius, J.C., 1781. Species Insectorum 1: i-viii+1-552.— Hamburg & Cologne.
- Fabricius, J.C., 1793. Entomologia systematica emendata et aucta, 2: i-viii+1-519.— Copenhagen.
- Fabricius, J.C., 1798. Entomologicae systematicae supplementum: 1-572.— Copenhagen.
- Fabricius, J.C., 1804. Systema piezatorum: i-xiv+1-15+1-440+1-30.— Brunswick.
- Field, J., 1992. Guild structure in solitary spider-hunting wasps (Hymenoptera; Pompilidae) compared with null model predictions.— *Ecol. Ent.* 17: 198-208.
- Fox, W.J., 1898. The species of *Pepsis*, inhabiting America north of Mexico.— *Proc. ent. Soc. Wash.* 4 (2): 140-148.
- Gauld, I.D. & L.A. Mound, 1982. Homoplasy and the delineation of holophyletic genera in some insect groups.— *Syst. Ent.* 7: 73-86.

- Gentry, A.H., 1979. Distribution patterns of Neotropical Bignoniaceae: some phylogenetic implications: 339-354. In: Larsen K. & L.B. Holm-Nielsen (eds) Tropical Botany.— London.
- Giner Mari, J., 1944. Algunos Himenópteros del Museo de Barcelona (Fams): “Sphecidae, Psammocharidae y Mutillidae” (Him. acul.).— Boln R. Soc. esp. Hist. nat. 42: 345-369.
- Grant, P.R., 1972. Convergent and divergent character displacement— Biol. J. Linn. Soc. 4: 39-68.
- Gribodo, J., 1894. Hymenopterorum novorum diagnoses praecursoriae.— Miscnea ent. 2: 2-3.
- Guérin-Ménéville, F.E., 1831. In: Duperrey, M.L.I. Voyage autour du monde, ... sur ... La Coquille, pendant ...1822-1825. Zoologie 2 (2), ch.13, div. 1, Insectes.— Paris [1830].
- Guérin-Ménéville, F.E., 1838. Dictionnaire pittoresque d'histoire naturelle 7.— Paris.
- Haupt, H., 1952. Alte und neue *Pepsis*-Arten (Hymenoptera-Sphecioidea).— Nova Acta Leopoldina N.F. 15 (109): 309-414.
- Hurd, P.D., 1948. Systematics of the California species of *Pepsis* Fabricius (Hymenoptera; Pompilidae).— Univ. Calif. Publs Ent. 8: 123-150.
- Hurd, P.D., 1952. Revision of the Nearctic species of the genus *Pepsis* (Hym. Pompilidae).— Bull. Am. Mus. nat. Hist. 98 (4): 257-334.
- Klug, J.C.F., 1848. See Erichson (1848).
- Latreille, P.A., 1809. Genera crustaceorum et insectorum 4: 1-399.— Paris & Strasbourg.
- Latreille, P.A., 1810. Considérations générales sur l'ordre naturel des animaux ... insectes: 1-444.— Paris. [Table des genres avec l'indication de l'espèce qui leur sert de type: 421-444.]
- Lawson, T., 1994. Stuck on sticks.— BBC Wildlife, London 12(8): 40-44.
- Lepeletier de Saint-Fargeau, A.M.L., 1845. Histoire Naturelle des Insectes. Hyménoptères 3: 1-646.— Paris.
- Lincecum, G., 1867. The tarantula killers of Texas.— Am. Nat. 1: 137-141.
- Lucas, R., 1895. Die Pompiliden-Gattung *Pepsis*.— Berl. ent. Z. 39 (4): 449-840 [1894].
- Lucas, R., 1897. Neue *Pepsis*-Arten aus der Sammlung des Herrn Herbert H. Smith (USA).— Ent. Nachr. Berlin 23 (19): 291-296.
- Lucas, R., 1919. Pompiliden-Studien 1.— Arch. Naturgesch., A. 83 (5): 1-180.
- MacLean, B.K., L. Chandler & D.B. Maclean, 1978. Phenotypic expression in the paper wasp *Polistes fuscatus* (Hymenoptera: Vespidae).— Gt Lakes Ent. 11 (2): 105-116.
- Maddison, R., 1994. Phylogenetic methods for inferring the evolutionary history and processes of change in discretely valued characters.— A. Rev. Ent. 39: 267-292.
- Malaise, R., 1937. Fabricius as the first designator and original inventor of genotypes.— Ent. News 48: 130-134.
- McKenzie, H.L., 1933. Note on the tarantula hawk wasps.— Pan-Pacif. Ent. 9 (4): 159.
- Mocsáry, A., 1885. Species novae vel minus cognitae generis *Pepsis* Fabr.— Természetr. Füz. 9: 236-271.
- Mocsáry, A., 1887. Studia synonymica.— Természetr. Füz. 11: 12-20.
- Mocsáry, A., 1894. Species novae vel minus cognitae generis *Pepsis* Fabr.— Természetr. Füz. 17: 1-14.
- Montet, G., 1921. Hyménoptères nouveaux du genre *Pepsis* Latr. de la collection du Muséum d'histoire Naturelle de Genève.— Revue Suisse Zool. 28: 205-219.
- Müller, P., 1986. Biogeography. i-x+1-377.— New York.
- Packard, A.S., 1869. List of hymenopterous and lepidopterous insects collected by the Smithsonian expedition to South America, under Prof. James Orton.— Rep. Peabody Acad. Sci: 56-69.
- Papavero, N., 1973. Essays on the history of neotropical Dipterology 2: 1- iii+217-446.— São Paulo.
- Passmore, L., 1936. Tarantula and tarantula hawk.— Nature Mag. 27: 155-159.
- Pate, V.S.L., 1946. The generic names of the spider wasps (Psammocharidae *olim* Pompilidae) and their type species (Hymenoptera: Aculeata).— Trans. Am. ent. Soc. 72: 65-137.
- Perty, J.A.M., 1830-1834. Delectus animalium articulorum, quae in itinere per Brasiliam ... collegerunt Dr. J.B. de Spix et Dr. C.F.Ph. de Martius, 3 (1833): 125-224.—Munich.
- Punzo, F., 1990. The hemolymph composition and neurochemistry of the spider wasp, *Pepsis formosa* (Hymenoptera, Pompilidae).— Comp. Biochem. Phys. 96A: 341-345.
- Punzo, F., 1991. Neurochemical events associated with learning and hunting behaviour in the spider wasp, *Pepsis formosa* (Say) (Hymenoptera, Pompilidae).— Fla Scient. 54: 51-61.

- Punzo, F., 1994a. The biology of the spider wasp, *Pepsis thisbe* (Hymenoptera, Pompilidae) from Trans Pecos, Texas. I. Adult morphometrics, larval development and the ontogeny of larval feeding patterns.— *Psyche*, Camb. 101: 229-241.
- Punzo, F., 1994b. The biology of the spider wasp, *Pepsis thisbe* (Hymenoptera, Pompilidae) from Trans Pecos, Texas. II. Temporal patterns of activity and hunting behaviour with special reference to the effects of experience.— *Psyche*, Camb. 101: 243-256.
- Punzo, F. & B. Garman, 1989. Effects of encounter experience on hunting behavior of the spider wasp, *Pepsis formosa* (Say) (Hymenoptera: Pompilidae).— *SWest. Nat.* 34: 513-518.
- Raup, D.M., 1993. Extinction - bad genes or bad luck?: 1-210.— Oxford.
- Roig A., 1987. Contribución al conocimiento de los Pepsinae sudamericanos. 4. El género *Sphictostethus* Kohl (Hymen., Pompilidae).— *Revta Soc. ent. Argent.* 44 (3-4): 277-315.
- Salman, K.A. 1928. On a new species of *Pepsis* (Family Psammocharidae, order Hymenoptera).— *Pan-Pacif. Ent.* 5: 23-25.
- Schrottky, C., 1909. Himenópteros de Catamarca.— *Annl. Soc. cient. argent.* 68: 233-272.
- Schulz, W.A., 1904. Materialien zu einer Hymenopterenfauna der westindischen Inseln.— *Sber. bayer. Akad. Wiss.* (1903) 33 (3): 451-488.
- Schulz, W.A., 1906. Spolia hymenopterologica: i-iii+1-356.— Paderborn.
- Shimizu, A., 1994. Phylogeny and classification of the family Pompilidae (Hymenoptera).— *Bull. nat. Hist. Tokyo Metropolitan Univ.* 2: 1-142
- Smith, F., 1855. Catalogue of hymenopterous insects in the collection of the British Museum. Part 3. Mutillidae and Pompilidae: 1-206.— London.
- Smith, K.G.V., 1987. Darwin's Insects.— *Bull. Br. Mus. (nat. Hist.) [Historical Series]* 14: 1-143.
- Starr, C.K. & Hernández L., L.R. , 1995. A daytime resting aggregation of male *Pepsis sericans* Lep. (Pompilidae).— *Sphecos* 29: 12-13.
- Taschenberg, E., 1869. Die Pompiliden des Museums der Universität zu Halle.— *Z. ges. naturw. Halle* 34: 25-75.
- Tiesheng, L. & Schmidt, J., 1992. Chinese wasp venoms.— *Sphecos* 23: 67.
- Townes, H., 1957. Nearctic Wasps of the subfamilies Pepsinae and Ceropalinae.— *Bull. U.S. nat. Mus.* 209: 1-286.
- Verhoeff, P.M.F., 1948. Systematisches Verzeichnis der niederländischen *Oxybelus*-Arten (*Oxybelus* Latr., Hym. Sphec.).— *Tijdschr. Ent.* 89: 157-208 (1946).
- Williams, F.X., 1928. Studies in Tropical Wasps - Their Hosts and Associates.— *Bull. Hawaiian Sug. Pls' Ass. Exp. Stn (Ent. Series)* 19: 1-179.
- Williams, F.X., 1956. Life history studies of *Pepsis* and *Hemipepsis* wasps in California (Hymenoptera, Pompilidae).— *Ann. ent. Soc. Am.* 49 (5): 447-466.
- Woollatt, L.H., 1945. Sawfly records from Cothill, Berks, including one new to the British list (Hym., Symphyta).— *Entomologist's mon. Mag.* 81: 154-155.
- Woollatt, L.H., 1946. Some biological notes on *Sciapteryx consobrina* Klug (Hym., Symphyta: Tenthredinidae).— *Entomologist's mon. Mag.* 82: 18-19.
- Zimsen, E., 1964. The type material of I.C. Fabricius: 1-656.— Copenhagen.

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(Junior synonyms and other invalid names are in *italics*.)

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