

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

Part 2. The *P. grossa*- to *P. deaurata*-groups

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In this Part, 37 species of the genus, belonging to eight species-groups, are described and figured, and their phylogenetics and biogeography are discussed. Seven of the species are described as new: *P. ecuadorae*, *friburgensis*, *marthae*, *onorei*, *pulawskii*, *riopretensis*, *yucatani*. One species-name, *P. tolteca* Lucas, 1895, is recalled from synonymy and one name, *P. lycaon* Banks, 1945, is upgraded from varietal to species status. The following 49 names are newly synonymized (valid names first): *P. grossa* (Fabricius, 1798) = *P. formosus* Say, 1823, *P. affinis* Dahlbom, 1845, *P. obliquerrugosa* Lucas, 1895, *P. nephele* Lucas, 1895, *P. theresiae* Kriechbaumer, 1900, *P. colombica* Brèthes, 1926, *P. pattoni* Banks, 1945, *P. pellita* Haupt, 1952; *P. aquila* Lucas, 1895 = *P. pyramus* Lucas, 1895, *P. pallidipennis* Haupt, 1952; *P. elevata* Fabricius, 1804 = *P. cristata* Haupt, 1952; *P. marginata* Palisot de Beauvois, 1809 = *P. reaumuri* Dahlbom, 1845; *P. terminata* Dahlbom, 1843 = *P. ferruginea* Lepeletier, 1845, *P. venusta* Smith, 1855, *P. albolimbata* Mocsáry, 1885, *P. pulchripennis* Mocsáry, 1885, *P. cyanosoma* Lucas, 1895, *P. acroleuca* Lucas, 1895, *P. mancoi* Banks, 1946, *P. fuscorubra* Brèthes, 1914; *P. brevicornis* Mocsáry, 1894 = *P. depressa* Brèthes, 1908; *P. cassiope* Mocsáry, 1888 = *P. cassandra* Mocsáry, 1888, *P. lilloi* Brèthes, 1908, *P. heterochroa* Brèthes, 1914, *P. elisa* Montet, 1921, *P. brethesi* Montet, 1921, *P. arizonica* Banks, 1921, *P. hirsuta* Salman, 1933, *P. iolanthe* Banks, 1946, *P. adusta* Haupt, 1952; *P. aurozonata* Smith, 1855 = *P. apicalis* Lepeletier, 1845; *P. aurifex* Smith, 1855 = *P. niphe* Mocsáry, 1885; *P. plutus* Erichson, 1848 = *P. opulenta* Mocsáry, 1894; *P. apicata* Taschenberg, 1869 = *P. alcimeda* Banks, 1946, *P. amalthea* Banks, 1946; *P. defecta* Taschenberg, 1869 = *P. fumata* Enderlein, 1901, *P. cleantes* Banks, 1946; *P. ricspidata* Gribodo, 1894 = *P. lativalvis* Mocsáry, 1894, *P. astarte* Banks, 1945; *P. pulszkyi* Mocsáry, 1885 = *P. aurocincta* Mocsáry, 1894; *P. sumptuosa* Smith, 1855 = *P. colossica* Stål, 1857, *P. apollinariii* Brèthes, 1926; *P. optima* Smith, 1879 = *P. andrei* Mocsáry, 1885; *P. toppini* Turner, 1915 = *P. selvatica* Brèthes, 1920; *P. bonplandi* Brèthes, 1914 = *P. eubule* Banks, 1946; *P. hyperion* Mocsáry, 1894 = *P. gigantea* Lucas, 1895, *P. altitarsus* Enderlein, 1901; *P. deaurata* Mocsáry, 1894 = *P. speciosa* Smith, 1855, *P. auricoma* Lucas, 1895. Keys to all forms are given. Lygarochromy and two mimicry-groups are defined and described and the occurrence of large individuals on islands is briefly discussed.

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Introduction

Completely new aspects of the genus *Pepsis* are dealt with in this second Part [Part 1: see Vardy, 2000], which is based on the examination of 4,775 specimens. Since several additional species-groups have now been studied, it has become possible to gain further insights into their phylogeny and biogeography by comparing these groups with each other and with the *P. rubra*-group (treated in Part 1). In the course of the present work it has also become apparent that the speciose *P. rubra*-group, whose distributional range virtually coincides with that of the genus, represents a good standard for comparison with other species-groups. The subject of mimicry-groups is introduced here, as two of them concern the taxonomic groups treated in this part. The phenomenon of lygarochromy, here defined as the sympatric occurrence of unusual colour forms not forming a clear mimicry-group, is further treated. Also the phenomenon of larger-sized individuals in island populations is mentioned.

Abbreviations and special terms

AE index =	Antennal/eye index: AS3 divided by UID, multiplied by 100; exceptional values in parentheses, e.g. (82-)91-108;
APT =	Anterior propodeal tubercle;
AS3 =	Antennal segment 3 (or its length);
Axial =	Denotes a vein which is parallel, or nearly so, to the longitudinal axis of the wing;
BL =	Body length, given in millimetres; exceptional values in parentheses;
DTC =	Dorsal transverse carinae of propodeum;
Lacuna =	A bubble-like space, found as sub-basal pairs inside some SGPs;
MG =	Median groove of propodeum;
MPN =	Metapostnotum;
MT =	Mesopleural tubercle;

PDV =	Postero-distal veinlet of SMC2 in forewing;
PFC =	Posterior face carinae of propodeum;
PPT =	Posterior propodeal tubercle;
PPV =	Postero-proximal veinlet of SMC2 in forewing;
Propodeal hair =	As used in comparison with PST or MPN length, the hair located just behind and below the APT;
PST =	Postscutellum;
PTC =	Posterior transverse carina of propodeum (divides dorsal and posterior faces)
S =	Sternite; S.6 is sixth sternite, etc.
SGP =	Subgenital plate in male;
SMC =	Submarginal cell of forewing;
Stigmal fenestra =	In the forewing, the narrow translucent band running obliquely inwards from the base of the stigma; sometimes reduced to a narrow line;
T =	Tergite; T.1 is the first tergite, etc.
UID =	Upper interocular distance (minimum, at level of ocelli);
VR =	Vertical ridges of propodeal posterior face.

Abbreviations of depositories

List of depositories and their staff, and private collectors, whose loans or gifts of material are gratefully acknowledged:

AEIG =	American Entomological Institute, Gainesville, Florida (Dr D. Wahl)
AFZD =	Agricultural and Forest Zoology Department, University of Helsinki (Dr M. Koponen, Dr M. Viitisaari)
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 The Natural History Museum, London] (Mr T. Huddleston)
BONELLI =	Padre B. Bonelli, Cavalese (private coll.)
BPBM =	Bernice P. Bishop Museum, Honolulu (Dr G.M. Nishida)
BRIO =	Biosystematics Research Institute, Ottawa (Dr J. Huber)
CARRASCO =	Prof. F. Carrasco, Cusco (private coll.)
CAS =	California Academy of Sciences, San Francisco (Dr W.J. Pulawski)
CMNH =	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (Dr J.E. Rawlins, Dr C.W. Young)
COOPER =	Mr M. Cooper, Lyme Regis (private coll.)
CSU =	Colorado State University, Fort Collins (Dr B. Kondratieff)
CUNY =	Cornell University, Ithaca, New York State (Dr E.R. Hoebeke, the late Mr B. Alexander)
EMMSU =	Entomology Museum, Michigan State University, East Lansing (the late Prof. R.L. Fischer, Prof. F.W. Stehr)
ETHZ =	Entomologisches Institut, Eidgenossische Technische Hochschule, Zürich (Dr B. Merz; now Dr A. Müller & Dr M. Schindler)
FDAG =	Florida Department of Agriculture, Gainesville (Dr L.A. Stange, Dr J.R. Wiley)

- FRITZ = Sr. M.A. Fritz, Salta (private coll.); to be deposited in AMNH
- GILLASPY = Prof. J.E. Gillaspay, Austin, Texas (private coll.)
- HENSEN = Drs R.V. Hensen, Utrecht (private coll.); subsequently deposited in RMNH
- IMLT = Instituto Miguel Lillo, Tucumán (the late Dr A. Willink, Dr M.V. Colombo de Correa, Sr A. Aguilera)
- INBIO = Instituto Nacional de Biodiversidad de Costa Rica (Dr A. Solís, Dr P. Hanson)
- INPA = Instituto Nacional de Pesquisas da Amazônia, Manaus (Dr J.A. Rafael)
- INTAC = Instituto Nacional de Tecnología Agropecuaria, Castelar, provincia de Buenos Aires (Dr A. Vetrano, now Ing. R. Larosa)
- LACM = Los Angeles County Museum, Los Angeles, California (Dr R.R. Snelling)
- LEBRAS = Laboratorio de Ecologia, Universidade de Brasilia, Brasilia, D.F. (Dr A. Raw)
- MACN = Museo Argentino de Ciencias Naturales, Buenos Aires (Dr A. Bachmann, Dr A. Roig A., Dr J.F. Genise, Sr R. Abas)
- MCSNGO = Museo Civico di Storia Naturale, Genoa (Dr R. Poggi, Dr V. Raineri)
- MCZ = Museum of Comparative Zoology, Cambridge, Massachusetts (Prof. J.M. Carpenter, Dr G. Chavarría, Mr S. Cover, Mr C. Vogt)
- MEM = Mississippi Entomological Museum, Mississippi State (Dr T.L. Schiefer)
- MHNGV = Museum d'Histoire Naturelle, Geneva (Dr C. Besuchet; Dr I. Löbl; now Dr B. Merz)
- MHNLIM = Museo de Historia Natural "Javier Prado", Lima (Dr G. Lamas M.)
- MHNNEU = Musée d'Histoire Naturelle, Neuchâtel, Switzerland (Dr J.-P. Haenni)
- MICR = Museo de Insectos, Universidad de Costa Rica (Dr H. Lezama)
- MIZAM = Museo del Instituto de Zoología Agrícola, Maracay (Dr J.E. Lattke, Dr J.L. García)
- MIZSU = Museo ed Istituto di Zoologia Sistemática dell' Università, Turin (Dr P.P. d'Entrèves, Dr O. Elter); material now transferred to Museo Regionale di Scienze Naturali di Torino (Dr P.L. Scaramozzino)
- MLP = Facultad de Ciencias Naturales y Museo, Universidad de La Plata (the late Dr R. Ronderos; Dra M. Loíacono)
- MLU = Martin-Luther Universität, Halle (Dr M. Dorn)
- MNCN = Museo Nacional de Ciencias Naturales, Madrid (Dra I. Izquierdo)
- MNHNPG = Museo Nacional de Historia Natural de Paraguay, Asunción (Dr J. Kochalka, Dr B. Garcete, Dra B. Barrios C., Dr C. Aguilar)
- MNHNPS = Muséum National d'Histoire Naturelle, Paris (the late Dr S. Kelner-Pillault, Dr J. Casewitz-Weulersse)
- MNHNSA = Museo Nacional de Historia Natural, Santiago, Chile (Dr A. Camouseight M., Dr M. Elgueta D.)
- MNHU = Museum für Naturkunde der Humboldt-Universität zu Berlin (Dr F. Koch, Mrs I. Wegener)
- MNRJ = Museu Nacional, Rio de Janeiro (Dr Miguel Monne, Dr Paulo Magno, Dra Marcela Monne)
- MNS = Museum für Naturkunde, Stuttgart (Dr T. Osten, Dr C. Schmid-Egger)

- MPEG = Museu Paraense "Emilio Goeldi", Belém do Para (Dr W.L. Overal)
MZEL = Museum of Zoology and Entomology, Lund (Dr R. Danielsson)
MZLAU = Musée de Zoologie, Lausanne (Dr M. Sartori)
MZUSP = Museu de Zoologia de la Universidade de São Paulo (Dr C.R.F. Brandão, Dr S.T.P. Amarante)
NHMBAS = Natural History Museum, Basle (Dr M. Brancucci)
NMV = Naturhistorisches Museum, Vienna (Dr M. Fischer, Dr S. Schödl)
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PMA = Provincial Museum of Alberta, Edmonton (Dr A. Finnamore)
PORTER = Dr C. Porter (private coll.); partly, including *Pepsis*, to Florida State Collection of Arthropods, Gainesville (Dr J.R. Wiley)
RMNH = Rijksmuseum van Natuurlijke Historie [now Nationaal Natuurhistorisch Museum, Leiden (Dr C. van Achterberg)
ROIG = Dr A. Roig A., Buenos Aires (private coll.)
RSM = Royal Scottish Museum, Edinburgh [Royal Scottish Museums, Natural History (Edinburgh)] (Dr M. Shaw)
SEMKU = Snow Entomological Museum, Kansas University, Lawrence, Kansas (Dr R.W. Brooks)
SMF = Natur-Museum Senckenberg, Frankfurt-am-Main (Dr J.-P. Kopelke, Dr D.S. Peters)
TEXAM = A & M University, College Station, Texas (Mr E.G. Riley)
TMB = Természettudományi Múzeum, Budapest (Dr J. Papp)
UCALB = University of California at Berkeley (Dr H.V. Daly, Dr J.A. Chemsak)
UCALD = University of California at Davis (Prof. R.M. Bohart)
UCMB = University of Colorado Museum, Boulder (Dr U.N. Lanham, Dr M. Weissman, Dr P. Robinson)
UCV = Universidad Católica de Valparaíso (specimens seen by courtesy of Prof. H. Toro, UMCE)
UFPCUR = Universidade Federal de Paraná, Curitiba (Dr V. Graf)
UFVIC = Universidade Federal de Viçosa, Minas Gerais (Dr J.R. Cure)
UMB = Übersee Museum, Bremen (Dr H. Hohmann)
UMCE = Universidad Metropolitana de Ciencias de la Educación de Santiago (Prof. H. Toro)
UMOX = Hope Entomological Collections, University Museum, Oxford, England (Mr C. O'Toole)
UNALM = Universidad Nacional Agraria, La Molina, Lima (Dr C.E. Vergara, Dr M. Ortiz)
UNAN = Universidad Nacional Autónoma de Nicaragua, Museo Entomológico (now Museo Entomológico de León, Nicaragua) (Dr J.-M. Maes)
UNCBOG = Universidad Nacional de Colombia, Bogotá (Dr F. Fernández, Dr W. Cubillos)

- UNCUS = Universidad Nacional de Cusco (Dr J.A. Escalante G., Dr W. Tagle E.)
 UNLAMB = Universidad Nacional P. Ruiz Gallo, Lambayeque (Dr Bravo Calderón, Dr D. Ojeda)
 UNPBOG = Universidad Nacional Pedagógica, Bogotá (Prof. R. Torres N., Sr C.E. Sarmiento, Srta A.R. Amarillo)
 UNTRUJ = Universidad Nacional de Trujillo (Dr G. Ayquipa A.)
 UPAN = Universidad de Panamá: Museo de Invertebrados G.B. Fairchild, Dept. de Zoología, Facultad de Ciencias Naturales (Dr Diomedes Quintero A., Sr. Roberto Cambra, Sr. Alberto Mena)
 USNM = United States National Museum [now National Museum of Natural History], Washington, D.C. (Dr A.S. Menke)
 USPRIB = Universidade de São Paulo, Riberão Preto (Dr R. Zucchi, Dra M. R. Mechi)
 USU = Utah State University, Logan (Dr F.D. Parker, Dr T. Griswold)
 UZMC(K) = University Zoological Museum, Copenhagen (Kiel collection) (the late Dr B. Petersen, Dr O. Lomholdt)
 WAHIS = Monsieur R. Wahis, Chaudfontaine, Belgium (private coll.)
 WASBAUER = Dr M.S. Wasbauer, Sacramento, California (private coll.)
 WILLIAMS = Mr D.M. Williams, Santa Ana, California (private coll.)
 ZIUK = Zoologisches Institut der Universität, Kiel (Dr V. Haeseler, Dr R. König, Dr P. Ohm)
 ZMHEL = Zoological Museum, Helsinki (Dr P. Nuorteva, Dr A. Jansson)
 ZMMICH = Zoological Museum, University of Michigan, Ann Arbor (Dr M.F. O'Brien)
 ZMMOSC = Zoological Museum, University of Moscow (Dr A. Antropov)
 ZMPUCEQ = Zoology Museum, Pontífica Universidad Católica del Ecuador, Quito (Dr G. Onore)
 ZSM = Zoologische Staatssammlung, Munich (Dr E. Diller)

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Mislabelling

Some important instances of multiple mislabelling have come to light during the course of this work. These are:

MCZ: many specimens are labelled "NW part Trinidad; Ballou, Urich and Fenah". At least some of these specimens are mislabelled; the most likely correct label is "Ecuador, Bucay". Examples of specimens whose provenance is certainly west coastal Ecuador, but bear the Trinidad label, are *P. grossa* (Fabricius, 1798) (endemic, lygarochromic colour form), *P. gracilis* Lepelletier, 1845 (endemic colour and structural

form; including some type-material of *P. ierensis* Banks, 1945) and *P. lycaon* Banks, 1945 (endemic species).

UZMC: specimens are labelled "VEN. Therida"; this should be Venezuela, Merida.

TMB: Many labels apparently transcribed from old records are unreliable; for instance, the well-known Panamanian locality Chiriqui is given on various labels as occurring also in two additional, widely-separated South American countries, which is most unlikely to be the case.

ZSM: specimens from "Colombia, Puerto Berrio, middle Rio Magdalena" are evidently mislabelled. This is apparent from comparing Kriechbaumer's (1900: 102) account with the specimens of *P. grossa* that he saw; some of these pertain to the lygarochromic form which is otherwise unknown from that area; neither do the numbers and sexes of individuals entirely coincide with his account.

Host records

In Part 1 (Vardy, 2000: 25-26) it is stated that host records subsequent to Hurd (1952: 268) are given under the species concerned. However, for easier reference a summary of the neotropical ones is given here, as follows (for nearctic species, see Williams, 1956; Punzo 1994, a,b; Punzo & Garman, 1989):

Part 1, *P. rubra*-group: *P. heros* (Fabricius, 1798).

Part 2, *P. elevata*-group: *P. marginata* Palisot de Beauvois, 1809 (only in Hurd, 1952).

Part 3, *P. inclyta*-group: *P. xanthocera* Dahlbom, 1843; *P. montezuma*-group: *P. montezuma* Smith, 1855, *P. smaragdina* Dahlbom, 1843; *P. ruficornis*-group: *P. gracillima* Taschenberg, 1869; *P. viridis*-group: *P. atripennis* Fabricius, 1804.

Wing structure

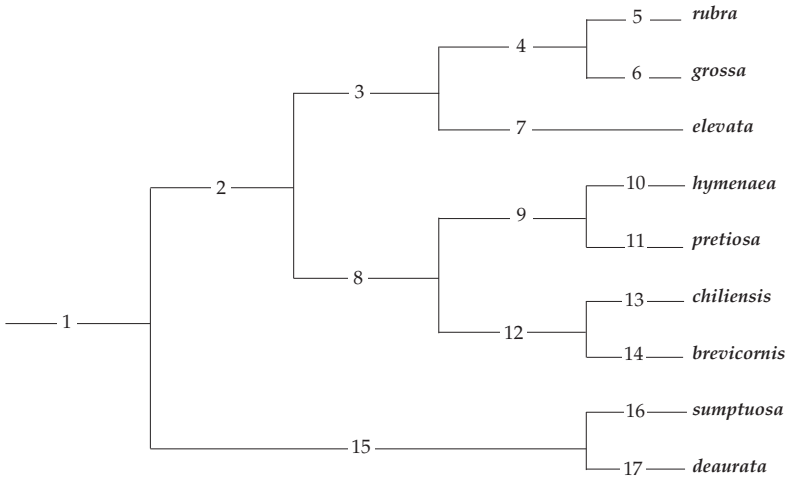
In the light of further study of the genus *Pepsis*, an interesting structural phenomenon has become apparent, involving two ways of solving the same problem. Females of the *Pepsis rubra*- and *grossa*-groups are remarkable in possessing a group-character in their venation *viz.* the radial vein meets the costa at a very shallow angle, i.e. ends on the costa much closer to the pterostigma than is normal for the genus. Unlike in other species-groups which have a group-character, this is not reflected in the males. However, the smaller the specimen, or species, the less pronounced this character becomes, approaching the usual state for the genus, i.e. a radial cell more-or-less symmetrically curved apically. The changed shape in large specimens and species of the *P. rubra*-group has the effect of placing a greater proportion of the radial vein in an axial position, thus enhancing the longitudinal strength of that part of the wing. Since large specimens of other species-groups do not have this structural arrangement, it prompts the question of how they cope with this problem. The answer is that the apex of the radial cell is markedly extended into a fairly symmetrical V-shape: this has the same effect as in the *P. rubra*-group, inasmuch as the proportion of the increased axial element which cannot be gained anterior to the apex (beside the costa) is instead gained posteriorly. This alternative adaptation holds good for the *P. sumptuosa*-group, where the females of most of the species are gigantic; it is also true of very large females of other species-groups, for

example *P. inclyta* Lepeletier, whereas small females of the same species do not display the phenomenon. An important corollary is that this phenomenon confirms the group-character of the *P. rubra*- and *grossa*-groups.

In all large *Pepsis* females (irrespective of group) there is found a concomitant adaptation which strengthens the middle part of the wing: the vein 1 r-m turns from its normal near-transverse position to a strongly axial one; thus the entire anterior half of the wing is strengthened – precisely the part which takes most stress when the wasp is in flight.

Phylogeny

Cladogram for the species-groups



Legenda for cladogram for the species-groups:

1. Male SGP more or less strongly modified; male sternites 5-6 or none with modified hairs; forewing apex pale; small to very large species.
2. Male SGP with strong elevation(s); body with dark hair.
3. Male SGP without lacuna; male SGP with more or less strong median keel; no male sternal hairs modified; female PTC very strong; wings sometimes bright crimson or with silver markings.
4. Female forewing costa/radius junction extremely shallow; female S.2 groove lateral extension strong; male digitus with strong, apical hair-tuft.
5. Male SGP carina with transverse element; female anterior femur not pilose below.
6. Male SGP with blunt median keel and coarse hair; female anterior femur long-pilose below; head strongly swollen.
7. Male SGP with strong, sharp median keel; lateral extension of female S.2 groove absent or very weak.
8. Male SGP with lacuna; forewing costa/radius junction more or less angulate and thickened; male S.5 and 6 hairs modified; digitus "swan-necked"; APT very strong; DTC very coarse; female head strongly constricted behind eyes.
9. Body slender, gaster cylindrical; propodeum tapered apicad; female hind tibia with elongate inner spur; female AS3 very long.
10. Male SGP with tooth, spine or strong keel; forewing apex narrowly pale; gaster dull.

11. Male SGP with low keel; forewing with very broad white apex; gaster metallic blue; antenna short.
12. Body robust; gaster dorsoventrally flattened, T.1 with median groove; propodeum parallel-sided; body with very dense hair.
13. Forewing PPV axial, very long; female clypeus strongly, arcuately emarginate, with strong ridge above emargination; last 3 segments of maxillary palp subequal.
14. Female hind femur with extremely sharp inner, posterior carina; female hind tibia with inner spur extremely long; antenna very short; body hair in the form of strong bristles.
15. Male SGP without strong elevations; body very large, robust; body with abundant golden hair; female SMC3 elongate.
16. Male SGP with polished and pilose areas; with basal tubercle; male paramere with tooth on inner side; female hind tibia with inner spur extremely short, with very strong hair-comb; last segment of female hind tarsus strongly curved; female AS3 long.
17. Female back of head extremely strongly swollen; female clypeus strongly rectangularly emarginate; male sternites 3-4 with modified hairs; female fore femur without hairs; male digitus with apical projection obtuse.

Character reversals.— The groups given in square brackets are those in which the character concerned represents the usual state.

1. At individual level. A female *P. albocincta* (*P. rubra*-group) has the facial hair entirely golden [*P. sumptuosa*- and *deaurata*-groups]. A male *P. cassiope* (*P. brevicornis*-group) has the PPV axial [*P. chiliensis*]. A female *P. cassiope* has abundant silvery-golden body hair [*P. sumptuosa*- and *deaurata*-groups]. This may represent only membership of the *P. plutus* mimicry-group. Two female *P. aquila* (*P. elevata*-group) have the inner spur of the hind tibia extremely short and with a strong hair fringe [*P. sumptuosa*- and *deaurata*-groups]. A female *P. albocincta* (*P. rubra*-group) has the radial vein slightly angulate near the costa [*P. hymenaea*- and *pretiosa*-groups]. A few of the male *P. tricuspidata* (*P. sumptuosa*-group) from Costa Rica and north coastal Colombia have the body hair golden, as in Amazonian specimens of the same group.

2. At population level.

In some western Mexican males of *P. terminata* (*P. elevata*-group) the white apex of the forewing is extremely broad and the SMC3 very short [*P. pretiosa*-group]. In males of the lygarochromic form of *P. grossa* (*P. grossa*-group), the anterior half of T.1 has a short median groove [*P. chiliensis*- and *brevicornis*-groups].

3. At species level.

P. rubra-group (18 species) (see Part 1 of this work): *P. vinipennis*, especially the male, has broad, white wingtips [*P. pretiosa*-group].

P. elevata-group (5 species): in *P. aquila* (variably), *terminata* and *lycaon* the fore wing radius/costa junction is slightly angulate and thickened [*P. hymenaea*-, *pretiosa*-, *chiliensis*- and *brevicornis*-groups]; in *P. lycaon* and *terminata* the male forewing apex is broadly white [*P. pretiosa*-group]; in *P. aquila* and *marginata* the female AS3 is long [*P. hymenaea*- and *pretiosa*-groups]. *P. hymenaea*-group (6 species): in *P. tolteca* the PPV varies to axial [*P. chiliensis*-group]; in *P. stella* and *marthae* the lateral extension of the female S.2 groove is weak [*P. elevata*-group].

P. chiliensis-group (1 species): male SGP lacuna lost (as far as can be ascertained in the thick chitin) [various groups].

P. sumptuosa-group (16 species): female S.2 groove lateral extension weak in *P. aurifex*, *bonplandi* and *hyperion* [*P. elevata*-group]; male digitus "swan-necked" in those males which are united by character 2 in the *P. sumptuosa*-group cladogram; female head strongly constricted behind eyes, and AS3 very long in *P. pulszkyi* and *yucatanii*; male SGP with lacunae in *P. apicata*, *aurifex*, *aurozonata* and *defecta*; male forewing with angulate radius/costa junction in *P. yucatanii* [all in *P. hymenaea*-, *pretiosa*-, *chiliensis*- and *brevicornis*-groups]; male T.1 flattened, with short median groove in *P. hyperion* [*P. chiliensis*- and *brevicornis*-groups]; female AS3 short in *P. defecta* [various groups].

Apart from the more easily definable characters given in the cladogram and above, various species of the *P. sumptuosa*-group show many similarities to species of the four groups united by cladogram character 8. However, none of these characters occur on a group basis, and the strongest characters of the *P. sumptuosa*-group (male SGP shape, female hind tarsal claw position) are not found elsewhere. Therefore it is not feasible to connect the major groups (i.e. characters 3, 8 and 15 in the cladogram) in any other way.

4. At group level.

P. rubra-group (18 species): female subfemoral hair lost. This hair is more or less strongly present in all other groups whose males possess a modified SGP, except for the distantly related *P. deaurata*-group.

P. deaurata-group (2 species): male S.4 and 5 with strongly modified hairs; female subfemoral hair lost (see also *P. rubra*-group above).

These characters are also effectively species-group apomorphies.

The proposed higher linkages between the groups shown in the cladogram must remain tentative until the remaining groups of the genus are treated. However, the associations of the species-pairs with their immediately adjacent groups, and that of the *P. elevata*-group with those of *P. rubra* and *P. grossa*, are sufficiently well supported. The phylogeny thus displays a clear, repeated pattern; this internal consistency is strong circumstantial evidence for its validity.

The modified sternal hairs found in the *P. deaurata*-group do not resemble those found in its sister-group (*P. sumptuosa*-group; or indeed those in any other groups with strongly modified SGP). However, the position of the hairs on the gaster (i.e. the sternites on which they occur) is probably more important than the form they take. In this respect, the hairs of the *P. deaurata*-group resemble those generally found in those groups of the genus treated in Part 3 of this revision. This suggests that these two groups are more closely related to the rest of the genus than are the other groups with strongly modified male SGPs. This, taken together with the differential patterns of incidence of the lacuna in all the groups with modified SGPs, implies that the *P. sumptuosa*-group (and its sister-group) is not so closely related to the *P. hymenaea*- and *chiliensis*-groups (and their sister-groups) as the two latter are to each other.

Distinctness of the species-pairs.— The strong structural distinction in the number of antennal segments between male *P. grossa* and *P. chacoana* places their specific dis-

tinctness beyond doubt; the other species-pairs exhibit characters also considered as specific, even though they are less obvious. This maintains consistency between groups regarded as occupying comparable phylogenetic positions. Further support for this scenario is afforded by Brown & Wilson (1956: 63) who state, "It is entirely possible that by the time an isolated population attains an ascertainable level of character concordance, it has already passed the species line, i.e. the more sharply defined an isolated subspecific population is by conventional standards, the less likely it is to be infraspecific in reality".

From the frequency and distribution of character reversals among the various taxa, it appears that many characters (including group-characters) are really ancestral ones resurrected. Indeed, such is the prevalence of these that one is tempted to wonder whether any true apomorphies exist at all. A possible mechanism is not far to seek. The effects of mutations (apart from neutral ones, not further discussed here) can be either "constructive" or "destructive". A constructive mutation is the addition to, i.e. further complication of, a probably already complicated set of genes controlling any given character. In order for it to survive, it must already be functionally perfect. A destructive mutation is a breakdown in a given gene-set; however, this breakdown need not be fatal provided it takes the form of a reduction to an earlier gene-set. In this latter case, the result will be the production of a probably still-functional ancestral character in the phenotype. Thus there is a considerably greater chance of reversal to an ancestral character, than of a new one appearing. Furthermore, in the single-provisioning Pompilidae, the fact that females must deal with formidable prey as large as themselves places a powerful limitation on change, so that any character innovation in that sex (as opposed to an already tried-and-tested ancestral character) is even less likely to be successful than in a multiple-provisioning wasp not in potential danger from its prey.

Character reversals may manifest at any level: individuals, populations, single or multiple species. Their occurrence is apparently not entirely random; it seems that the closer the relationship, the more frequently resemblances due to reversals appear. For example, both sexes of both *P. decorata* and *roigi* (both members of the *P. rubra*-group, although not particularly closely related within it) display extremely similar and detailed silvery wing-patterns; however, a silvery basal band on the forewing is found in both sexes of *P. equestris* (*P. rubra*-group) but only in the females of *P. terminata* and *P. lycaon* (both *P. elevata*-group).

Biogeography

Basic patterns.— The phylogenetic schemes of the groups so far studied constitute a clear, repeated pattern which consists of major groups each of whose sister-groups are a species-pair. There are three exceptions to this pattern: the *P. elevata*-group lacks a sister-pair; instead, its sister-group is formed by the *P. rubra*- and *grossa*-groups together (sister-groups of each other), suggesting that the *P. elevata*-group originated earlier than the others. The second exception is the *P. chiliensis*-group where a single species occupies the phylogenetic position of a multiple species-group; however, as it inhabits the higher Andes it may well have avoided competition from its close allies by adapting to this extreme habitat after its divergence from the ancestor of its sister-group, thereby avoid-

ing the need to evolve further in response to competition; it may be regarded as a relict. The third exception is the *P. pretiosa*-group with three species rather than a pair, two of them being sympatric. Since these exceptions are each of a different nature, they do not detract from the basic, repeated theme which thus remains sufficiently clear to impart internal consistency – strong evidence for its validity.

The species-pairs.— The constitution and distribution of the major groups (except for *P. chiliensis*) are not particularly unusual within the genus, but their sister-groups (usually pairs of species) do share certain remarkable characteristics. The species of each pair are very closely related to each other and exhibit one or more unusual, sometimes bizarre, apomorphies unique or virtually so within the genus; the pairs also show a striking similarity in their distribution patterns, in which one has a north-west South American, trans-Andean range, while the other has a much more restricted one with a south-eastern bias. These facts point to the ancestors of the species-pairs having shared a common territory, where they remained for a long time before a single event split all the ancestral populations in comparable ways.

Effects of isolation.— Although *Pepsis chiliensis* Lepeletier must be as old as the ancestor of the *P. brevicornis* species-pair (its sister-group), its isolated high-altitude habitat appears to have constrained its evolution in ways other than by competition; most of its unusual characters are extrapolations of those found in other montane species. By definition, isolation (in whatever habitat) implies removal of competition from close relatives; however, intraspecific competition remains operative, as also do climatic effects and genetic drift. We can gain an idea of what results intraspecific competition between males can produce, by reference to Eberhard's (1985) work; he explains runaway evolution in secondary sexual characters by invoking female selection. Even more fascinating is that a comparable phenomenon may exist in plants: for example, Morley (1983: 799) stated that in the variation found in the plant *Mouriri guianensis* (Melastomataceae), "High specialization appears to have accompanied isolation, for reasons that are unclear." Obviously, if plants also develop unusual characters when isolated, they likewise need a mechanism. Marshall (1998) has demonstrated the feasibility of sexual selection in plants, wherein pollen grains from some donors consistently fertilized more ovules than did others. However, the results of sexual selection may be more difficult to assess in plants, where the sexes are combined in the great majority of taxa. A considerable part of any creature's energy budget must be devoted just to survival needs if it is competing with other species – if extinction is a threat, nothing else matters. When a creature is isolated, that energy becomes available for other application. How *Pepsis* might react to climatic change can be gauged by considering the adaptive tendencies found in montane wasps on a world basis: much denser hair cover, yellow markings change to white, and sometimes (e.g. in montane *Pepsis* species) a more slender build. In view of the extreme conditions which these relatively small adaptations cater for, it seems unlikely that the remarkable changes seen in some species-pairs of *Pepsis* are brought about by climatic influences. This leaves intraspecific competition (between males for females and between females for prey) and genetic drift as possible agents for these changes. The extra energy available during isolation, re-applied to accelerate these mechanisms, might well result in exceptional characters – with chance governing what form they take. If conspicuous but relatively minor characters such as the distribution and con-

figuration of male sternal hairs and SGP shape can be modified so easily, how much greater could be the changes possible when more time and energy become available. These unusual characters are sometimes less strongly expressed in one sex, but not always the same one; in any case the differences between sexes are not sufficient to suggest any mating or prey-catching functions in either. Genetic drift seems to offer the best explanation for these unusual characters. Once developed, their owners appear well able to survive when they again meet potential competitors; in no case so far examined is there any suggestion that one of such a pair has become extinct, since these unusual species are always paired. Perhaps all potential competition, except perhaps that between sister-species of a pair (to judge by their ranges, they may be mutually exclusive) has been bypassed. What an ironic paradox, if defence against potential competition were best acquired during the absence of it!

Striking dissimilarities between large groups.— Interesting contrasts result from comparing the distribution patterns of the two largest species-groups of *Pepsis* so far studied, the *P. rubra*- and *sumptuosa*-groups. The former is well represented in North and Central America and has two species endemic to the West Indies, whereas the *P. sumptuosa*-group is absent from North America and the West Indies and is only poorly represented in Central America. A comparable situation exists in southern South America. Since these two groups occupy parallel phylogenetic positions, it is likely that they began to proliferate at about the same time; if so, then the considerable differences between their ranges could most simply be explained by the *P. rubra*-group ancestor being pre-adapted to higher altitudes than that of the *P. sumptuosa*-group, enabling the former to cross the Andes, Guyana Shield and Brazilian highlands from Amazonia much earlier. Indeed, this adaptation may have been acquired before the bifurcation of the ancestors of the main groups from those of their sister-groups; in the *P. grossa*-group, sister of the *P. rubra*-group, *P. grossa* itself is trans-Andean, while *P. chacoana* has achieved a distant southerly range (high latitude being climatically somewhat similar to high altitude). However, in the *P. deaurata*-group, sister of the *P. sumptuosa*-group, both species are restricted to low altitudes; *P. frivaldszkyi*, although trans-Andean, appears to have circumvented the Andes via a north-coastal route rather than crossed them. Unlike its counterpart *P. grossa*, it is nowhere found at even moderate altitudes. Further evidence of the greater degree of altitude adaptation in the *P. rubra*-group, compared with the *P. sumptuosa* group, is that no species of the former has an eastern, i.e. lowland, bias in South America. Indeed, the ranges of all except two species, today restricted to the West Indies, are at some point contiguous with the New World western mountain chain (the Andes northwards). However, the ranges of no less than seven species of the *P. sumptuosa*-group exhibit an eastern (lowland) bias, including some which are exclusively eastern.

The key factor.— If this explanation is correct, then it follows that the degree of altitude adaptation is crucial in determining whether a group can cross a given mountain pass during a given elevation of temperature. Janzen (1967) argued that, as the range of temperatures in the tropics is narrower than that in temperate regions, tropical animals and plants will be less adaptable and therefore have greater difficulty in crossing mountain passes. Finely-tuned altitude adaptation has been demonstrated in plants: Kelly *et al.* (1994) gave a list of 181 very diverse species in an area of Venezuela, of which 28 occupy altitude zones of only 100-500 m, and Burger (1992)

examined altitude distribution zones of species-pairs of plants belonging to diverse families on the Caribbean coast of Costa Rica, where the only variable factor appeared to be altitude (accompanied by a temperature difference of only 3-4°C); some zones were as narrow as 200 m. There have been perhaps fewer studies of altitude zonation in animals because the phenomenon is more difficult to document in mobile creatures.

Comparison with butterflies and proposed explanations.— Adams (1985) reported on studies of pronophiline (Satyridae) butterflies in the Colombian Andes. Although he does not give tables of altitude zonation like those of Burger (1992), the zones are nevertheless comparable with those of plants. Burger suggested that these altitude restrictions are mediated in plants by fungal pathogens which attack seedlings germinating outside the preferred zones. This seems unlikely, but if true, the zonation of the pathogens would then have to be explained. Pendry & Proctor (1996: 241) conclude that "forest differences with altitude are most likely to be related to changes in temperature". They also conclude that soil type and nitrogen supply are of much less importance.

Adams (loc. cit.) offers a theory of speciation which purports to explain how altitudinal zonation patterns form. Although his ideas are interesting and have stimulated further thought on the phenomenon, insufficient consideration is given to the events brought about by the actual onset of individual glacial periods; since this phase would appear to be crucial to the processes involved, the explanation is incomplete and hence unable to account for the phenomenon as a whole. He says, "Recently evolved allopatric species [isolated on mountainsides during interglacials] established contact during glacial periods, by crossing the lowlands between the mountains in which they originated. Rather than face extinction through competition, or alter their ecological niches while remaining sympatric, the pronophilines moved into mutually-exclusive bands of altitude." But how could they? If the previously-isolated taxa were driven down to lowlands by an interglacial, by the same means they would certainly have been held there for a considerable time, and in a highly competitive situation. This must have resulted in wholesale extinctions, especially since the first taxa to be brought together again would have been the most recent isolates, i.e. the closely-related offspring of very few parent populations formerly inhabiting the lowlands. It is unclear how these closely-related and recently-merged taxa would have been able to escape competition by almost immediately ascending the mountains again ("begin to partition the altitude gradient" in his fig. 13.3), as Adams suggests, "because of flexibility in larval foodplants or because their preferred species occupied a wide range of altitudes". If the altitude-adapted butterflies were driven downwards, their foodplants would likewise have been. A new interglacial could certainly not have intervened before most of the competitive interaction was complete; without it, a long time would have had to pass before taxa could re-adapt to the new conditions and begin to ascend the mountains again. Furthermore, the translocated foodplants would also have been brought into competition with each other, with much extinction resulting; this may have worked to augment still further the number of extinctions among the butterflies dependent on them.

Adams then goes on to say, "Since dozens of less closely-related pronophiline species can coexist sympatrically (e.g. 41 between 2,800 and 2,900 m in the Central Cordillera [of Colombia]), niche space at such altitudes cannot be limiting and compe-

tion seems to be the most likely cause of the species' spatial separation." This is difficult to understand because it is precisely extremely specialized niche spaces, delimited and enforced by competition, which enable larger numbers of species to coexist. He also seems to be confusing "niche space" (niches) with physical space. He further states that, "in damaged cloud-forest, species are much more often found out of their normal altitude range, suggesting that parapatry depends on the habitat being intact." Indeed, but surely this merits further explanation: since damaged forest constitutes a different habitat, different species will promptly invade, while the species originally in occupation will retreat; after a probably short transitional period, parapatry will still be maintained, but at new boundaries. Adams also states that the higher the altitude, the greater the number of endemic species; he ascribes this situation to the upper species being more isolated than the lower, which are more likely to spread to other mountain ranges during glacials. However, as already pointed out above, these lower-altitude taxa are also more liable to extinction at such times; again the explanation appears incomplete. It seems more likely that the situation results from additional species repeatedly colonizing from below during inter-glacial cycles, which would cause intense competition at the boundaries between taxa, resulting in a strong upward compression of altitude zones and hence niches; these would tend to accumulate and therefore become narrower higher up, until the upper limits are reached. In summary: according to Adams' explanation, the situation would simply revert to what it was before the glacial cycle, so no new altitude zones would have formed; it is clear that other factors must be involved. The following account, wherein glacial cycles do not in themselves produce altitude zonation, but do so by punctuating a continuously ongoing process, is believed fully to explain the phenomenon.

An alternative explanation.— When *Eucalyptus gunnii* F. Müller seeds were first imported into England from Australia, the introduction was unsuccessful because the resulting seedlings were killed or severely stunted by frost in their first winter. Then seeds from montane populations of the same species were tried; these produced frost-hardy saplings. It is reasonable to conclude from this that, given sufficient time, lowland species will usually produce mutations able to colonise higher altitudes; this process will gradually produce populations at higher levels which are at least physiologically different from the parent population. As adaptation proceeds, more noticeable anatomical differences may also appear, concomitant with increasing genetic differences between the upper and lower altitudinal extremes. The latter (as well as actual distance) will increasingly work to reduce gene-flow between upper and lower limits; for example, any lower-altitude adapted plant genotype will not survive much beyond the germination stage at the upper altitude limits, and much the same principles will apply to animals. This process can be expected to continue until certain limits are reached; these may be imposed by sheer harshness of climate, reduced oxygen concentration, lack of suitable soil in the case of plants, or lack of foodplants or prey in the case of animals. However, it is worth noting here that warm-blooded animals have the great advantage of an internal heating system whose maintenance is more dependent on finding food than on ambient temperature, with considerable consequences for adaptation to colder altitudes and latitudes.

When an ice age intervenes in this situation, populations of all creatures will be driven downwards; but the uppermost fraction of a population will not be driven so

low as the remainder, and may thus remain isolated at moderate altitude. It will accordingly not be subject to the multiple extinction events occurring due to competition between the newly-merged populations of many formerly lower-montane species. When this situation is again changed by the advent of a new interglacial period, the already-adapted lower-montane population (probably no longer accompanied by its parent population) will ascend to higher altitude than previously, since it is already partly adapted; any closely-related lower-level species will compete with it at the new boundary when it too, begins to adapt to altitude; a lower-level species not in competition will in time probably become at least partly sympatric with the next species up. These processes will, of course, affect any number of species from different, compatible groups simultaneously.

Evidence of habitat preferences.— As far as geographical distribution of habitat is concerned, one finds that the lower the latitude, the higher the altitude (also, desertic and montane habitats have much in common climatically at comparable latitudes). This is well demonstrated by taxa such as *Hypodynerus* (Eumenidae) or *Pepsis montezuma* Smith; both taxa are (from Ecuador southwards) increasingly widespread at lower altitudes the further south they occur in the Andes. Despite the fact that these taxa are at different taxonomic levels and have different origins (circum-antarctic and Amazonian respectively) they are nonetheless comparable in this respect. From this, it follows that some populations of the lowland species surviving interglacial-induced competition will move further from the equator to avoid increasing temperatures (as well as competition).

Multiple events.— So far, only the situation pertaining to a single glacial cycle has been considered. Successive repetitions of these processes mediated by further glacial cycles will produce additional zones below, forcing the ones above to move higher

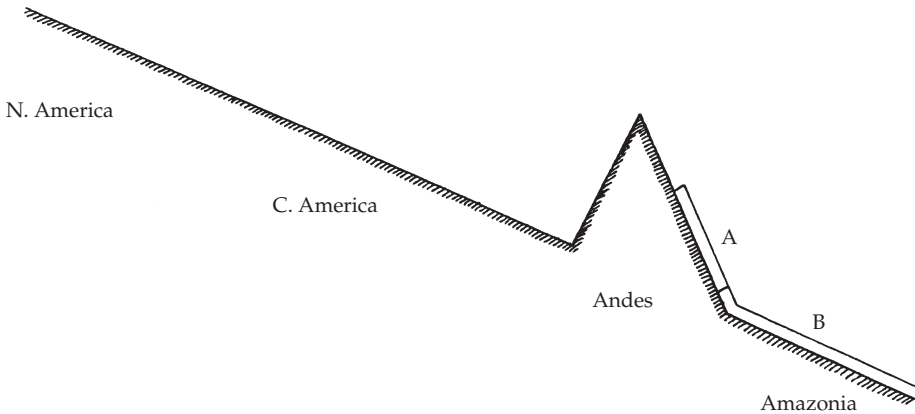


Fig. 1. Glacial period, cold; stable situation with species A adapted to moderate altitudes and B, low. Species A could belong to, for example, the *P. rubra*-group and B to the *P. sumptuosa*-group.

and producing zones whose compression increases with altitude, since there is no escape at the upper limits – barring extinction. This will of course only apply if a glacial cycle is long enough for a certain degree of altitude adaptation to have developed in the lowland population; if not, the situation will revert to its last interglacial condition. In those cases where new zones are formed, the differences in degree of relationship between the closely-related taxa involved may be explained by the irregularity of the interruptions, and also to some extent by the topography; see for example Funk & Brooks (1990: 27), in which the authors showed a remarkable degree of coincidence between a cladogram of tepui/river topography in Venezuela and one of the plant genus *Stenopadus* (Asteraceae). The situation where an interglacial period is warm enough to enable a population to cross a mountain barrier to previously-inaccessible territory will differ from the foregoing in the following ways, using Mesoamerica as an example.

In the following figures, the shaded land surface represents latitude and altitude combined; the blocks, populations of different taxa. Single arrows represent extension of range; opposed arrows, competition.

The present-day situation.— The three oldest species of the *P. rubra*-group found north of the Andes, inhabit the USA and Mexican mountains and are sufficiently distantly related (i.e. not in competition) that they can live sympatrically; but each of the younger, Central American, species on the same branch of the cladogram is allopatric, or at least parapatric, to the others; the last is true also of all the species on the other branch of the cladogram, but species on opposite branches are sometimes sympatric. In short, degree of compatibility is related to taxonomic distance as well as to altitudinal and latitudinal adaptation.

In the above scenario, much extinction must have occurred during the fluctuations

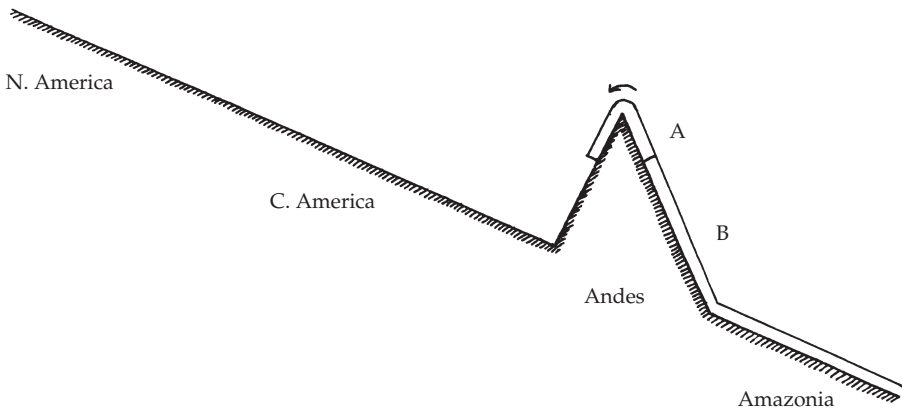


Fig. 2. Interglacial period, warm; in maintaining the temperature regimes to which they are adapted, both species elevate their altitude zones, but only species A sufficiently to cross an Andean pass northwards towards Central America. Only an exceptionally warm interglacial would allow species B to do so as well; for the sake of simplicity, it does not happen in this example, but similar principles would apply; one difference would be that at times of maximum warmth, species A would temporarily colonize altitudes higher than those necessary for it to cross the mountains.

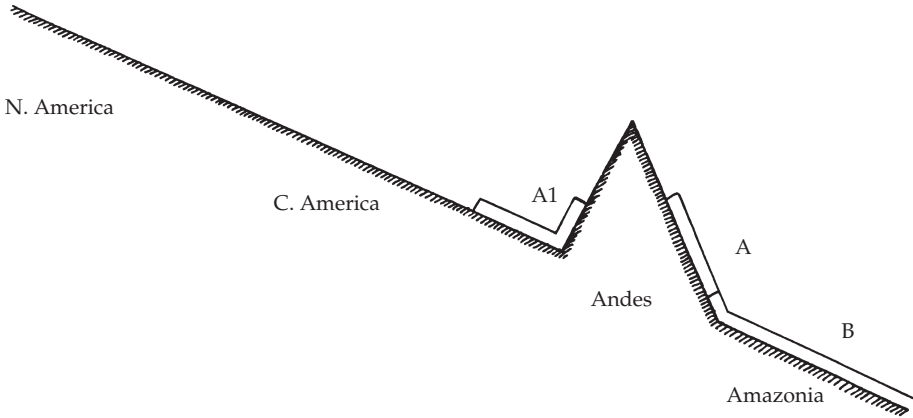


Fig. 3. Glacial; the northern fraction of A (A1) is isolated; if the new lowland habitat in Central America is sufficiently similar to that of adjacent Amazonia, little adaptation will be necessary to avoid extinction during the onset of renewed glaciation; it is simply that this new, suitable habitat was previously inaccessible. Furthermore, the uppermost fraction of a population, already at least partially altitude-adapted, will have been the first (possibly the only one) to cross the Andes, and hence stand the best chance of adapting to lower temperatures, whether these result from higher altitude or increasing latitude. In time, gradually increasing adaptation will enable the population to spread northwards. The fraction remaining south of the Andes, although not subject to these conditions, also begins to evolve independently, partly due to genetic drift. Species B simply returns to its former situation.

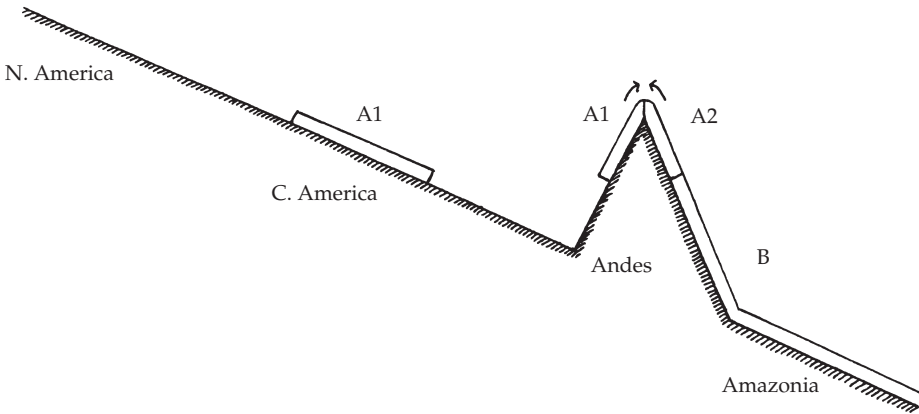


Fig. 4. Interglacial; the northern fraction of A (A1) is now further isolated, adapting to both increased altitude and latitude. (Some of the old species of *Pepsis rubra*-group found in the USA, e.g. *P. pallidolimbata* Lucas, have ranges extending into Mexico; the further south the records, the higher the altitude, until the limits of heat-tolerance are reached in the highest peaks of southern Mexico.) However, the southern fraction now meets a new Amazonian taxon (A2) evolved from the ancestor of the two; whatever the latter's status, they may compete because of their relatively recent divergence. Perhaps the Amazonian taxon is more likely to extinguish the other in view of its more recent origin and possibly greater vigour; it is assumed to be the victor in this example.

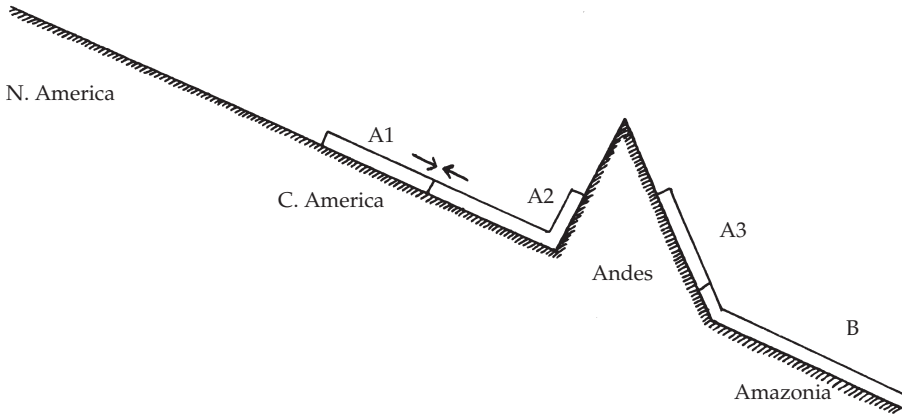


Fig. 5. Glacial; the survivor (A2) of this competition meets the original northern fraction, but by now the latter is better adapted to higher altitude and latitude than the newcomer; this will limit the competition, resulting in some extinction of individuals only at the newly-formed boundary.

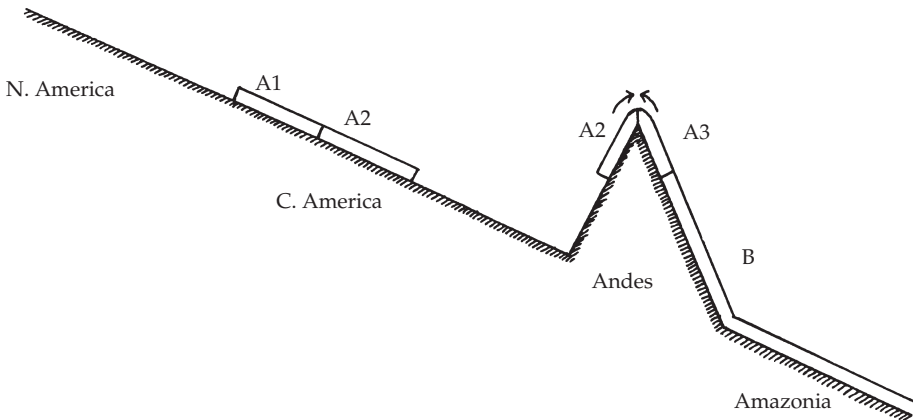


Fig. 6. Interglacial; this is basically a repeat of the situation in fig. 4, except that now there are two species which have "come to an agreement" in the extreme north.

of climatic regimes, because the taxa constituting successive waves of invasion, being more-or-less closely related, would often have been in close competition with each other; yet the number of glacial cycles must have limited the number of such vicariance events which occurred overall. In the above scenario extinction occurs mainly at lower levels during glacial periods, but at higher ones during interglacials. The repetition of such a succession of events can be expected to produce a more-or-less distinct latitudinal banding, modified mainly by higher ground; furthermore, the older the species, the higher the altitude and/or latitude it is likely to inhabit; this is indeed the situation we see today.

The southern counterpart.— Although a comparable situation is present south

of the Brazilian Highlands, it is more difficult to discern because of the vastly greater width of the land-mass and its more varied topography. A few of the oldest species which evidently spread at an early stage of their respective groups' history, for example *P. caridei* Brèthes (*P. rubra*-group), *limbata* Guérin and *thoreyi* Dahlbom (both *P. montezuma*-group), managed to cross a low pass in the southern Andes into Chile. The fact that there is today an especially high degree of endemism (frequently involving the oldest extant species of their respective species-groups) south-east of the Brazilian Highlands is most likely due to the area being easiest to colonize from Amazonia (either via a coastal route or over the rather low Highlands) with only moderate interglacial warming – a very early vicariance event. However, it is less easy to understand just how the endemism is maintained in this case; it may depend on climatic factors or competition from species better adapted to surrounding areas.

Adaptive mechanism.— It is possible that the temperature-sensitivity of enzyme systems may be responsible for this finely-tuned zonation. Somero (1978) stated that "...[two of four] aspects of enzyme structure may be destabilized by high and low [italics mine] extremes of temperature." Other aspects are affected only by high temperatures. Also, "many enzymes ... are incorporated into multi-enzyme pathways or are components of highly integrated physiological systems". He further believed that, "... the effects of temperature on enzyme structure and function may be instrumental in establishing the thermal optima and tolerance limits of metabolic function and, thereby, of the organism itself". Somero also expressed the hope that, "this discussion will help to provide a bridge between the interesting new discoveries of enzyme chemists and interests of ecologists, systematists, and zoogeographers". Hochachka & Somero (1984: 356) added that, "... very small temperature changes have large effects on reaction rates ... the mechanisms responsible for this relationship are fundamental".

Large individuals on islands

The population of *Pepsis terminata* in the West Indies exhibits a much greater average body size than anywhere else in its very wide distributional range. The phenomenon of large body size in island populations has been discussed by Carlquist (1974: 603-607) and Williamson (1981: 48-50), among others. (Use of the term "island gigantism" is avoided here because it may comprise several different phenomena, *teste* Paul Eggleton, pers. comm.)

Table 1. Relative body lengths of mainland and West Indian populations of *Pepsis terminata* Dahlbom.

	Males			Females		
	Mean	Range	Sample size	Mean	Range	Sample size
Mainland	18	12-23	47	24	17-30	29
West Indies	24	15-29	7	30	20-40	11

This is one of only two species which are found commonly both in the West Indies and on the neotropical mainland. The other, *P. grossa*, is the same size in the West Indies as it is on the mainland. However, since it is already a large species on the mainland, this may militate against its becoming larger still in the West Indies. How-

ever, it is possible to draw a comparison between some West Indian species and their mainland counterparts; for example, *P. rubra* (endemic to the West Indies) with *P. mexicana* or *P. equestris* (occupying allopatric ranges on the mainland). All three are very closely-related small species but there is no appreciable size difference between them. No size differences are apparent in any other species-group where those include closely-related West Indian and mainland species; it is possible that *P. terminata* reached the West Indies before any other species and therefore had more time in which to acquire unusual characteristics (see discussion of phylogeny of the *P. elevata*-group).

The mimicry-groups in *Pepsis*

Many of the species in this large genus belong to groups of distinctive colour mimics, in which they form (at least in the female sex) probably the strongest Müllerian element.

Simple black-winged, amber-winged and transitional specimens (sometimes forming geographical clines) are not treated as belonging to distinct mimicry-groups because they are so variable. This kind of variation is correlated with the degree of humidity experienced by the late pupal stage (MacLean et al., 1978) and is more related to changeable local environmental conditions than to major geographical region (although the two may coincide). Such variations may form several loose mimicry complexes which are difficult to define in terms of phenotype characterization and distributional range; they are therefore treated only in the main keys to species. However, like the more distinct mimicry-groups, they form part of larger groups which include many different insects and other creatures including Batesian mimics.

The four clearly-defined mimicry-groups recognized are named the *Pepsis atripennis*-, *completa*-, *discolor*- and *plutus*-groups; the two latter groups are discussed here because they include members of the *P. sumptuosa*-group. They differ in character to the extent that the *P. discolor* mimicry-group includes species of diverse phylogeny and size, whereas most of the *P. plutus*-group is made up of species belonging to the *P. sumptuosa*-(taxonomic)group and includes mainly very large species. The *P. atripennis*- and *completa*-groups comprise small species with yellow to off-white, broad, transverse wing-bands; they are comprised of members of species-groups which will be treated in Part 3 of this work.

Many species or sexes belonging to the mimicry-groups also occur outside (and occasionally also within) the group-area in a different colour form. Curiously, transitional forms are common in some species towards the periphery of the mimicry area, whereas in others they are very rare. Sometimes only the males of a species belong to a distinct mimicry-group (as defined here); this applies especially to the *P. plutus* mimicry-group.

Within the genus *Pepsis*, some species form the only known representative of a particular mimicry-group in a particular area; however, such groups usually include many taxa of insects, including other pompilid genera such as a female ?*Anacyphononyx* Haupt, 1950 (Hymenoptera: Pompilidae) (det. M.C. Day) from Paraguay (TMB) which belongs to the *P. completa* mimicry-group.

In those species which are poorly represented in collections, both sexes have been

included in the following keys even though one sex may not so far be known to occur in the colour-form concerned; the status of all forms is given before the keys.

The *Pepsis discolor* mimicry-group

The colour pattern of this group is less well defined than in others. The whole insect, except sometimes part of the antenna, has a more or less dark greenish tint. The hindwing is usually at least slightly paler than the forewing; the bases of both are often much paler than the rest of the wings; the forewing apex is sometimes also pale, but less so than the base.

The following species are included: *P. australis* Saussure, 1868: some specimens of both sexes; *P. decorata* Perty, 1833: all specimens of both sexes; *P. defecta* Taschenberg, 1869: all specimens of both sexes; *P. discolor* Taschenberg, 1869: all specimens of both sexes; *P. flavescens* Lucas, 1895: females only; *P. foxi* Lucas, 1897: all specimens of both sexes; *P. minarum* Brèthes, 1914: all specimens of both sexes; *P. roigi* Vardy, 2000: all specimens of both sexes; *P. smaragdina* Dahlbom, 1843: all specimens of both sexes.

The species of this group are phylogenetically diverse, and hence more varied in size than those of any other mimicry-group. It includes some of the largest and smallest species in the genus.

Compared with other mimicry-groups, the *P. discolor*-group occupies a relatively small area, centred on south-eastern Brazil. It is better defined than other groups, in the sense that all specimens of most species concerned belong to the mimicry-group when they occur within the area, but only differently coloured individuals occur outside. The main exception is *P. australis*, which occurs in sharply different colour-forms; this and *P. minarum* are the only species endemic to the area.

Since this group is thus defined by geographical region rather than by the ranges of its constituent species (as opposed to other mimicry-groups), climatic and topographic influences may play a greater part in its formation and maintenance than in other groups.

Key to males of the *Pepsis discolor* mimicry-group

1. SGP with raised pre-apical carina
 *P. foxi*, *decorata* and *P. roigi* of *P. rubra*-group (Part 1)
- SGP without raised pre-apical carina 2
2. SGP with distinctly separated polished and pilose areas (figs 140-141)
 *P. defecta* p. 108
- SGP entirely covered with hairs 3
3. Sternites 2, 3, 4, and to a lesser extent 5, with dense hairs (figs 7-12)
 *P. australis* Saussure (Part 3)
- Only sternite 4 with dense hairs 4
4. Claws, especially hind ones, sharply bent at the middle; small species, BL 19-21
 (figs 13-17) *P. minarum* Brèthes (Part 3)
- Claws evenly curved; species often larger 5
5. S4 with lateral hairs long, forming a narrow brush, the tips of those of opposite
 sides meeting in the middle, altogether forming a distinct arc; a few shorter hairs

- inserted centrally (figs 18-23) *P. smaragdina* Dahlbom (Part 3)
- S.4 hairs all long, slightly curved and forming a single, broad patch not differentiated into brushes (figs 24-29) *P. discolor* Taschenberg (Part 3)

Key to females of the *Pepsis discolor* mimicry-group

1. Radial vein meeting costa at a very shallow angle; PTC strong
..... *P. foxi*, *decorata* and *P. roigi* of *P. rubra*-group (see Part 1)
- Radial vein meeting costa at a steep angle; PTC often weak 2
2. Hindleg with claw-tooth placed 0.20-0.25 distance from apex of claw (in middle leg slightly more), the overlying setae bent around it (cf. figs 207, 209); last tarsal segment strongly curved; inner spur of hindleg short, robust, about equal to outer and reaching to 0.25-0.3 basitarsus length; large species (BL 32-55); antenna often with orange or brown colour towards apex (map fig. 243) *P. defecta* p. 108
- All claw-teeth placed further from apex, the overlying setae straight (cf. fig. 213); last tarsal segment almost straight; inner spur of hindleg various; medium to small species; antenna with or without paler markings 3
3. Small species (BL 23-27); gaster dorsoventally flattened, tergites 2-5 emarginate behind, all tergites usually highly polished due to early abrasion; antenna sometimes paler apicad *P. australis* Saussure (Part 3)
- Size various; gaster normal (almost circular in cross-section), tergites not emarginate behind, not polished; antenna black 4
4. Inner spur of hindleg very short and robust, at most 1.2 times as long as outer and reaching to only 0.2-0.25 basitarsus length; AS3 with bristles on inner side; small species (BL 20-25) *P. minarum* Brèthes (Part 3)
- Inner spur of hindleg markedly longer than outer, reaching further along basitarsus; AS3 without bristles; medium species 5
5. Propodeal hairs long, about as long as PST + 1/2 MPN together
..... *P. flavescens* Lucas (Part 3)
- Propodeal hairs short, equal to or slightly shorter than PST length 6
6. Antenna usually with some apical segments orange; hindwing less infuscate but the same basic colour as the fore wing; smaller species, BL 18-29
..... *P. smaragdina* Dahlbom (Part 3)
- Antenna entirely black; hindwing more contrasting, yellow-amber; larger species, BL 22-37 *P. discolor* Taschenberg (Part 3)

The *Pepsis plutus* mimicry-group

The species belonging to this group are characterized by usually golden (sometimes silver-white or ashy-white) body pubescence, usually dense and often forming well-defined patterns.

The following *Pepsis* species are included (*P. asteria* Mocsáry, 1894 and *P. optimatis* Smith, 1873 are not closely related to the other species and will be more fully treated in Part 3 of this work): *P. aurifex* Smith: males only, all specimens; *P. apicata* Taschenberg: males only, Amazon basin specimens, becoming darker southwards; *P. asteria* Mocsáry: both sexes, most specimens in western Amazon basin (but mimicry-group

colours weak and variable), no mimicry-group colours in specimens west of the Andes; *P. aurozonata* Smith: both sexes, all specimens; *P. bonplandi* Brèthes: both sexes, northern specimens (eastern Brazil), becoming totally dark in north-eastern Argentina (Misiones); *P. cassiope* Mocsáry: probably both sexes, but no males known from western Ecuador, only one female specimen known from there; *P. deaurata* Mocsáry: both sexes, all specimens; *P. ecuadorae* spec. nov.: at least females (male unknown), all specimens; *P. onorei* spec. nov.: both sexes, all specimens; *P. optimatis* Smith: both sexes, all specimens in Amazon basin, becoming darker southwards; *P. plutus* Erichson: both sexes, all specimens; *P. pulszkyi* Mocsáry: males only, all specimens; *P. riopretensis* spec. nov.: males only, all specimens; *P. sumptuosa* Smith: females only, all specimens; *P. tricuspidata* Gribodo (Central American species): a minority of males only.

This mimicry-group largely coincides with the taxonomic group of *P. sumptuosa*; the only species which do not belong to this latter group are *P. deaurata* (*P. sumptuosa* sister-group), *P. cassiope* (*P. brevicornis*-group), *P. optimatis* and *asteria* (both *P. inclytata*-group). In no other mimicry-group of this genus is there such a close correlation with a taxonomic group; all the species included in it are medium to very large.

The range of the group is basically Amazonian including the Guianas, but also includes the higher Andes of Colombia (one species); it also occurs in the western watershed of the Andes in Colombia and Ecuador but here the pubescence is transmuted to silver- or ash-white. It is especially interesting that a minority of males (7 of 24 seen) of *P. tricuspidata*, an essentially Central American species, display evident character-reversal to the typical Amazonian colour; this strongly suggests a fairly recent Amazonian origin for this species (no similarly-coloured specimens of any other species have been seen from Central America). In the Amazon basin and the Guianas, the hair colour is at its brightest; with increasing southerly latitude, the colour becomes gradually darker on average, i.e. the proportion of totally dark specimens increases southwards, and the dark colour is more extensive in more specimens. Many specimens with intermediate colour (e.g. *P. apicata*) are found in the Brazilian highlands, especially the Mato Grosso, and Bolivia. In northern Paraguay, at least the males of *P. optimatis* (one of the few species of this mimicry-group to reach so far south; no females have been seen from there so far) have an entirely black body. Within the *P. sumptuosa*-group, *P. bonplandi* is exceptional in that its distributional range does not extend as far north as the Amazon. In accordance with this, its body-hairs are never as brightly coloured as those of typical members of the group; nevertheless, they become darker southwards, as in *P. apicata* and *optimatis*, becoming entirely black in northeastern Argentina (Misiones province). Some west-Amazonian specimens of the trans-Andean species *P. asteria* belong to this group (usually indistinctly); the west-Andean watershed specimens do not. Only a single specimen of *P. cassiope* (a female from the west-Andean watershed of Ecuador) has been seen which belongs to this group. It matches the local version of the mimicry-group (represented by two species of the *P. sumptuosa*-group) very well; the colour of *P. cassiope* is extremely variable in any case.

One of the most remarkable phenomena in this mimicry-group is the existence of three different categories in the *P. sumptuosa*-group species which occur in Amazonia (including the Guianas): (1) non-membership of the *P. plutus* mimicry-group (represented by *P. toppini* only), (2) membership of one sex (the male in most species) and (3) membership of both sexes (six species). In the other mimicry-groups (which are

not centred on Amazonia), and in other species-groups, one or both sexes can be members of two different colour-groups in the same area; this is unknown in the *P. sumptuosa*-group. Evans (1968, 1969) discussed category (2) in relation to the pompilid genera *Chirodamus* Haliday, 1836 and *Austrochares* Banks, 1947; he realised that previously unassociated sexes, until then placed in different genera, were congeneric. He believed that the two sexes belong to different mimicry-groups because of their differing behaviour: the males (non-stinging) fly mainly among vegetation (well above ground-level) in the company of social wasps (whose appearance they strongly resemble) and thus constitute Batesian mimics, whereas the females spend most of their time hunting for spiders on the ground and are at the centre of Müllerian mimicry-groups frequenting that habitat. However, he also stated (1968: 9) that not all examples of sexual dimorphism in Pompilidae follow this pattern (e.g. category 3 above); he believed that these belong to mimicry-groups based on different criteria [perhaps both sexes fly above the ground and the females hunt arboreal spiders?]. Unfortunately, no records are available for these species.

However, a female *Pepsis xanthocera* Dahlbom, 1843 (to be treated in Part 3) in MIZAM has a spider, *Avicularia* species, pinned with it. This is the first record of a *Pepsis* species preying on an arboreal spider, and as such poses interesting questions. If a *Pepsis* female stings a terrestrial spider, it jumps back to avoid the spider's attack while waiting for the venom to work; only when it is safe to do so does the wasp drag the spider into a burrow for storage, oviposition etc. It is difficult to imagine this being successful in a tree, where the spider could easily fall to the ground and be lost. Clyne (1999: 62) relates how in Australia the cicada-killer wasp [*Sphecius pectoralis* (Smith, 1856); see Bohart & Menke (1976: 510)] "seeks out a cicada in a tree and paralyzes it with her sting. Dropping with it from the tree she drags it into her burrow..." This technique is possible because the cicada poses no threat to the wasp, but a tarantula sometimes kills a wasp during the latter's attempt to sting it. Observations are needed to establish how *Pepsis* wasps secure arboreal prey. The lack of observations on these species doubtless reflects the greater difficulty in studying them, compared with observations on terrestrial species; even these are only infrequently observed with prey.

It is interesting to note that intraspecific habitat division need not be correlated with mimicry-groups; for example, Walters (1991: 507) stated that "Although both sexes ... of the red-cockaded woodpecker, *Picoides borealis* (Vieillot, 1809) ... forage on the upper trunk ... of the longleaf pine, *Pinus palustris* P. Miller, 1768, only females regularly forage low on the trunk, and only males forage regularly on the twigs and limbs".

Key to males of the *P. plutus* mimicry-group

1. Fourth sternite, or fourth and fifth sternites, with strongly modified hairs 2
 - If sternites with modified hairs, they are only on S.5 & 6 3
2. Head in dorsal view with temple extremely strongly swollen; S.4 & 5 with strongly modified, almost identical hairs (Panamá, Guianas, middle to lower Amazon) (figs 47-51, 247) *P. deaurata* p. 127
 - Head much less swollen; S.5 with few modified hairs, very different from those on S.4 12

3. SGP strongly curved or bent downwards 4
 - SGP more or less in one plane 5
4. SGP very elongate, strap-like, and strongly curved down (Amazon basin, French Guiana) (figs 106-109, 240) *P. aurozonata* p. 97
 - SGP not very elongate, strongly bent down about the middle, strongly narrowed sub-basally (Lower Amazon) (figs 110-113, 241) *P. aurifex* p. 100
5. SGP with a strong, sharp lateral tooth at about mid-length, thence sharply constricted to a narrow, rounded apex (Amazon basin, Guianas) (figs 171-174, 243) *P. plutus* p. 102
 - If the SGP has a lateral tooth, it is rounded, and the SGP apex is distinctly bifid .. 6
6. SGP elongate, parallel-sided or slightly narrowed apicad 13
 - If the SGP is parallel-sided for much of its length, it is either very short (quadrate or wider), or constricted basally, with a strongly transverse tubercle (almost a carina), and lacks lacunae; last tergites of gaster and hindlegs without strongly contrasting, bright colours 7
7. SGP extremely short, quadrate, its apex truncate, forming a thin, sharp lamella, polished and without long hairs (eastern Brazil to north-east Argentina) (figs 121-123, 245) *P. bonplandi* p. 123
 - SGP more elongate and also otherwise of different shape, its apex with abundant, more-or-less long hairs 8
8. SGP apex evenly rounded, strongly constricted behind; pale golden pubescence extending back to gastral T.1 only (figs 175-177, 241) *P. riopretensis* p. 101
 - SGP apex more-or-less deeply bifid; if the sides are constricted, then they are parallel for most of their length 9
9. SGP gradually expanded from the base, then gradually curved inwards to form the apex (Central America and Caribbean coast of Colombia) (figs 150-152, 243) *P. tricuspidata* p.109
 - SGP parallel-sided for part of its length, strongly constricted before and after that part 10
10. Gaster with golden hair only on T.1, the rest black; parallel parts of SGP sides well delimited distally by a strongly raised, almost square, tooth (Colombian Andes) (figs 153-155, 245) *P. sumptuosa* p. 116
 - Gaster with golden hair on all tergites except the last; parallel parts of SGP sides poorly delimited distally, only slightly raised in a very weak angle 11
11. SGP with boundary between polished and pilose areas sharply defined; paramere with apical half parallel-sided, and apex broadly rounded; SGP gradually narrowed to the apex (Amazon basin, Guianas, eastern Brazil) (figs 159-161, 244) *P. pulszkyi* p. 114
 - SGP with boundary between polished and pilose areas indistinct; paramere with apical half gradually narrowed to the bluntly-pointed apex; SGP strongly narrowed to the apex (western watershed of Andes in Colombia and Ecuador) (figs 156-158, 244) *P. onorei* p. 111
12. Body very robust; propodeal dorsum virtually quadrate, with the PPT very strong, tooth-like; the longer hairs of S.4 forming dense, lateral brushes (Lower Amazon to northern Paraguay) (figs 30-35) *P. optimatis* Smith (Part 3)
 - Body elongate, slender; propodeal dorsum longer than quadrate, PPT only a raised

- ridge; the longer hairs of S.4 very sparse, extending more or less evenly across the segment (western Amazon basin) (figs 36-41) *P. asteria* Mocsáry (Part 3)
- 13. Modified hairs of S.5 & 6 dense, their apices strongly curved, strongly differing from those of previous segments; SGP with a virtually round basal tubercle, on either side of which is a lacuna clearly visible (especially by transmitted light) through the translucent amber colour, with a sharply-defined, depressed area beginning at the tubercle and expanding apicad, covered with long, strongly-curved hairs, while the remaining area is highly polished; last 2 gastral tergites entirely covered with dense, bright orange-golden hair; hind tibia and tarsi usually bright red-brown (east of the Andes from the Amazon mainstream to northern Argentina) (figs 135, 139, 242) *P. apicata* p. 105
- Modified hairs of S.5 & 6 sparse, gradually curved for most of their length, not very different from the unmodified hairs on previous segments; SGP with a more-or-less Y-shaped basal tubercle whose central arm points apicad and extends into a depressed, oval, pilose area, with a lacuna on either side, difficult to see through the dark colour, the hairs of the apical, depressed area only moderately long and only slightly curved, the surface of the remaining area somewhat irregular; last 2 gastral tergites, hind tibia and tarsi without strongly contrasting colours (west of the Andes in Ecuador) (figs 131-134, 239) *P. cassiope* p. 92

Key to females of the *P. plutus* mimicry-group

- 1. Back of head extremely strongly swollen; clypeus with a more-or-less rectangular emargination, ending in a strong, lateral tooth; PTC weak or absent; S.2 groove with very strong lateral extension; hind tarsus with last joint straight (Panamá, Guianas, mid to lower Amazon) (cf. figs 178-179; 247) *P. deaurata* p. 127
- Back of head moderately or not swollen; clypeus shallowly, arcuately emarginate, not ending in a lateral tooth; PTC usually present; lateral extensions of S.2 groove and last joint of hind tarsus variable 2
- 2. Inner spur of hind tibia about half as long as basitarsus; posterior edge of middle and hind femora with knife-sharp carina (west of Andes in Ecuador) (fig. 237) *P. cassiope* p. 92
- Inner spur of hind tibia much shorter; posterior edge of middle and hind femora less sharply, if at all, carinate 3
- 3. Gaster with weak or no golden, silver or ash-coloured hair 4
- Bright golden, silver or ash-coloured hair forming patterns on gaster as well as on rest of body 7
- 4. Propodeum transverse, its dorsal length shorter than distance between the tips of the PPTs, which are peg-like (virtually parallel-sided); head dorsally, mesoscutum, centre of scutellum and gaster with strong, deep blue sheen; last joint of hind tarsus straight; MPN with only fine carinae (Lower Amazon to northern Paraguay) *P. optimatis* Smith (Part 3)
- Propodeum tapered apicad, its dorsal length equal to or longer than distance between tips of PPTs, which are tooth-like (tapered apicad), or ridge-like; body parts black, sometimes with very weak blue or violet sheen; last joint of hind tarsus more or less distinctly curved; MPN usually with coarse carinae 5

5. Head and thorax (including propodeum) with bright golden pubescence forming strong patterns, in particular a virtually square patch on the central mesoscutum; very large species, BL 34-56 (Colombian Andes) (fig. 245) *P. sumptuosa* p. 116
 - Body with dull, yellow-brown pubescence not forming distinct patterns; smaller species, BL 25-42 6
6. Inner spur of hind tibia extremely short, no longer than maximum width of tibial apex, and about as long as outer spur; golden hair on postscutellum to propodeum (eastern Brazil to north-east Argentina) (fig. 245) .. *P. bonplandi* p. 123
 - Inner spur of hind tibia distinctly longer than maximum width of tibial apex and longer than outer spur; golden hair on all main body parts except gaster (western Amazon basin) *P. asteria* Mocsáry (Part 3)
7. Pubescence patterns silvery, ash-coloured or yellowish (west of the Andes) 8
 - Pubescence patterns bright golden (east of the Andes, including the Guianas) (map figs 240, 243) *P. aurozonata* and *P. plutus* p. 100
..... (see table under *P. aurozonata*)
8. Hind claw with tooth about 2/3 from base, setae straight where they pass over it; PTC rather narrow, almost tooth-like (western watershed of Andes in Colombia and Ecuador) (figs 213, 244) *P. onorei* p. 111
 - Hind claw with tooth about 3/4 from base, setae distinctly sinuate where they pass over it; PTC very wide, a transverse carina (coastal Ecuador) (figs 207, 243)
..... *P. ecuadorae* p. 111

General keys to species

Key to males

(continued from "Other groups" in Part 1 key)

Note.— The male of *P. ecuadorae* is unknown.

1. S.4 usually without strongly modified hairs. If any modified hairs are present on the gaster, they are usually on S.5 and 6 (if also on S.4, usually weakly); occasionally, entire body except T.2 onwards with long, dense, black hair; SGP usually strongly modified, either with a median tooth or keel (occasionally a pair), or basal tubercle or carina (most often transverse); the surface is commonly divided into polished and (usually long-)pilose areas; often more-or-less abruptly expanded or constricted anywhere along lateral margin. If strongly modified hairs are present on S.4 and 5, then the temples are very strongly swollen (fig. 48) and the body large (BL 25-35). Rarely, the SGP is entirely polished and with coarse but rather sparse hairs; or the SGP has a basal, raised triangle narrowing apicad to a weak keel (in one such species all the sternites except the anterior part of 2 have very dense, long hair); in all these cases except the last, the sternal hairs are as described 2
 - S.4 commonly with strongly modified hairs, often those of S.5 also modified but usually less strongly so and differently; SGP usually flat and strap-shaped, sometimes variously broadened or narrowed, occasionally transversely convex; usually entirely covered with fine, inconspicuous hair (sometimes with a longer apical fringe). If modified hairs are on S.3 & 4; or 5 more strongly than 4; or (rarely) very

- strong on 5 alone, then the SGP is as described; if the SGP is expanded apicad, with a very long apical hair fringe, and partly polished, then the sternal hairs are as described) other groups (Part 3)
2. Entire body including T1 and all sternites covered by long, dense, black hair; wings black; antenna partly orange; PPV of forewing (figs 45,46) usually exceptionally long; SGP & digitus figs 42-44. Map fig. 237 *P. chiliensis* p. 88
 - Fewer sternites with long hair; other characters often disagree 3
 3. Gaster with very strongly modified hairs on S.4 & 5, also very weakly on S.3 (fig. 47); head with temples strongly swollen (fig. 48). SGP & digitus figs. 49-51; (*P. deaurata*-group) 4
 - S.4 with at most weakly modified hairs; head at most only moderately swollen 5
 4. Body with abundant bright golden hair forming strong patterns; French Guiana, entire Amazon mainstream, and all its western headwaters from southern Colombia to central Perú; map fig. 247 *P. deaurata* p. 127
 - Body with pubescence at most dull yellow-violet, not forming patterns; Panamá, entire Caribbean coast of South America, Amazon mainstream west to Fonte Boa at 66°W. Map fig. 247 *P. frivaldszkyi* p. 128
 5. SGP (figs 52,53; 56,57) very thick, with a pair of longitudinal carinae converging apicad to form a U- or V-shape; insect entirely black except for amber wings; PPV variable in length; paramere & digitus figs 54, 55, 58, 59. Peruvian Andes. Map fig. 238 *P. tolteca* p. 78
 - SGP thinner, with at most a single longitudinal carina 6
 6. Apex of forewing broadly white (including at least a small part of SMC3); gaster deep metallic blue to violet; SGP virtually flat, without strong median carina; Panamá southwards; (*P. pretiosa*-group) (see also *P. vinipennis* in Part 1) 7
 - If apex of forewing is broadly white and species is found from Mexico to Nicaragua then the gaster is less bright, the SGP has a sharp basal point forming the beginning of a median carina, and its apex is strongly upcurved 9
 7. SMC3 very short, its anterior vein not longer than 2/3 the length of the proximal; APT weak, at most hemispherical; south-east Brazil 8
 - SMC3 of usual shape, its anterior vein at least slightly longer than the proximal; APT extremely strong and projecting; SGP & digitus figs 60-62; rare in south-east Brazil but more frequent northwards. Map fig. 239 *P. egregia* p. 84
 8. Small species, BL 15-20; SGP (figs 63,64) with apical half more shallowly rounded transversely than basal half, slightly expanded laterally; paramere broadly, obliquely truncate. Digitus fig. 65. Known only from a small area of southeast Brazil; map fig. 239 *P. friburgensis* p. 85
 - Large species, BL (17-)24-31; SGP (figs 66, 67) with apical half moderately expanded laterally, flattened and slightly concave; paramere narrowly, squarely truncate. Digitus fig. 68. Found along most of the southeastern coast of Brazil; a single record from inland. Map fig. 239 *P. pretiosa* p. 87
 9. SGP elongate, gradually narrowed apicad; with a strong but not sharp median carina, obsolescent towards the strongly upcurved apex; obscured by coarse, long, dense hairs, narrowly at the base, broadening apicad to cover the entire width, remainder of surface shining; (*P. grossa*-group) 10
 - If the SGP is narrowed apicad and has a strong median carina, then it does not

have dense hair covering an area becoming wider apicad	11
10. With 12 antennal segments; wings black except sometimes in the USA and northern Perú; forewing with a more or less distinct white apex; SGP & genitalia figs 69-72. USA to northern Perú and Guianas. Map fig. 234	<i>P. grossa</i> p. 58
- With 13 antennal segments; wings amber to orange with a dark apical band; SGP (figs 73,74) slightly expanded at apex. Paramere fig. 75. Eastern Bolivia southwards, map fig. 234	<i>P. chacoana</i> p. 57
11. SGP with a strong, central tooth or spine often bearing a tuft of long hair, apex more or less deeply bifid; mostly slender species; northern and central Andes	12
- SGP with a longitudinal carina, basal transverse carina, or with a weaker elevation	15
12. SGP with a strong, central tooth, beyond which it is entirely covered with dense hair, apex not strongly upturned; small, slender species (BL 17-28)	13
- SGP with extremely strong central tooth or spine, beyond which the surface is not entirely covered with hair, apex strongly upturned; mostly medium to large, more robust, species (BL 24-25)	14
13. Species of Venezuelan Andes. Map fig. 238. SGP & digitus figs 76-83	<i>P. hymenaea</i> p. 75
- Species of Ecuadorean Andes. Map fig. 238. SGP & digitus figs 84-89	<i>P. cofanes</i> p. 76
14. SGP (figs 90,91) with sub-basal tooth, triangular in cross-section, without hair on ventral surface, apex shallowly bifid; digitus fig. 92. Peruvian Andes. Map fig. 238	<i>P. pulawskii</i> p. 79
- SGP (figs 93,94) with central, laterally compressed spine whose sides bear tufts of long hair; apex extremely deeply bifid; digitus fig. 96; sternal hairs fig. 95. Colombian Andes. Map fig. 238	<i>P. stella</i> p. 77
15. SGP with a very high and sharp median carina	16
- If the SGP has a median carina, it is not simultaneously high and sharp	18
16. SGP carina (figs. 97,98) raised into a very strong, basal tooth; large species with orange-amber wings. Digitus fig. 99. West Indies, occasionally adjacent areas. Map fig. 235	<i>P. marginata</i> p. 67
- SGP carina not raised into a tooth	17
17. SGP carina in profile (figs 100,101) beginning basally with a short, straight edge (less than half visible SGP length); digitus fig. 102. Small species (BL 15-25) with white wing tips; western Andes of Ecuador and Perú. Map fig. 236	<i>P. lycaon</i> p. 71
- SGP carina in profile (figs 103,104) with a long, straight edge (more than half of visible SGP length); T.1 transversely swollen, angulate in profile. Digitus fig. 105. Large species (BL 24-33), entirely black. East of Andes. Map fig. 235	<i>P. elevata</i> p. 64
18. SGP in profile with main axis strongly curved or bent at or just beyond the middle	19
- SGP in profile at most weakly curved (occasionally a strong, transverse, basal elevation creates the illusion of strong curvature)	22
19. Base of SGP with a very strong, transverse-semicircular carinate tubercle; SGP translucent yellow-brown; body with much bright, golden hair	20

- Base of SGP without such a tubercle, dark brown or black; body hair less bright 21
- 20. SGP (figs 106,107) very elongate, almost parallel-sided. Digitus & sternal hairs 108-109. Widespread east of Andes. Map fig. 240 *P. aurozonata* p. 97
- SGP (figs 110,111) broad, strongly narrowed at the middle. Digitus & sternal hairs figs 112,113. Lower Amazon only. Map fig. 241 *P. aurifex* p. 100
- 21. Small species (BL 12-23); wings black with white tips; SGP (figs 114,115) black, gradually expanded apicad. Digitus fig. 116. Very widespread species. Map fig. 236 *P. terminata* p. 68
- Medium-sized species (BL 21-25); wings amber, antenna orange; SGP (figs 117,118) sharply expanded sub-basally then narrowed apicad. Sternal hairs & digitus figs 119,120. Urubamba valley at Machu Picchu, possibly also Chanchamayo valley. Map fig. 238 *P. marthae* p. 82
- 22. Base of SGP with a strong, transverse, arcuate tubercle; often with a sharp, lateral tooth; apex moderately to very narrow 36
- Base of SGP with at most a weak, transverse carina; if with a lateral tooth, it is rounded; apex broader, often emarginate centrally 23
- 23. SGP almost parallel-sided, strongly narrowed only at or just before apex 24
- SGP changing in width before apex 29
- 24. SGP (figs 124,125) essentially flat transversely, slightly curved upwards apicad; entirely polished and also covered rather sparsely with long, coarse hair. Sternal hairs & digitus figs 126,127. South-east and central Brazil. Map fig. 246 *P. hyperion* p. 125
- SGP surface divided into polished and pilose areas, or with median elevation, or both together 25
- 25. SGP (figs 121,123) very short, quadrate, the apex strongly truncate, forming a very thin, sharp, lamella with a more-or-less sinuate edge. Digitus fig. 122. Eastern Brazil to north-eastern Argentina. Map fig. 245 *P. bonplandi* p. 123
- SGP longer than quadrate, its apex thicker 26
- 26. SGP rather narrow, most of its surface more or less pilose; apex rounded, hairs short, scarcely projecting beyond apex 27
- SGP broad, the surface divided (usually sharply) into polished and pilose areas; apex more or less emarginate centrally; the hairs very long, curved, projecting well beyond apex 28
- 27. Gaster dorsoventrally flattened, T.1 with a median groove; wings orange-amber with a dark, apical band; antenna very short, scarcely longer than head, thorax and propodeum together; wings orange with black apical border. SGP & digitus figs 128-130. Chaco and southern Brazil. Map fig. 237 *P. brevicornis* p. 90
- Gaster evenly rounded, T.1 without median groove; antenna distinctly longer than head, thorax and propodeum together; wings very variable in colour, forewing often with white or pale apex. SGP & genitalia figs 131-134. Widespread species. Map fig. 237 *P. cassiope* p. 92
- 28. SGP (figs 135,136) with lateral margin thickened, distally raised, producing an obtuse angle between margin and apex, pale yellow-brown; sternal hairs & genitalia figs 137-139; apex of gaster with bright reddish hairs; wings without distinct, pale apical band; mainly Amazon, where the body has much bright golden hair;

- hair less bright southwards to Argentina, but gastral apex colour not changing. Map fig. 242 *P. apicata* p. 105
- SGP (figs 140,141) with the lateral margin scarcely thickened, apex and sides evenly rounded together; SGP and entire body black; digitus & sternal hairs figs 142,143; wings often with pale apical band; a mainly southern South American species. Map fig. 243 *P. defecta* p. 108
29. SGP (figs 145,146) almost spathulate, surface without obvious pilosity; with a fairly strong basal, triangular tubercle forming the beginning of a median keel, which is rapidly obsolescent apicad; the apex entire, rounded; the junction of side and apex strongly raised, leaving sides and apex depressed. Digitus fig. 144. North and Central America. Map fig. 235 *P. aquila* p. 63
- SGP not spathulate; part of surface strongly pilose, the rest polished; Mexico southwards 30
30. SGP gradually wider apicad, then rounded into the apex; lateral margin at most only slightly thickened distally, immediately before the pilose area reaches the margin; Central America and north-western South America only 31
- SGP virtually parallel-sided in the middle section; the side more or less abruptly expanded basally, distally ending in a raised "shoulder" forming the end of the polished area, beyond which it is more or less suddenly constricted, pilose, and narrows more gradually to the apex; widespread species 32
31. SGP (figs 147,149) short, length (measured from basal transverse carina) about 1.1 times maximum width; punctate area basally occupying much more than one-third of SGP width at that point; basal carina with distinct groove proximally; apical projection of digitus (fig. 148) with extremely short, very sparse bristles; propodeum with PPT and PTC not extremely strong, distance between tips of PPTs is obviously less than that between APTs; propodeal hair at least as long as MPN length; wings pale yellow-amber, forewing with apex slightly paler; smaller species (BL 32-34); Yucatan peninsula and Chiapas state. Map fig. 246 *P. yucatani* p. 121
- SGP (figs 150,152) appearing rather elongate, about 1.3 times as long as maximum width; punctate area basally occupying about one-third or less of SGP width at that point; basal carina without a groove proximally; apical projection of digitus (fig. 151) with fairly long, dense hair (about as long as complete aedeagus width); propodeum with PPT and PTC extremely strong, so that distance between tips of PPTs is about equal to that between tips of APTs; propodeal hair shorter than MPN length; wings orange-amber, with weakly infusate apical band; larger species (BL 31-41) southern Mexico to north-western South America. Map fig. 243 *P. tricuspidata* p. 109
32. Body with much bright golden or golden-silver pubescence forming conspicuous patterns 33
- Body with at most dull yellow-violet pubescence, not forming conspicuous patterns 35
33. Tergites from T.2 onwards with conspicuous golden apical hair-bands; apical projection of digitus strongly expanded on proximal side (as well as on distal), resembling a cobra's hood 34
- Tergites from T.2 onwards usually entirely black, occasionally with faint golden apical bands; apical projection of digitus not expanded on proximal side, thus

- slightly concave. SGP & digitus figs 153-155. Colombian Andes. Map fig. 245
 *P. sumptuosa* p. 116
34. Inner emargination of paramere with tiny but sharp tooth at its base; SGP (figs 156, 158) with junction between polished and pilose areas poorly defined, pilosity dark brown. Digitus fig. 157. Western watershed of Andes in Colombia and Ecuador. Map fig. 244 *P. onorei* p. 111
- Inner emargination of paramere without basal tooth; SGP (figs 159,161) with junction between polished and pilose areas sharp except basally, pilosity bright red-brown. Digitus fig. 160. Eastern Venezuela, Guianas and western Amazon basin from Colombia to Perú. Map fig. 244 *P. pulszkyi* p. 114
35. Wings black; SGP (figs 162,164) scarcely longer than quadrate, its apex projecting only a little beyond distal "shoulder" of lateral margin; pilose area depressed below polished area only beside "shoulder", elsewhere the junction between the two is very poorly defined. Digitus fig. 163. Eastern watershed of Andes in Ecuador and Perú. Map fig. 246 *P. toppini* p. 120
- Wings orange-amber; SGP (figs 165-168) clearly longer than quadrate, its apex projecting well beyond distal "shoulder" of lateral margin (for a distance about equal to length of straight part of lateral margin); entire pilose area depressed below surface of polished area, thus the two sharply separated everywhere. Digitus & sternal hairs figs 169,170. Mexico and Central America to coastal Venezuela and west-Andean watershed of Ecuador. Map fig. 245 *P. optima* p. 118
36. All gastral tergites with bright golden hair; hind legs partly red; SGP (figs 171,172) without sub-basal constriction; with a sharp, lateral tooth and very narrow apex. Digitus & sternal hairs figs 173,174. Venezuela, the Guianas, much of Amazon watershed. Map fig. 243 *P. plutus* p. 102
- Only T.1 with pale golden hair; legs all black; SGP (figs 175,176) with strong, sub-basal constriction; without sharp, lateral tooth, apex moderately narrow; digitus fig. 177. Central and south-eastern Brazil. Map fig. 241 *P. riopretensis* p. 101

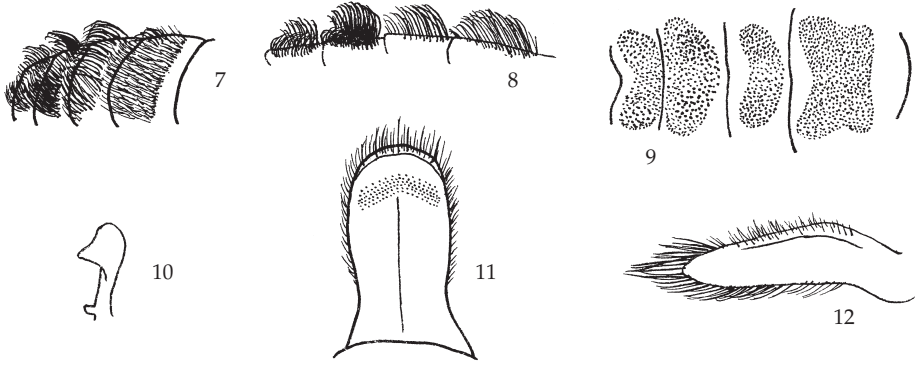
Key to females

(continued from "Other groups" in Part 1 key)

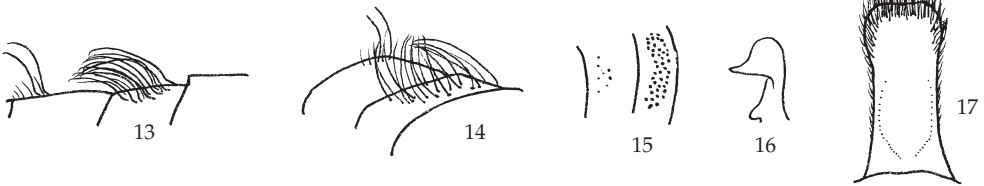
A key to separate "Part 2" females from those in the remainder of the genus would be too difficult to construct and to use; however, with the exceptions of *P. terminata*, *lycaon* and *aurifex* the sexes show little wing-colour dimorphism, although in the *P. sumptuosa*-group the body hair can be dark in one sex, golden in the other; the following notes will be useful in conjunction with the keys.

P. grossa-group (p. 56). Both species have the same venation character as the *P. rubra*-group, i.e. the forewing radius joining the costa at a very shallow angle (fig. 190); they also have much coarse hair below the front femur (see Distinctions under *P. grossa*), as do species of the *P. sumptuosa*-group, but all are included in this Part. *P. grossa*-group species never have golden body hair.

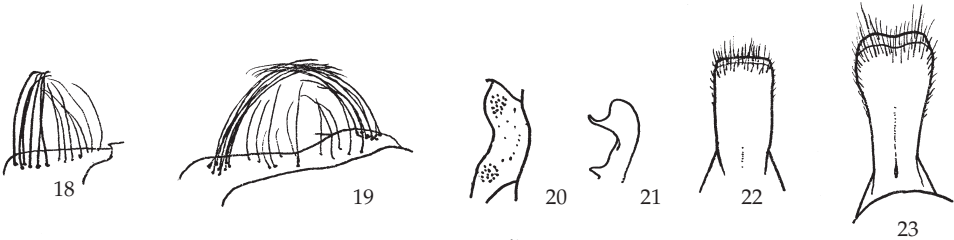
P. elevata-group (p. 61). All species usually lack the lateral extension of the S.2 groove (e.g. fig. 203) (occasionally very weakly developed), but are otherwise very varied; the detailed text descriptions must be consulted, especially in the case of *P. aquila*, whose female resembles those of other sympatric species.



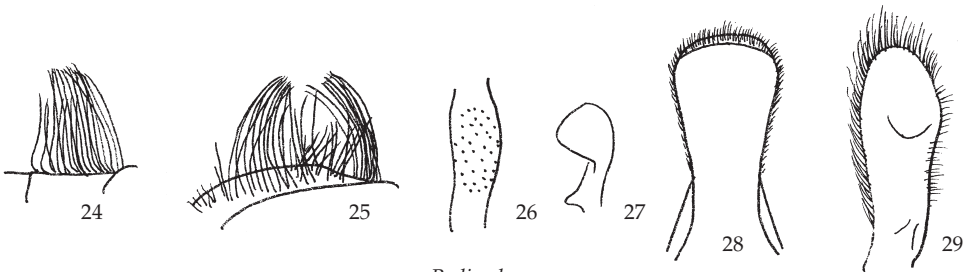
P. australis



P. minarum

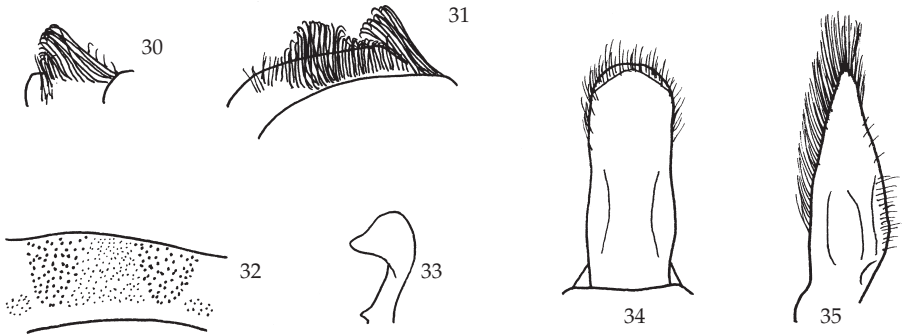


P. smaragdina

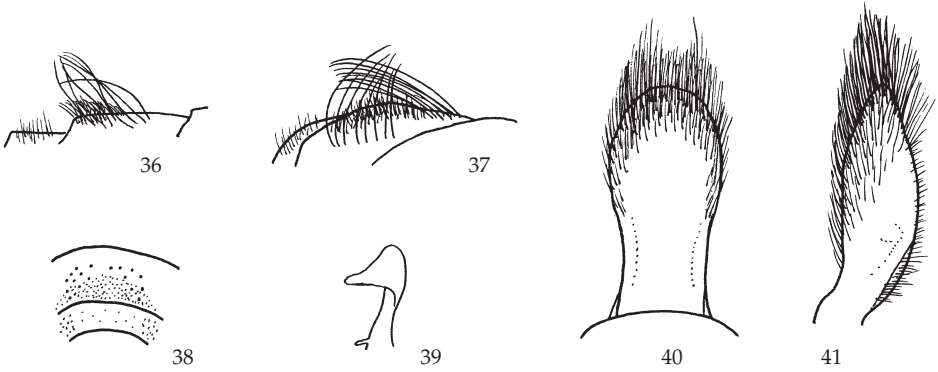


P. discolor

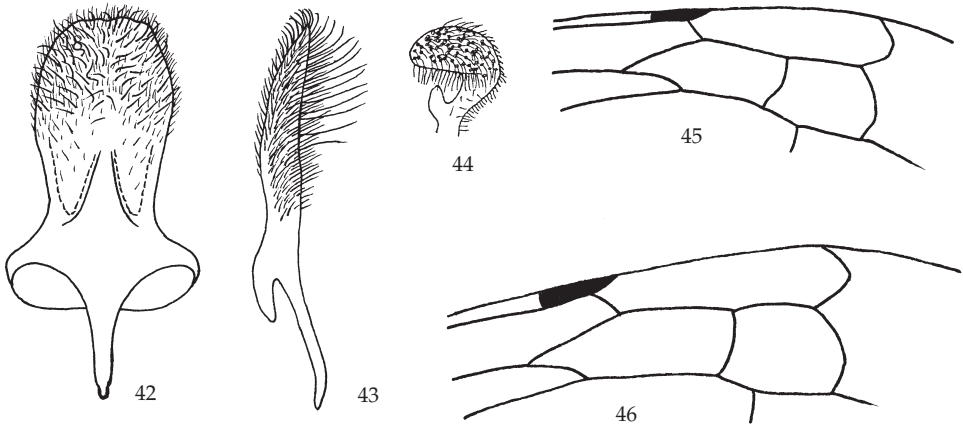
Figs 7-12. *P. australis* Saussure; 13-17, *P. minarum* Brèthes; 18-23, *P. smaragdina* Dahlbom; 24-29, *P. discolor* Taschenberg. 7-9, 13-15, 18-20, 24-26, sternal hairs and their insertion points; 11, 17, 22-23, 28, subgenital plate; 12, 29 paramere; 10, 16, 21, 27 digitus apex.



P. optimatis

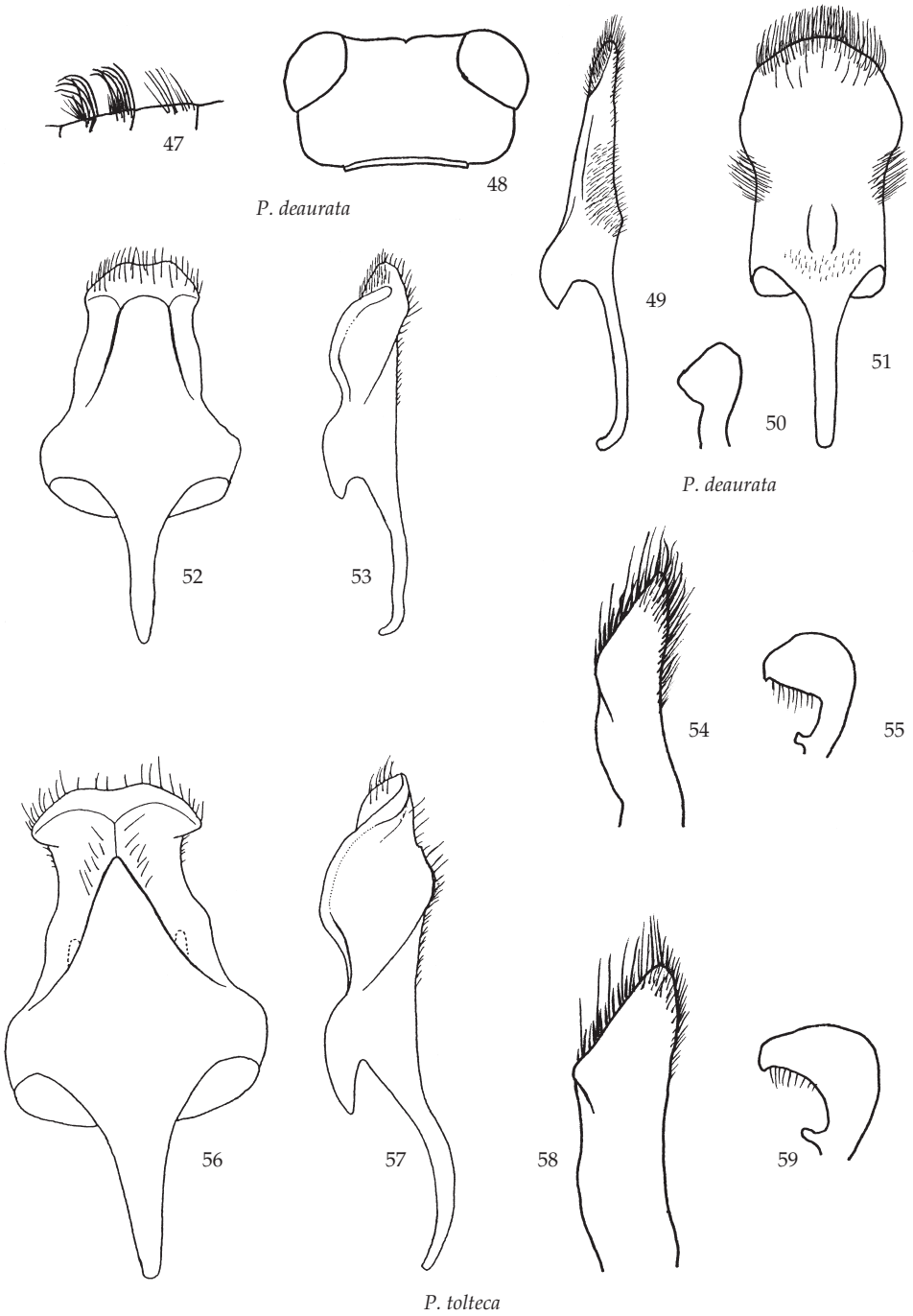


P. asteria

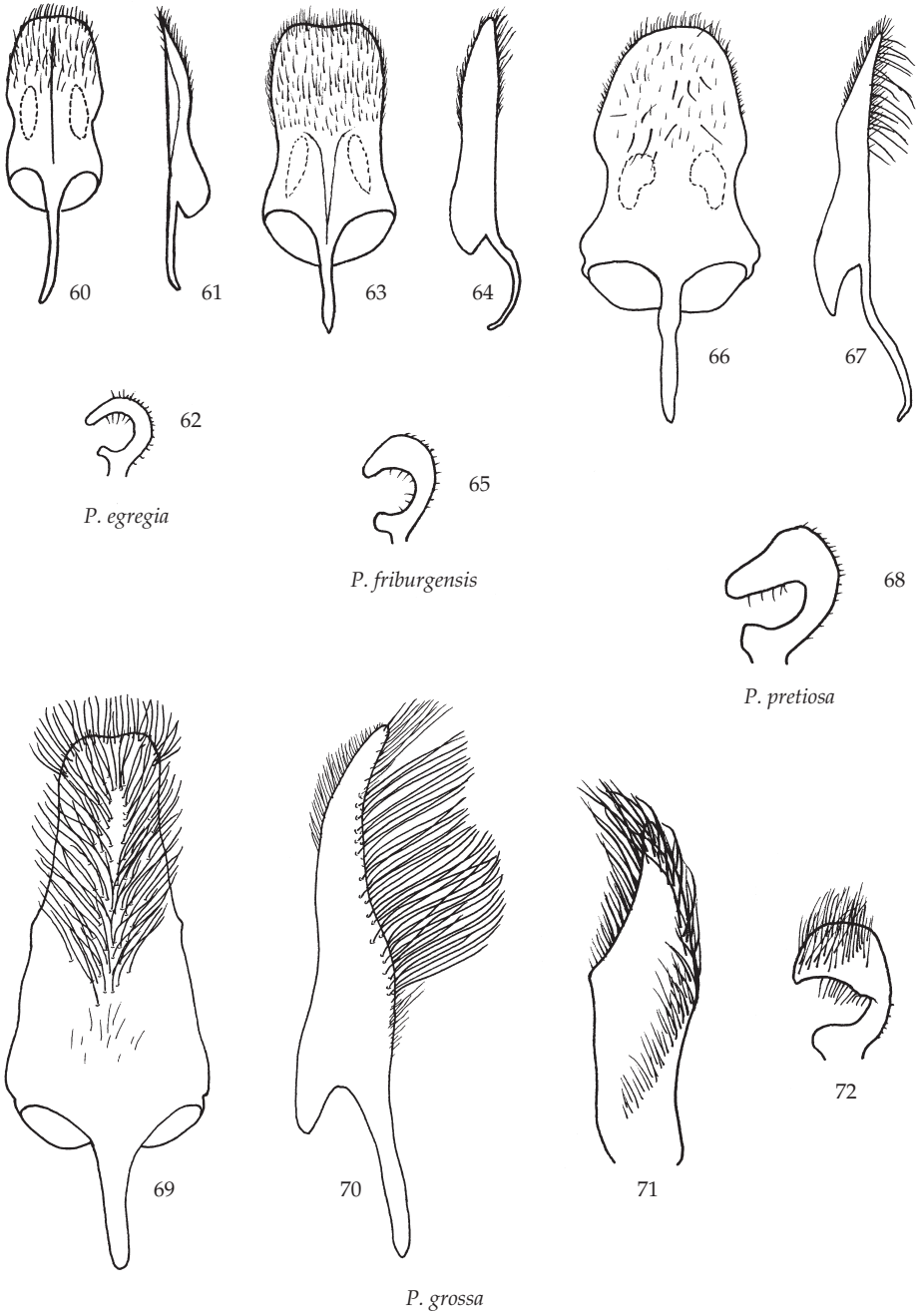


P. chiliensis

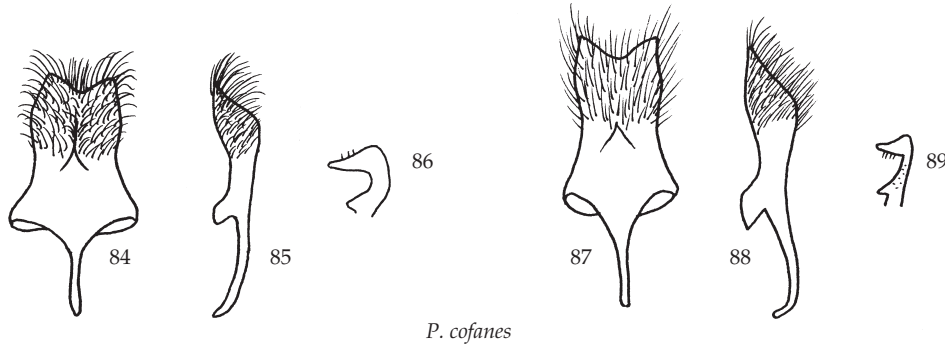
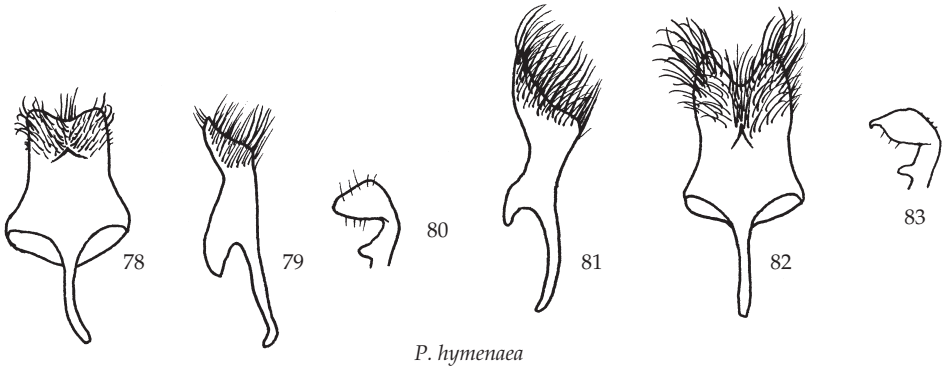
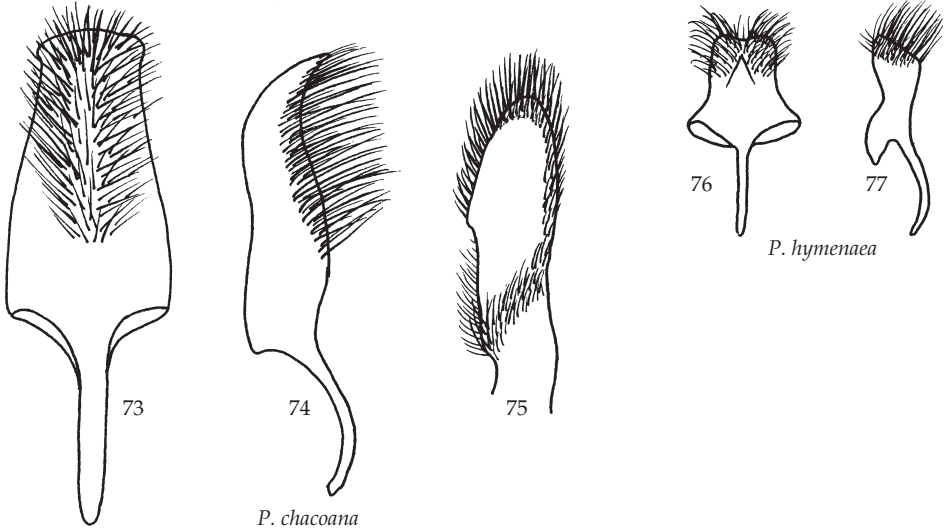
Figs 30-35. *Pepsis optimatis* Smith; 36-41, *P. asteria* Mocsáry; 42-46, *P. chiliensis* Lepeletier. 30-32, 36-38, sternal hairs and their insertion points; 34, 40, 42-43, subgenital plate; 35, 41 paramere; 33, 39, 44, digitus apex; 45-46, forewing.



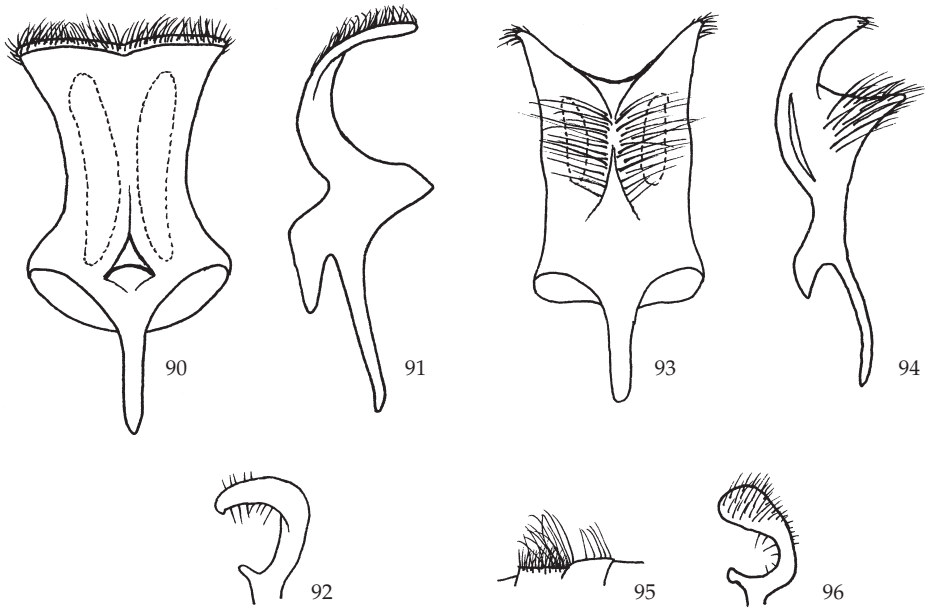
Figs 47-51. *Pepsis deaurata* Mocsáry; 52-59, *Pepsis tolteca* Lucas. 47, sternal hairs; 48, head, dorsal aspect; 49, 51, 52-53, 56-57, subgenital plate; 54, 58 paramere; 50, 55, 59, digital apex.



Figs 60-62. *Pepsis egregia* Mocsáry; 63-65, *P. friburgensis* spec. nov., 66-68, *P. pretiosa* Dahlbom; 69-72, *P. grossa* (Fabricius). 60-61, 63-64, 66-67, 69-70, subgenital plate; 71, paramere; 62, 65, 68, 72, digital apex.

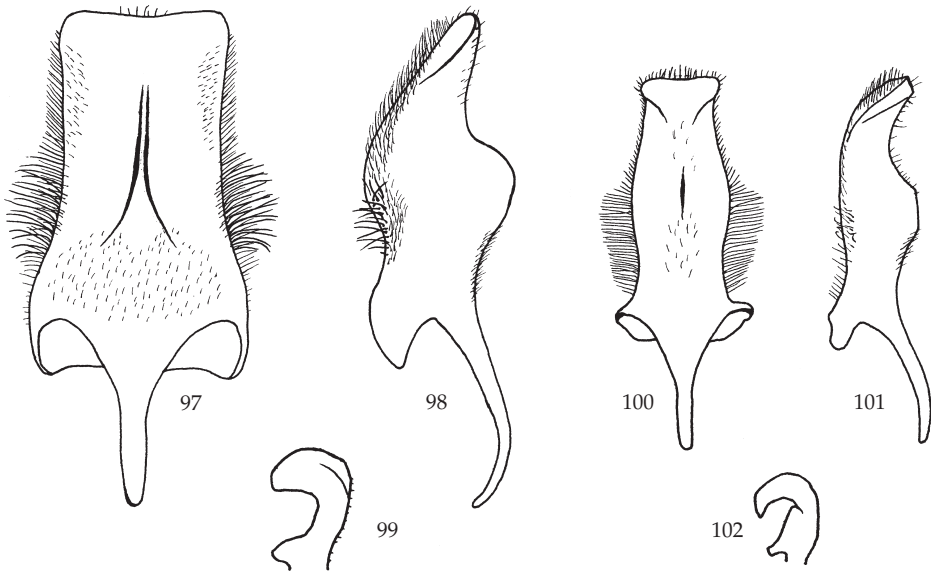


Figs 73-75. *Pepsis chacoana* Brèthes; 76-83, *P. hymenaea* Mocsáry; 84-89, *P. cofanes* Banks. 73-74, 76-79, 81-82, 84-85, 87-88, subgenital plate; 75, paramere; 80, 83, 86, 89, digital apex.



P. pulawskii

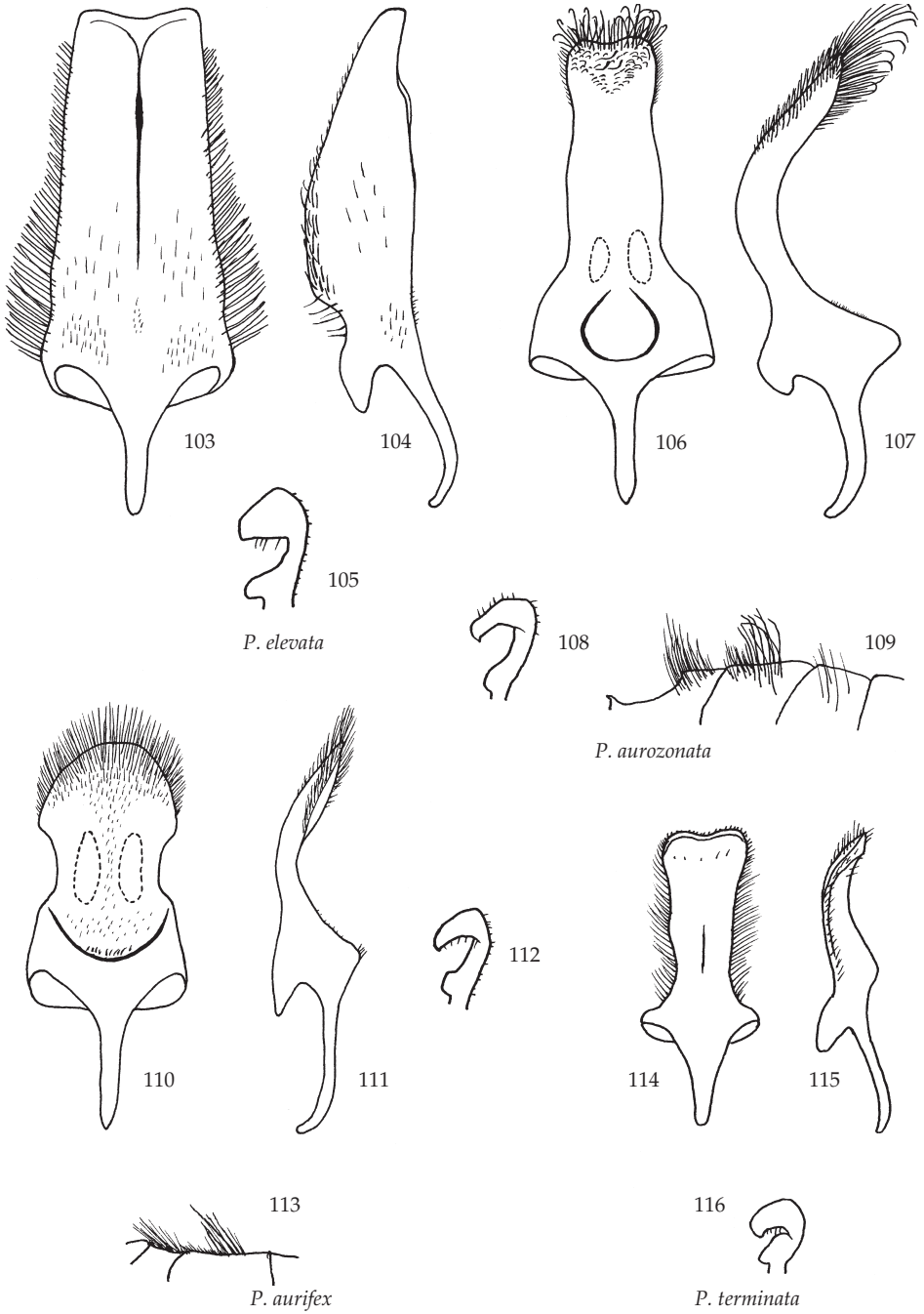
P. stella



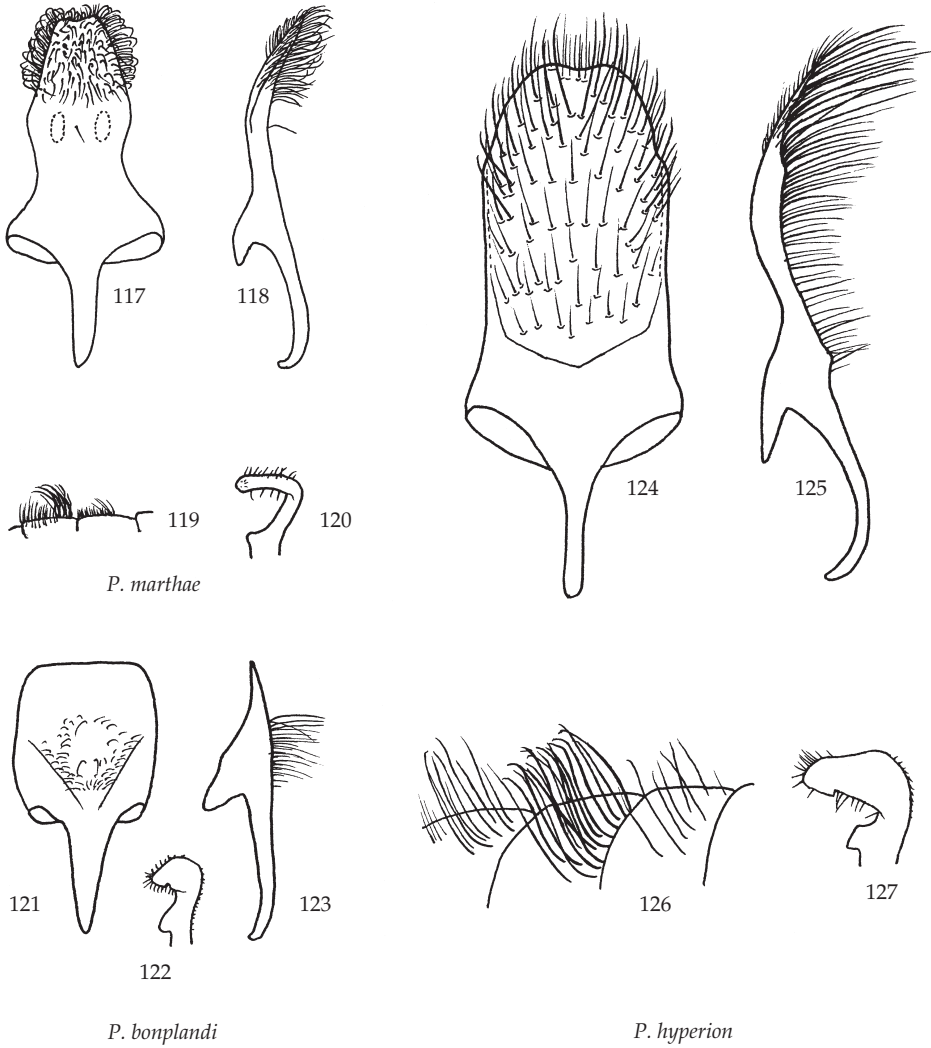
P. marginata

P. lycaon

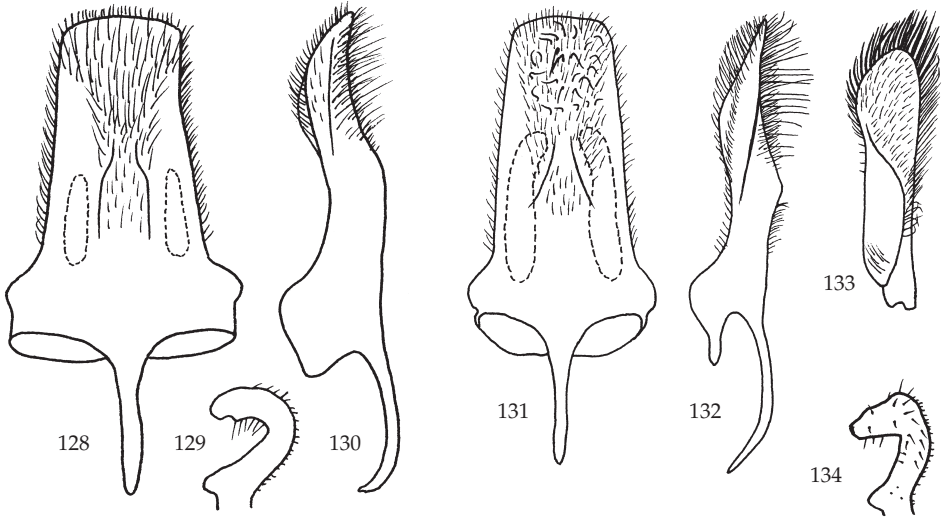
Figs 90-92. *Pepsis pulawskii* spec. nov.; 93-96, *P. stella* Montet; 97-99, *P. marginata* Beauvois; 100-102, *P. lycaon* Banks. 90-91, 93-94, 97-98, 100-101, subgenital plate; 95, sternal hairs; 92, 96, 99, 102, digital apex.



Figs 103-105. *Pepsis elevata* Fabricius; 106-109, *P. aurozonata* Smith; 110-113, *P. aurifex* Smith; 114-116, *P. terminata* Dahlbom. 103-104, 106-107, 110-111, 114-115, subgenital plate; 109, 113, sternal hairs; 105, 108, 112, 116, digital apex.

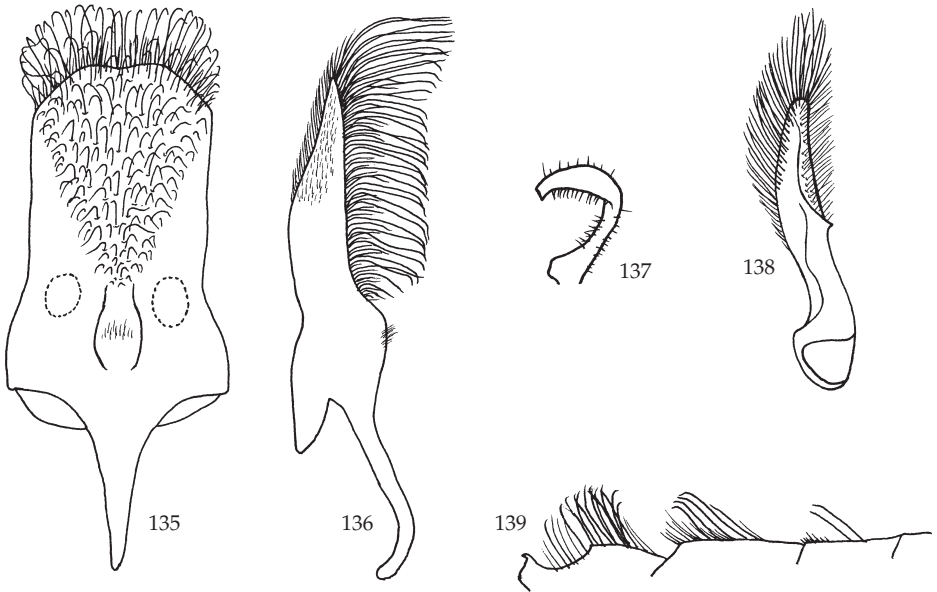


Figs 117-120. *Pepsis marthae* spec. nov.; 121-123, *P. bonplandi* Brèthes; 124-127, *P. hyperion* Mocsáry. 119, 126, sternal hairs; 117-118, 121, 123, 124-125, subgenital plate; 120, 122, 127, digital apex.



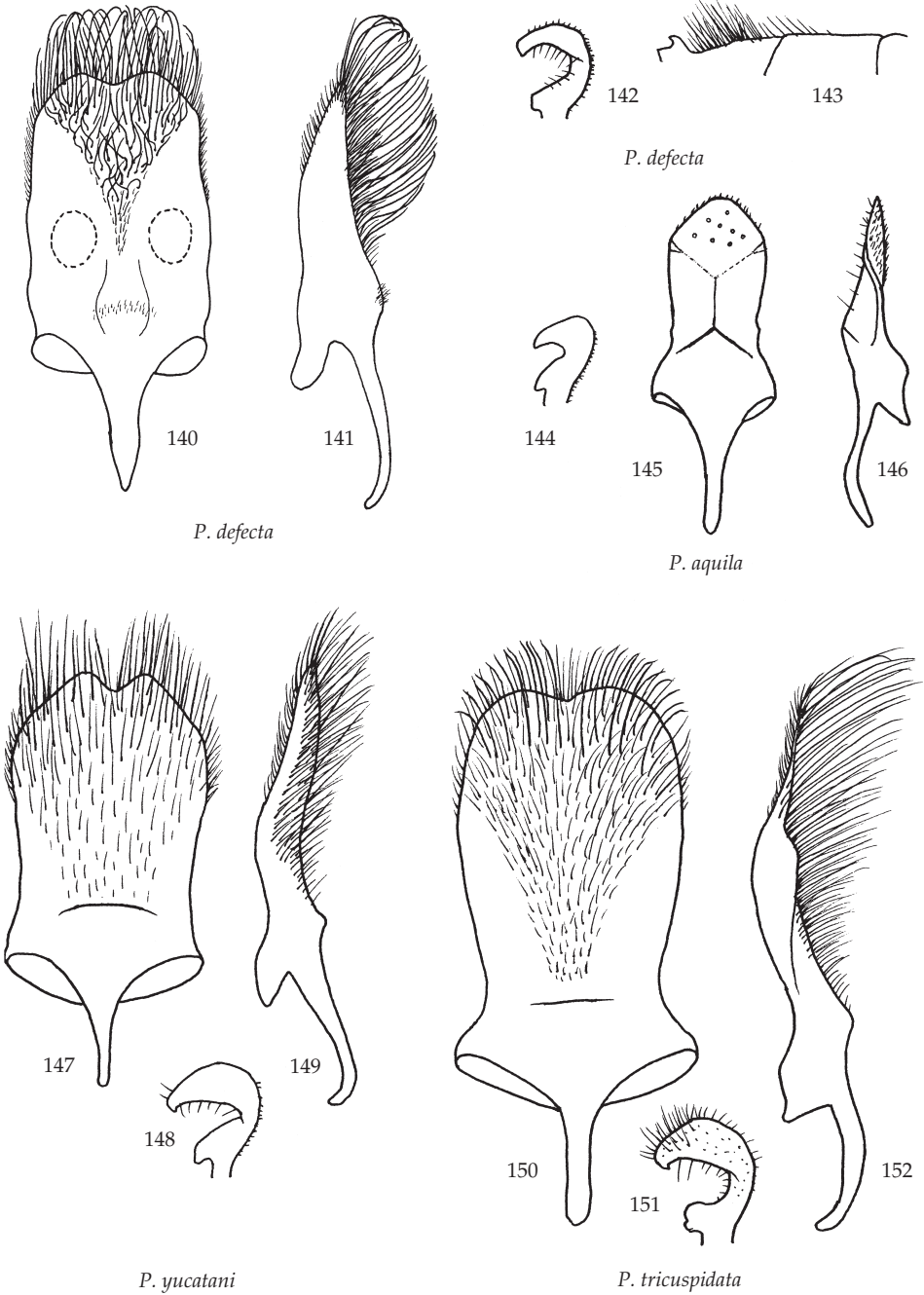
P. brevicornis

P. cassiope

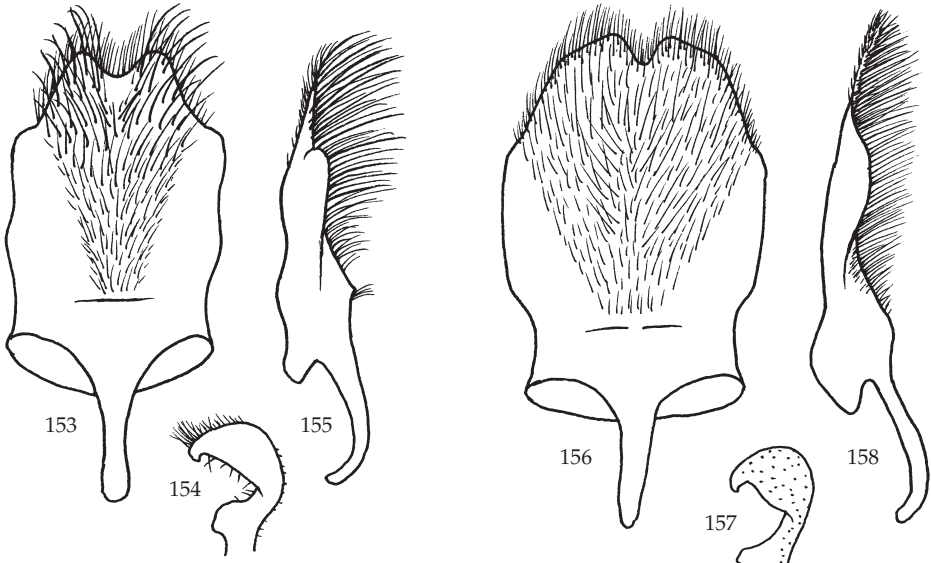


P. apicata

Figs 128-130. *Pepsis brevicornis* Mocsáry; 131-134, *P. cassiope* Mocsáry; 135-139, *P. apicata* Taschenberg. 128, 130, 131-132, 135-136, subgenital plate; 139, sternal hairs; 133, 138, parameres; 129, 134, 137, digital apex.

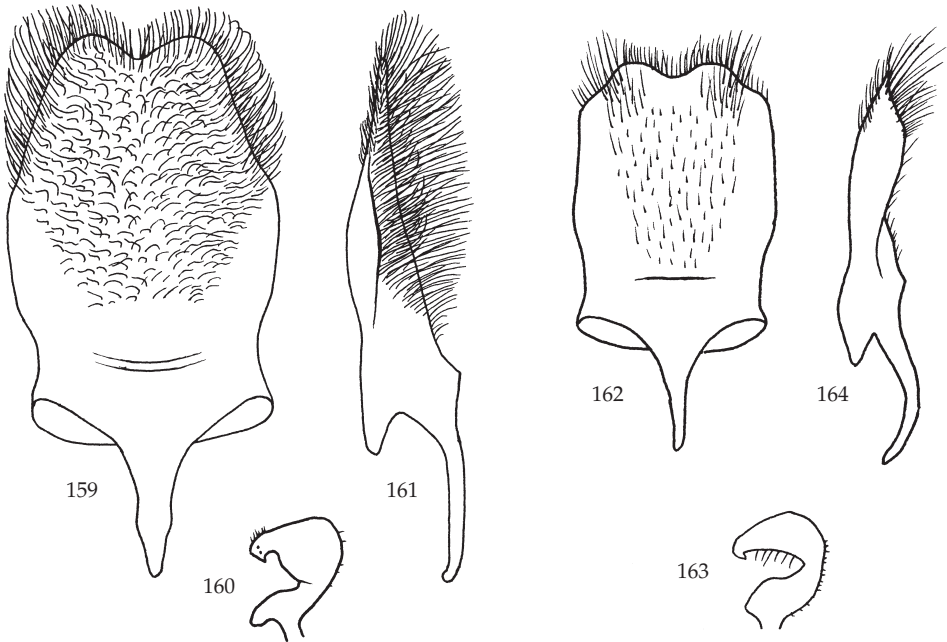


Figs 140-143. *Pepsis defecta* Taschenberg; 144-146, *P. aquila* Lucas; 147-149, *P. yucatani* spec. nov.; 150-152, *P. tricuspidata* Gribodo. 140-141, 145-146, 147, 149, 150, 152, subgenital plate; 143, sternal hairs; 142, 144, 148, 151, digital apex.



P. sumptuosa

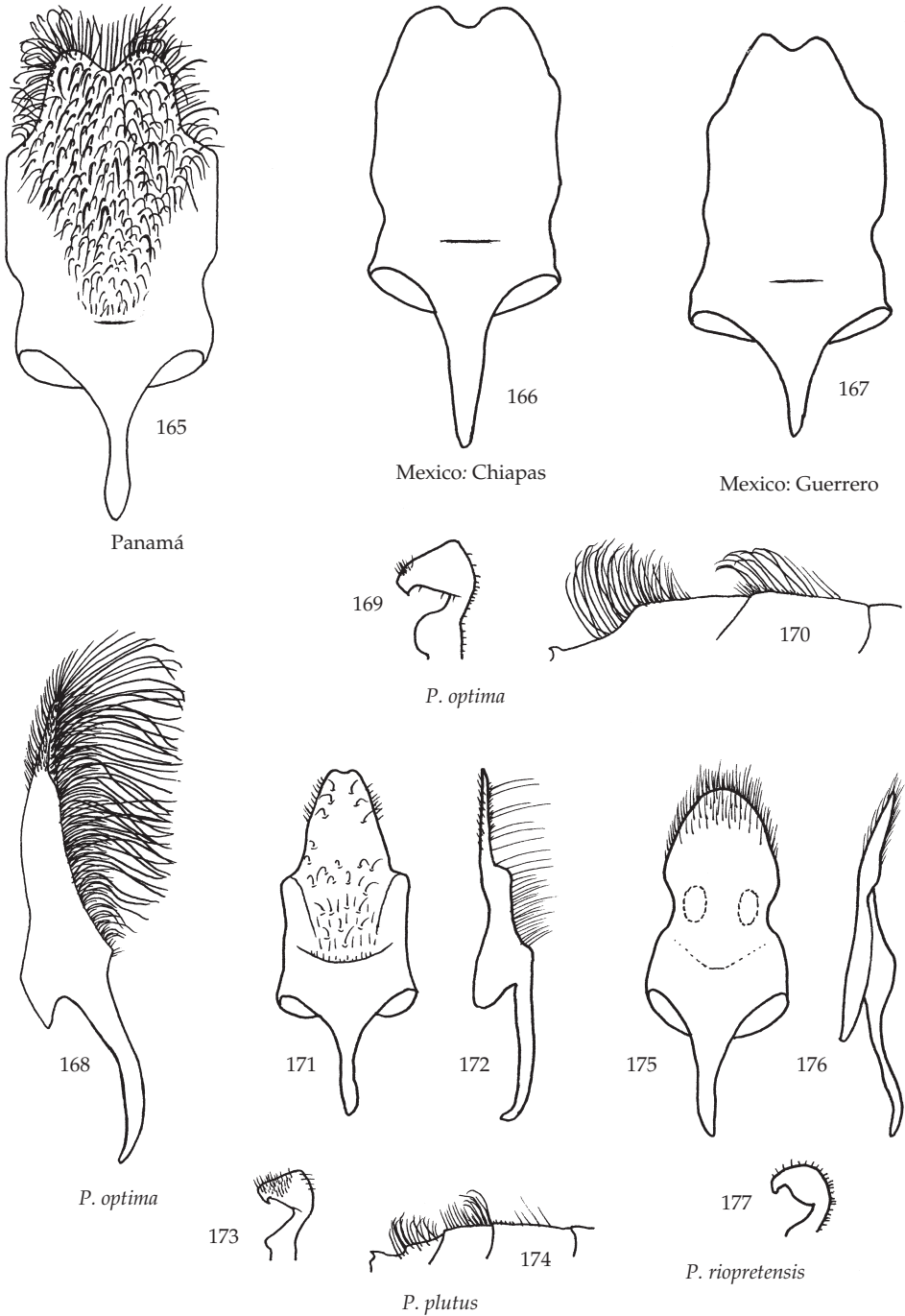
P. onorei



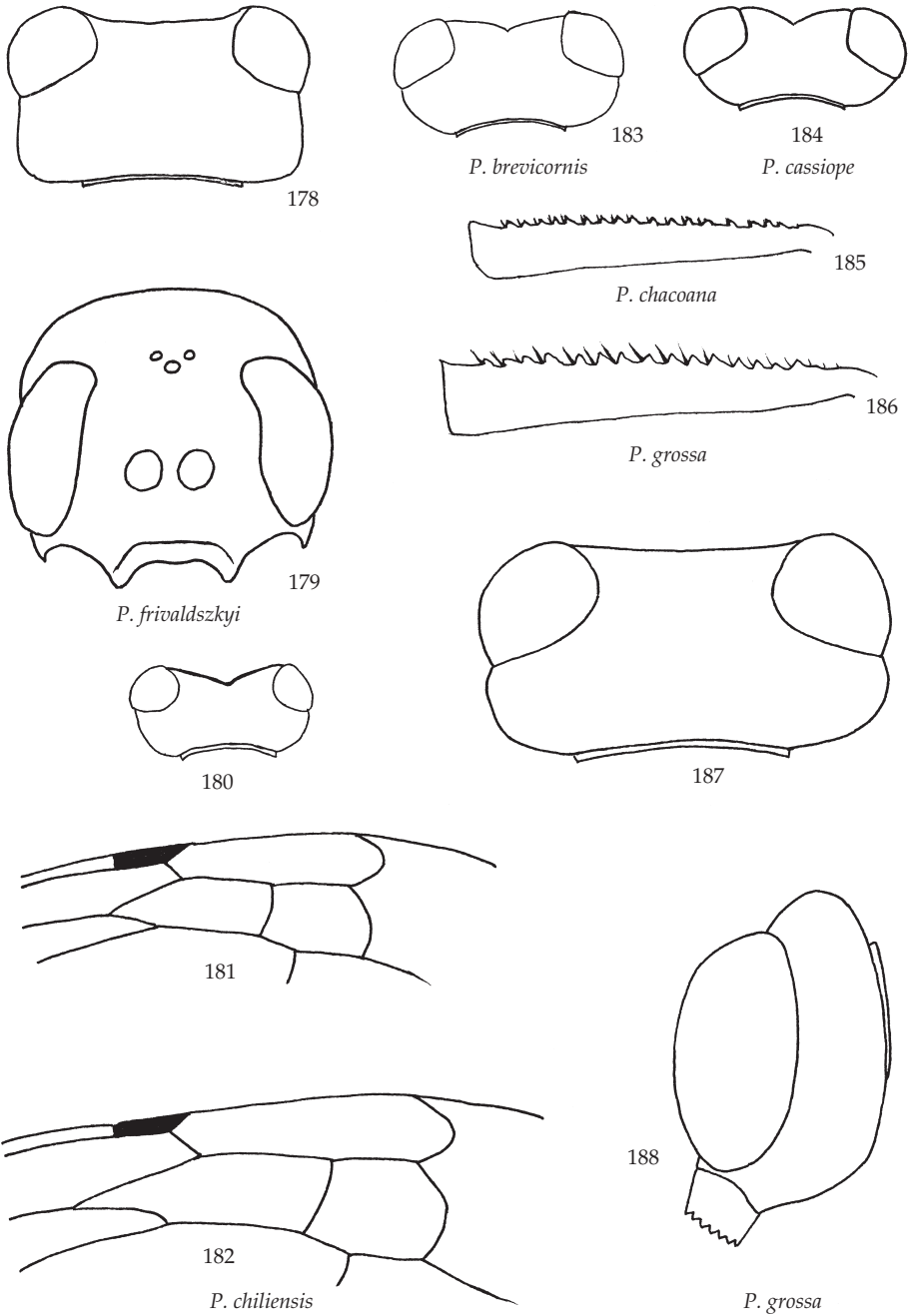
P. pulszkyi

P. toppini

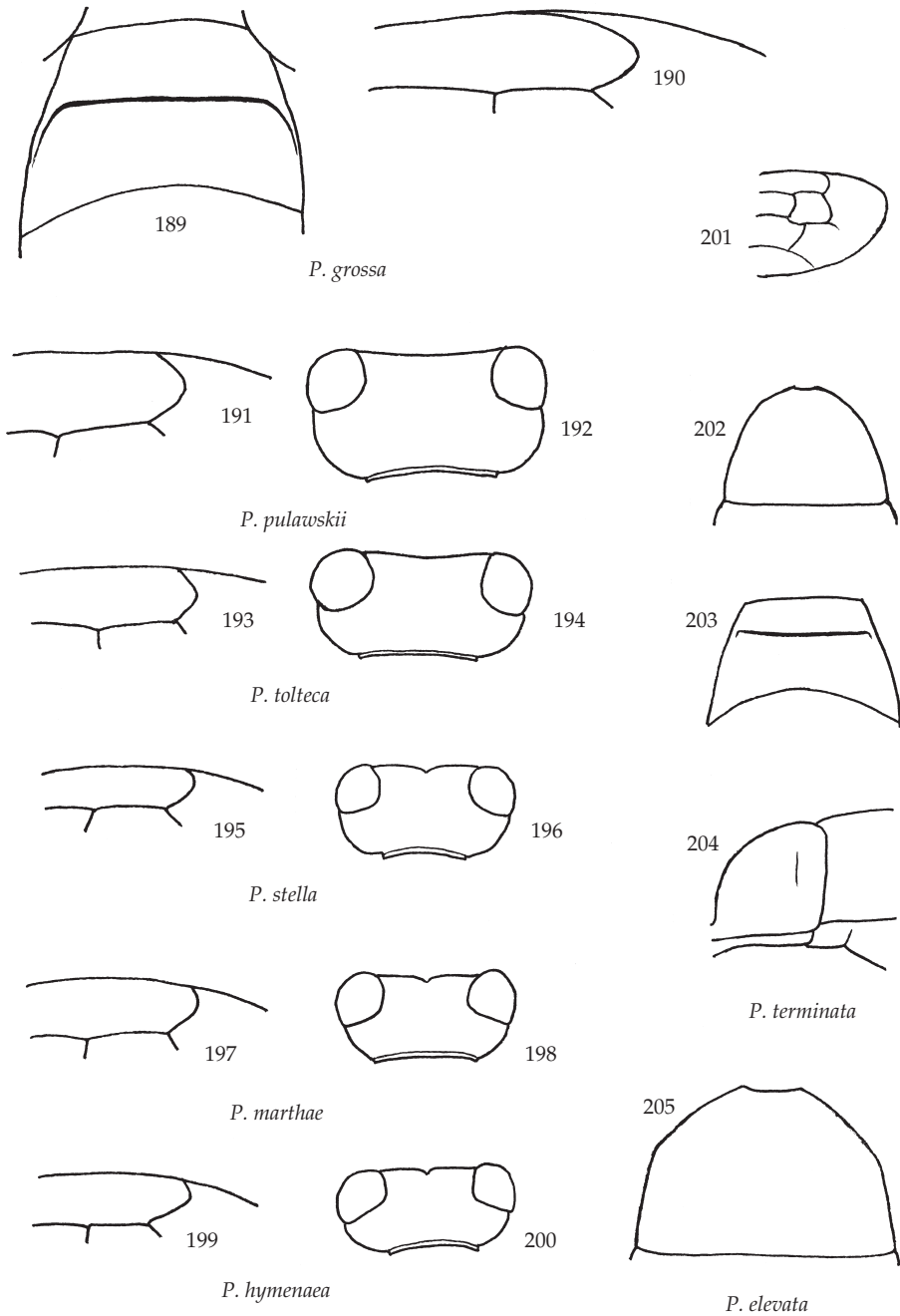
Figs 153-155. *Pepsis sumptuosa* Smith; 156-158, *P. onorei* spec. nov.; 159-161, *P. pulszkyi* Mocsáry; 162-164, *P. toppini* Turner. 153, 155, 156, 158, 159, 161, 162, 164, subgenital plate; 154, 157, 160, 163, digital apex.



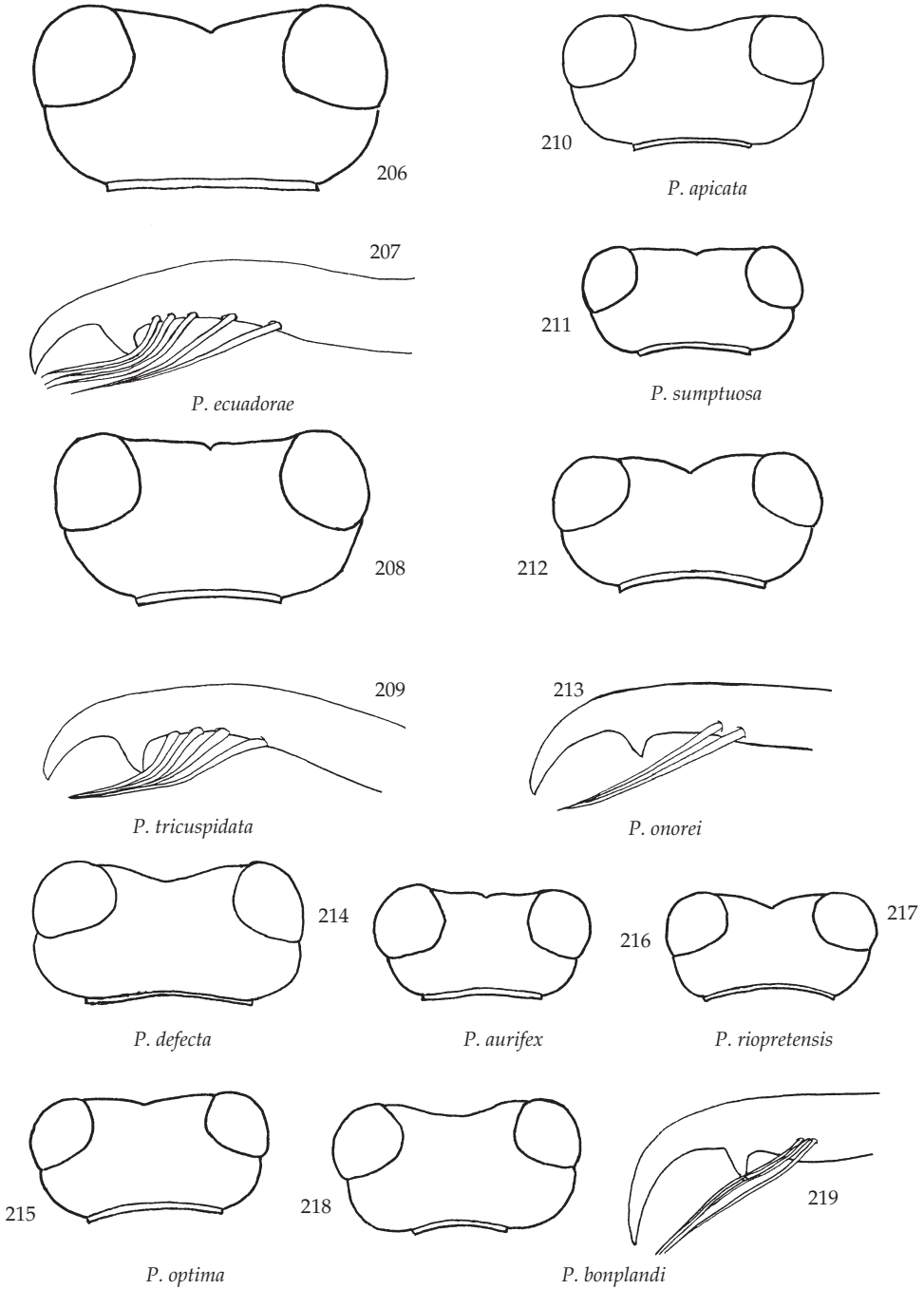
Figs 165-170. *Pepsis optima* Smith; 171-174, *P. plutus* Erichson; 175-177, *P. riopretensis* spec. nov.; 165-168, 171-172, 175-176, subgenital plate; 170, 174, sternal hairs; 169, 173, 177, digital apex.



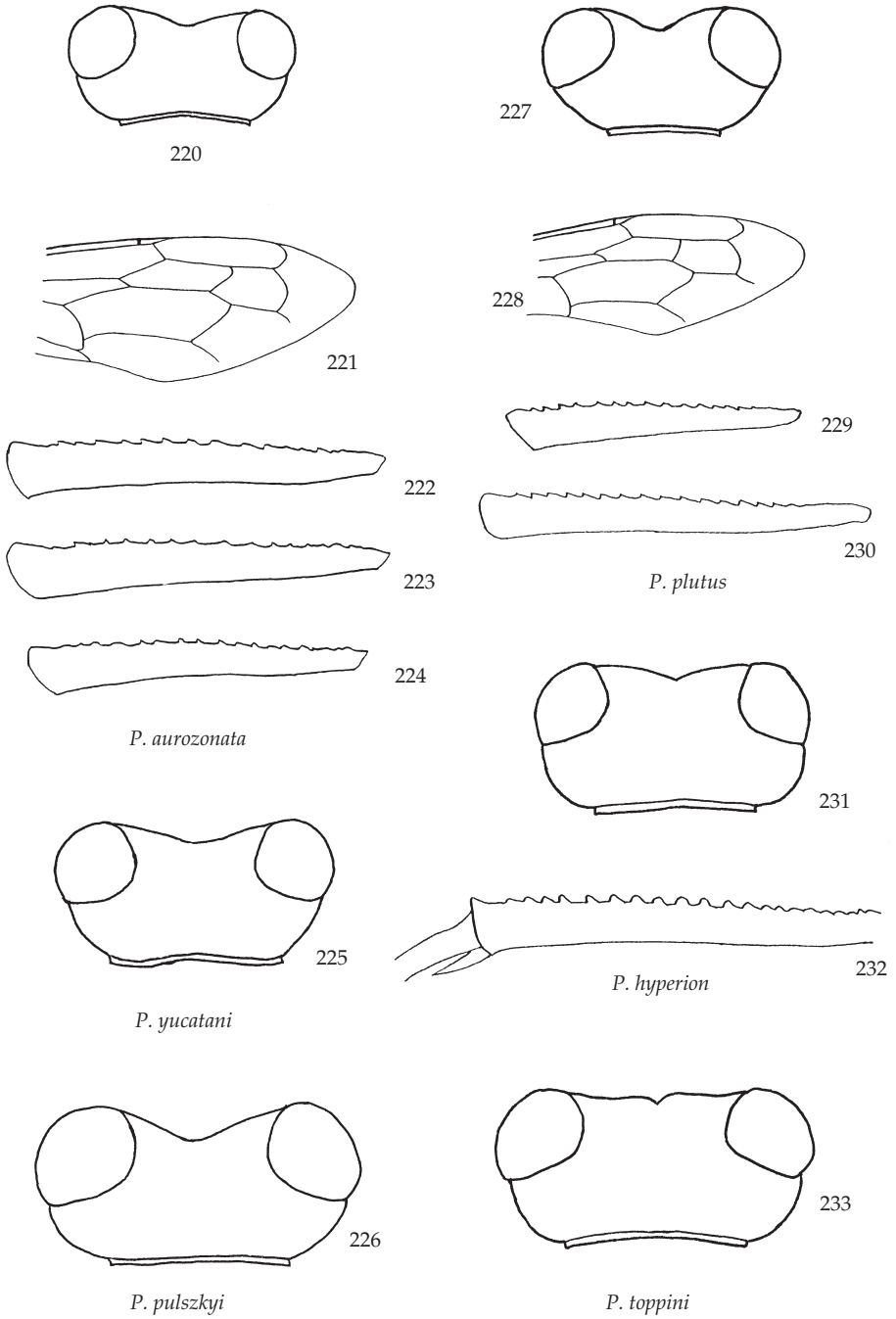
Figs 178-179. *Pepsis frivaldszkyi* Mocsáry; 180-182, *P. chiliensis* Lepeletier; 183, *P. brevicornis* Mocsáry; 184, *P. cassiope* Mocsáry; 185, *P. chacoana* Brèthes; 186-188, *P. grossa* (Fabricius). 178-179, 180, 183, 184, 187-188, heads, 178, 180, 183, 184, 187, dorsal aspect, 179, frontal aspect and 188, lateral aspect; 181-182, forewing; 185, 186, hind tibia.



Figs 189-190. *Pepsis grossa* (Fabricius); 191-192, *P. pulawskii* spec. nov.; 193-194, *P. tolteca* Lucas; 195-196, *P. stella* Montet; 197-198, *P. marthae* spec. nov.; 199-200, *P. hymenaea* Mocsáry; 201-204, *P. terminata* Dahlbom; 205, *P. elevata* Fabricius. 189, 203, second sternite; 190, 191, 193, 195, 197, 199, 201, forewing; 192, 194, 196, 198, 200, heads, dorsal aspect; 202, 204, 205, first tergite.



Figs 206-207. *Pepsis ecuadorae* spec. nov.; 208-209, *P. tricuspidata* Gribodo; 210, *P. apicata* Taschenberg; 211, *P. sumptuosa* Smith; 212-213, *P. onorei* spec. nov.; 214, *P. defecta* Taschenberg; 215, *P. optima* Smith; 216, *P. aurifex* Smith; 217, *P. riopretensis* spec. nov.; 218-219, *P. bonplandi* Brèthes. 206, 208, 210-212, 214-218, head, dorsal aspect; 207, 209, 213, 219, hind claw.



Figs 220-224. *Pepsis aurozonata* Smith; 225, *P. yucatani* spec. nov.; 226, *P. pulszkyi* Mocsáry; 227-230, *P. plutus* Erichson; 231-232, *P. hyperion* Mocsáry; 233, *P. toppini* Turner. 220, 225-227, 231, 233, head, dorsal aspect; 221, 228, forewing; 222-224, 229-230, 232, hind tibia.

P. hymenaea-group (p. 72). All species inhabit moderate to high altitudes in the Andes from Venezuela to Perú, although *tolteca* is sometimes found also on the desert coast of the latter country. The forewing radius joins the costa more or less perpendicularly, with the junction bent and often thickened (figs 191, 193, 195, 197, 199). The species are often slender, especially the antennae and legs.

P. pretiosa-group (p. 83). All species possess a broadly white forewing apex and dark steel-blue gaster (the males of two other species, *P. vinipennis* of the *P. rubra*-group and (sometimes) *P. terminata* of the *P. elevata*-group, also have similarly coloured wings).

P. chiliensis-group (p. 88). The single included species is entirely black except for orange antennae and is covered with long, dense hair; it inhabits the Andes and desert coast of Perú. It thus resembles the coastal form of *P. montezuma*, but that species has normal venation and is smaller.

P. brevicornis-group (p. 90). Both species are rather large and robust; the knife-like carina of the inner, hind edge of the hind femur, and the extremely long, inner spur of the hind tibia are characteristic.

P. sumptuosa-group (p. 94). Most of the giants of the genus belong here, with a few species medium-sized; the inner spur of the hind tibia is extremely short (e.g. fig. 232), often no longer than the apical width of the tibia; the claw-joint of the hind tarsus is often more or less strongly curved; the claw-tooth is often further than half-way from the claw base and the setae sometimes curved where they pass over it (figs 207, 208; contrast with figs 213, 219); some species have much bright golden body hair. A similar short spur is also found in a few species of the *P. sommeri*-group; these are mentioned in the following keys.

P. deaurata-group (p. 126). Both species are at once distinguished by the rectangularly emarginate clypeus (fig. 179) and extremely strongly swollen back of head (fig. 178).

- 1. Clypeus broadly, rectangularly emarginate; head in dorsal view with temple extremely strongly swollen (figs 178, 179); large species (BL 34-47); (*P. deaurata*-group) 2
- Clypeus shallowly, arcuately emarginate; head in dorsal view with temple at most strongly swollen; body size variable 3
- 2. Head, thorax & T.1 with bright, golden pubescence; species found along the entire Amazon, and its headwaters from southern Colombia to Perú. Map fig. 247 *P. deaurata* p. 127
- Body with at most dull, yellow-violet pubescence; species found from Panamá eastwards through Venezuela, the Guianas and Amazon westwards to Brazil, Fonteboa. Map fig. 247 *P. frivaldszkyi* p. 128
- 3. Hind tibia with inner spur extremely long, reaching 0.45-0.50 basitarsus length, and with deep groove on inner side of teeth; hind femur with inner, posterior carina very strong, knife-edged; fairly large, robust species (BL 29-41); all femora below, at least basally, with fairly dense, short hairs (not longer than femoral width, least dense on hind femur); (*P. brevicornis*-group) 4
- Hind tibia with inner spur usually shorter; if as long, species slender; without deep groove on inner side of teeth; hind femur with inner, posterior carina usually blunt, at most angulate 5

4. Propodeum strongly transverse, its dorsum distinctly shorter than distance between tips of PPTs; T.1 with broad, shallow median groove, obsolescent apicad; head fig. 183. Southern Brazil and northern Argentina. Map fig. 237 *P. brevicornis* p. 90
- Propodeal dorsum virtually quadrate, its length about equal to the distance between the tips of the PPTs; T.1 smoothly convex, without median groove; head fig. 184. Northern Argentina and Amazon basin to USA. Map fig. 237 *P. cassiope* p. 92
5. Forewing apex broadly milky-white, including at least part of SMC3; gaster shining, dark blue; (*P. pretiosa*-group) 6
- If forewing apex is pale, it is more narrowly or less brightly so; gaster less strongly shining, often differently coloured 8
6. SMC3 very short, anterior vein not longer than 2/3 proximal; APT not narrow or pointed; south-east Brazil 7
- SMC3 normal, anterior vein at least a little longer than proximal; APT narrow and pointed, often very strongly so. Rare in south-east Brazil but otherwise more widespread, especially northwards. Map fig. 239 *P. egregia* p. 84
7. Small species, BL 21; AEI 88; APT and PTC very weak, PPT absent; hind tibial teeth narrow, almost upright. Map fig. 239 *P. friburgensis* p. 85
- Large species, BL 32-43; AEI 111-128; APT and PPT moderately strong, PTC strong (though narrow); hind tibial teeth broad, directed strongly backwards. Map fig. 239 *P. pretiosa* p. 87
8. PPV of forewing very long, up to one-third length of total posterior length of SMC2 (figs 181,182); head fig. 180; clypeus with strong, transverse, pre-apical ridge; wings black; body covered with long, dense, black hair. Andes and desert coast of Perú and Ecuador. Map fig. 237 *P. chiliensis* p. 88
- If PPV very long, wings are not black; clypeus with at most a weak pre-apical ridge 9
9. Radial vein meeting costa at a very acute angle (often quite far from apex of radial cell)(fig.190); front femur with coarse, fairly dense hair below; head in dorsal view with temple strongly swollen (figs 187,188); PTC very strong; lateral extension of S.2 groove well developed (fig. 189); (*P. grossa*-group) 10
- Radial vein meeting costa at a more obtuse angle (closer to apex of radial cell); PTC usually moderate to weak; other characters variable 11
10. Spines of hind tibia about as high as teeth (fig. 185); wings orange-amber, with dark border; Bolivia southwards. Map fig. 234 *P. chacoana* p. 57
- Spines of hind tibia distinctly higher than teeth (fig. 186); wings usually black, sometimes paler in USA, Ecuador and northern Perú. Perú northwards. Map fig. 234 *P. grossa* p. 58
11. Small species, BL 17-33(-40 in West Indies), with lateral extension of S.2 groove absent or virtually so (fig. 203), tip of forewing white or pale (sometimes narrowly), T.1 swollen in middle (appearing hemispherical rather than conical or bell-shaped)(figs 202,204), AE index very low (69-98) and inner spur of hind tibia very short, reaching to only 0.20-0.35 basitarsus length 12
- If species are small with lateral extension of S.2 groove lacking or very weak, most (usually all) other characters disagree 13

12. Forewing without silvery sub-basal band, basic wing colour varying from amber through red to black; SMC3 short (fig. 201); widespread species. Map fig. 236 *P. terminata* p. 68
- Forewing with sub-basal silvery band, basic wing colour always black; habitat: coast and western watershed of the Andes in Ecuador and Perú. Map fig. 236 *P. lycaon* p. 71
13. Radial vein of forewing forming a rather wide angle with the costa (sometimes virtually perpendicular), and slightly bent and thickened at the actual junction; inner spur of hind tibia reaching to at least 0.30 of basitarsus length 14
- Radial vein of forewing forming a rather shallow angle with the costa, usually not bent or thickened at the junction; inner spur of hind tibia variable 20
Note: some species of the *P. sommeri*-group (not treated in this part) will run to here; they are distinguished by their extremely fine DTC.
14. Wings orange-amber with dark apical band; lateral extension of S.2 groove absent (occasionally vestigial, cf. fig. 203); USA to Panamá. Map fig. 235 *P. aquila* p. 63
- Wings usually otherwise coloured; lateral extension of S.2 groove often present; Andes and western desert coast of South America; (*P. hymenaea*-group) 15
15. Large, robust species with amber wings (BL 25-42); Andes and desert coast of Ecuador and Perú 16
- Species usually more slender and smaller; if large, then wings black or mainly so; always at moderate to high altitudes 17
16. Antenna orange. Forewing & head figs 191,192. North-western Perú only. Map fig. 238 *P. pulawskii* p. 79
- Antenna black. Forewing & head figs 193,194. Widespread in Andes and desert coast of Ecuador and Perú. Map fig. 238 *P. tolteca* p. 78
17. Larger species (BL 27-37) of the High Andes in Colombia; wings black, with or without circular orange-yellow patch near apex of forewing. Forewing & head figs. 195,196. Map fig. 238 *P. stella* p. 77
- Medium to small species (BL 20-31) found elsewhere; wing colour variable 18
18. Medium-sized species (BL 25-31) of eastern Perú: Urubamba valley at Machu Picchu, possibly also Chanchamayo valley. Forewing & head figs 197,198. Map fig. 238 *P. marthae* p. 82
- Smaller species (BL 20-28); forewing & head figs 199, 200; found elsewhere. Map fig.238 19
19. Ecuadorean Andes: Baños and Mérida (12k east of Baños). Map fig. 238 *P. cofanes* p. 76
- Venezuelan Andes. Map fig. 238 *P. hymenaea* p. 75
20. T.1 transversely swollen, so that sides are slightly angulate in dorsal view (fig. 205); large, entirely black species with lateral extension of S.2 groove absent or very weak; Guianas and Amazon southwards. Map fig. 235 *P. elevata* p. 64
- If T.1 is swollen, sides are evenly rounded, not angulate 21
21. Large species of West Indies, occasionally Florida (BL 30-55); lacking lateral extension of S.2 groove; wings orange-amber with dark apical band. Map fig. 235 *P. marginata* p. 67
- If species large and occurring in West Indies, the lateral extension of the S.2

- groove is well-developed and the wings are differently coloured 22
22. Hind tarsus with claw-tooth subapical, at least 3/4 from claw base, and setae strongly sinuate where they pass over the tooth (figs 207, 209) 23
- Hind tarsus with claw-tooth sometimes beyond the mid-point, but not subapical; setae not or scarcely sinuate where they pass over the tooth (figs 213, 219) 26
23. Body including gaster with abundant ashy-white pubescence forming strong patterns; head & hind claw figs 206, 207. Western watershed of Ecuadorean Andes. Map fig. 243 *P. ecuadorae* p. 111
- Body without obvious pubescence patterns 24
24. Species of Central America, occasionally north-western South America but not reaching Amazon mainstream, map fig. 243. Head & hind claw figs 208, 209 *P. tricuspidata* p. 109
- Species of Amazon mainstream southwards 25
25. Head in dorsal view with temple quite strongly swollen (fig. 214), AE index lower (94-113); forewing with more or less distinct pale apex; a mainly southern South American species, not reaching Amazon. Map fig. 243 *P. defecta* p. 108
- Head in dorsal view scarcely swollen (fig. 210), AE index higher (113-136); forewing with at most a very indistinct pale apex; fairly common along the Amazon and extending southwards as far as *P. defecta*, but less commonly so; map fig. 242 *P. apicata* p. 105
26. Head, thorax and propodeum (usually also at least T.1 of gaster) with golden or silver-golden pubescence forming strong patterns 27
- Note: *P. optimatis* Smith (Part 3) will run here, but it is distinguished by its strongly transverse propodeum (shorter than quadrate) and from the majority also by its smaller size, BL 24-38.
- Body with at most dull metallic pubescence, not forming strong patterns (sometimes dull golden with violet tinge in parts, continuous on most surfaces) 29
27. Wings very dark brown; on gaster, bright golden pubescence usually extending to T.1, only little if any on T.2 onwards; head fig. 211. Colombian Andes, map fig. 245 *P. sumptuosa* p. 116
- Wings amber to orange; bright pubescence forming apical bands on most tergites; habitat usually elsewhere 28
28. Pubescence silver-golden; head fig. 212; hind claw fig. 213; western watershed of Andes in Colombia and Ecuador, map fig. 244 *P. onorei* p. 111
- Pubescence golden; species of the Guiana lowlands, Amazon basin and eastern Brazil. *P. aurozonata* & *P. plutus* (maps figs 240, 243) (see table under *P. aurozonata*) p. 97
29. Rather large species (BL 33-38) of Lower Amazon only, map fig. 241; wings smoky-amber, forewing with pale apex; AE index 125-137; lateral extension of S.2 groove very weak; inner spur of hind tibia reaching to at most 0.15 hind basitarsus length; head fig. 216. *P. aurifex* p. 100
- Note: two species to be treated in Part 3 are similar to *P. aurifex*, but are not known from the Lower Amazon; they also differ as follows: *P. asteria* Mocsáry: most specimens have the inner spur of the hind tibia much longer; *P. minarum* Brèthes is smaller (BL 20-25) and has a much lower AE index (73-86).
- If the species is found on the Lower Amazon, other characters do not coincide .. 30

30. Very large, entirely dark species, (BL 38-58) of central, eastern and south-eastern Brazil; AE index 113-118; hind tibia with teeth usually rounded (fig. 232) and inner spur reaching to at most 0.20 basitarsus length; lateral extension of S.2 groove weak or absent; head fig. 231; map fig. 246 *P. hyperion* p. 125
 - If the species is very large, other characters do not coincide 31
31. Face and especially clypeus with very distinct reticulation, head fig. 217; map fig. 241 *P. riopretensis* p. 101
 - Face and clypeus with only the usual puncturation 32
32. Inner spur of hind tibia very short, reaching to at most 0.20 basitarsus length (scarcely longer than maximum width of tibial apex); at least one MPN carina very strong 33
 - If the inner spur of the hind tibia is as short, all MPN carinae are extremely fine (several species of the *P. sommeri*-group, to be treated in Part 3)
33. AE index very high (143-162), head in dorsal view with temple scarcely swollen (figs 225, 226) 34
 - AE index high (105-136), head in dorsal view with temple fairly strongly swollen (figs 215, 218, 233) 35
34. Habitat widespread east of the Andes, map fig. 244; very large species (BL 40-55); head fig. 226; wings dark orange-amber *P. pulszkyi* p. 114
 - Habitat southern Mexico (Yucatan and Chiapas), map fig. 246; large species (BL 33-47); wings usually pale yellowish-amber and forewing with more or less distinct pale apex (some specimens from higher altitudes in Chiapas have orange wings, sometimes with the forewing apex dark); head fig. 225 *P. yucatani* p. 121
35. Lateral extension of S.2 groove absent or almost so; medium-sized species (BL 27-41); habitat south-eastern South America, map fig. 245; head fig. 218; hind claw fig. 219 *P. bonplandi* p. 123
 - Lateral extension of S.2 groove well-developed; large to very large species (BL 37-57); found elsewhere 36
36. Habitat Mexico and Central America, occasionally north of the Venezuelan Andes and west of the Ecuadorean Andes, map fig. 245; AE index high (112-118); large species (BL 37-52); head fig. 215 *P. optima* p. 118
 - Habitat eastern watershed of Andes in Ecuador and Perú, map fig. 246; AE index 119-136; very large species (BL 42-57); head fig. 233 *P. toppini* p. 120

The species-groups
The *P. grossa*-group

Definition.— Male SGP elongate, with blunt median ridge, apically upcurved, mostly covered with very coarse hair. Female anterior femur with much coarse hair below; forewing radius joining costa at a very shallow angle (fig. 190 – as in the *P. rubra*-group); S.2 groove lateral extension well developed (fig. 189); head with temple and vertex strongly swollen. Both sexes with strong PTC.

Description.— Large, robust species (BL males 23-40, females (20-)30-51). Body hair and antennae black (tips of the latter more or less orange). Wings orange-amber (*P. chacoana*) or orange-amber with a black border or entirely black, sometimes with amber markings.

Distribution.— Found from the U.S.A. and West Indies to north coastal Perú, western Amazon basin and the Guianas; and south-central Brazil, Paraguay, northern Argentina and Uruguay.

Phylogenetics.— This sister-pair forms the sister-group of the *P. rubra*-group, based on the strong apomorphy of the shallow radius/costa junction in the female forewing; however, the male SGP shape also indicates a fairly close relationship with the *P. elevata*-group.

Of the four species-pairs so far studied this one has perhaps the strongest structural character distinguishing its two species from each other: the male of *P. grossa* has only 12 antennal segments, as in the female (the normal male number is 13). Not only is this species thus unique in the genus, but the character also strongly confirms the distinct species status of the two taxa. This in turn strongly suggests similar status for the other species-pairs which occupy a comparable phylogenetic position.

Biogeography.— The very wide, transandean range of *P. grossa* on the one hand, and the very restricted southern range of *P. chacoana* on the other, illustrate well the generally allopatric patterns of the species-pairs; however, the range of *P. grossa* is more extensive in the north than that of the northern component of any other species-pair (i.e. species of comparable phylogenetic position); not only is it widespread in the U.S.A., but it has also reached the West Indies. Furthermore, it also occurs in western Ecuador and northwest Perú, albeit in a strange colour form (see Lygarochromy discussion in Part 1); *P. chacoana* has also reached a more southerly position than usual. These facts suggest that the pair spread more rapidly than the others due to greater altitude/latitude adaptability.

Pepsis chacoana Brèthes, 1908
(figs 73-75, 185, 234)

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

Type-material.— Lectotype: I have seen two conspecific ♂ syntypes in MACN. The one I have labelled lectotype has badly abraded wings but better-condition antennae than the paralectotype. Both are labelled "Colonia Popular" but the lectotype is further labelled "35 k.N.O. de Resistencia, Chaco". A ♀ standing under the name *P. chacoana* in MACN is without type status, since Brèthes did not describe that sex; it belongs to a species of a different group.

Description.— ♂. BL 23-33. Body and legs black with blue-green sheen, and violet tinge especially on legs. Antenna black with up to 3 apical segments orange on outer side. Wings orange with variably distinct dark border, sometimes weakly entering cells; extreme apex of forewing often slightly pale; base of wings narrowly infusate, forewing with a usually very narrow sub-basal band of silvery pubescence. S.5 with slightly denser hairs than on the preceding sternites; S.6 with the hairs denser still but shorter. SGP (figs 73, 74) very similar to that of *P. grossa* but with the apex more rounded and more strongly upturned. Paramere (fig. 75) scarcely angulate on the inner side.

♀. BL 39-45. AE index 76-93. Colour as in male, except apices of antennal segments 3 onwards, and last 2-3 segments more extensively, dull brown. Dark border of wings obscure, but sub-basal band of silvery pubescence broader. Head in dorsal view with

vertex and temples very strongly swollen. MT weak. MPN a little shorter than PST, its furrow broad; carinae mostly fine. Propodeum: APT weak to moderate, PPT small but sharp. DTC fairly strong, weaker and a little denser posterad. PTC strong, flat-topped. Propodeal hair about as long as PST. Posterior face: VR absent, PFC quite strong above, a little weaker below, covering whole of face. Lateral extension of S.2 groove strong. Anterior femur with much coarse hair below. Hind tibia (fig. 185): teeth rather small, the subtending spines scarcely higher. Inner spur reaching to 0.25-0.3 basitarsus length (a little longer than tarsal segment 3) and 1.3-1.4 times as long as outer spur.

Variation.— Only as given above.

Distinctions.— Structurally similar to *P. grossa*, but distantly allopatric and in colour somewhat resembling only the geographically most distant form of that species in the USA; the male of *P. chacoana* has the normal number (13) of antennal segments; its SGP apex is slightly wider, more rounded and more strongly upturned; the parameres exhibit parallel differences. *P. chacoana* strongly resembles the orange-winged species of the *P. rubra*-group which are sympatric in Argentina; the male SGP is diagnostic for that sex, and the female is distinguished by its very strongly swollen vertex and temples, hind tibial spines scarcely longer than teeth (fig. 185) (spines distinctly longer than teeth in *P. rubra*-group species), and coarse hair below the anterior femur.

Distribution.— Found only in the Chaco and adjacent areas of Argentina, Uruguay, Paraguay and Bolivia, at low altitudes (map fig. 234).

Material.— 101 ♂♂, 34 ♀♀; AEIG, BMNH, COOPER, CUNY, EMMSU, FRITZ, IMLT, MACN, MCZ, MHNGV, MNHNPS, MNHNPY, MNRJ, MZUSP, NRS, OSUC, RMNH, WAHIS, WASBAUER.

Pepsis grossa (Fabricius, 1798)
(figs 69-72, 186-190, 234)

Sphex grossa Fabricius, 1798: 245, no. 89-90. India [incorrect locality]. Lectotype ♂ (UZMCK), here designated [examined].

Pepsis grossa (Fabricius) 1804: 214, no. 32.

Pompilus formosus Say, 1823: 76, ♀. Arkansas River within 100 miles of the Rocky Mts. (lost).

Pepsis affinis Dahlbom, 1845: 464, no. 9. Lectotype ♀ (MZEL), here designated [examined]. **Syn. nov.**

Pepsis formosa (Say); Neotype ♂, New Mexico (CAS). [Designated by Hurd, 1948:135]. **Syn. nov.**

Pepsis obliqu rugosa Lucas, 1895: 576, no. 51. Lectotype ♀ (MNHU), here designated [examined]. **Syn. nov.**

Pepsis nephele Lucas, 1895: 739, no. 138. Lectotype ♀ (TMB), here designated [examined]. **Syn. nov.**

Pepsis pseudoformosa Cockerell, 1898: 146 (no type-material). [Synonymized by Hurd, 1952: 285].

Pepsis formosa var. *theresia* Kriechbaumer, 1900: 102. Lectotype ♂ (ZSM), here designated [examined].

Syn. nov.

Pepsis colombica Brèthes, 1926: 9. Lectotype ♂ (MACN), here designated [examined]. **Syn. nov.**

Pepsis pattoni Banks, 1945: 181. Holotype ♀ (MCZ) [examined]. **Syn. nov.**

Pepsis pellita Haupt, 1952: 400. Lectotype ♂ (MLU), here designated [examined]. **Syn. nov.**

[*Pepsis terminata* Dahlbom; Alayo, 1969: 9. Misidentification].

Type-material.— *P. grossa*: I have seen a single, headless type-material ♂ labelled "*grossa*" and labelled it lectotype. *P. affinis*: I have seen a single type-material ♀ bearing the labels: "*affinis* nov. sp."; and another (written in Latin) indicating that the author thought that this species was intermediate between his *P. terminata* and Fabricius' *P. elevata*; the latter label also says "Surinam. Roger. Dufour.". I have labelled this specimen lectotype. *P. obliqu rugosa*: I have seen two conspecific ♀ syntypes, and

have labelled the one (locality "Cuba") in MNHU as lectotype. The paralectotype in NMV bears no locality, although Lucas gives St. Thomas. *P. nephela*: I have seen a single type-material ♀ and labelled it lectotype. *P. colombica*: I have seen two conspecific syntypes, one of each sex, and labelled the ♂ as lectotype; the ♀ is a paralectotype. *P. pellita*: I have seen a single type-material ♂ and labelled it lectotype; it belongs to the lygarochromic form of its species. *P. theresiae*: I have seen a single type-material ♂ and labelled it lectotype.

Description.— ♂. BL 24-40. Body and legs black with mainly blue-green sheen, often with violet or copper tinge. Antenna black, usually with tip of last segment

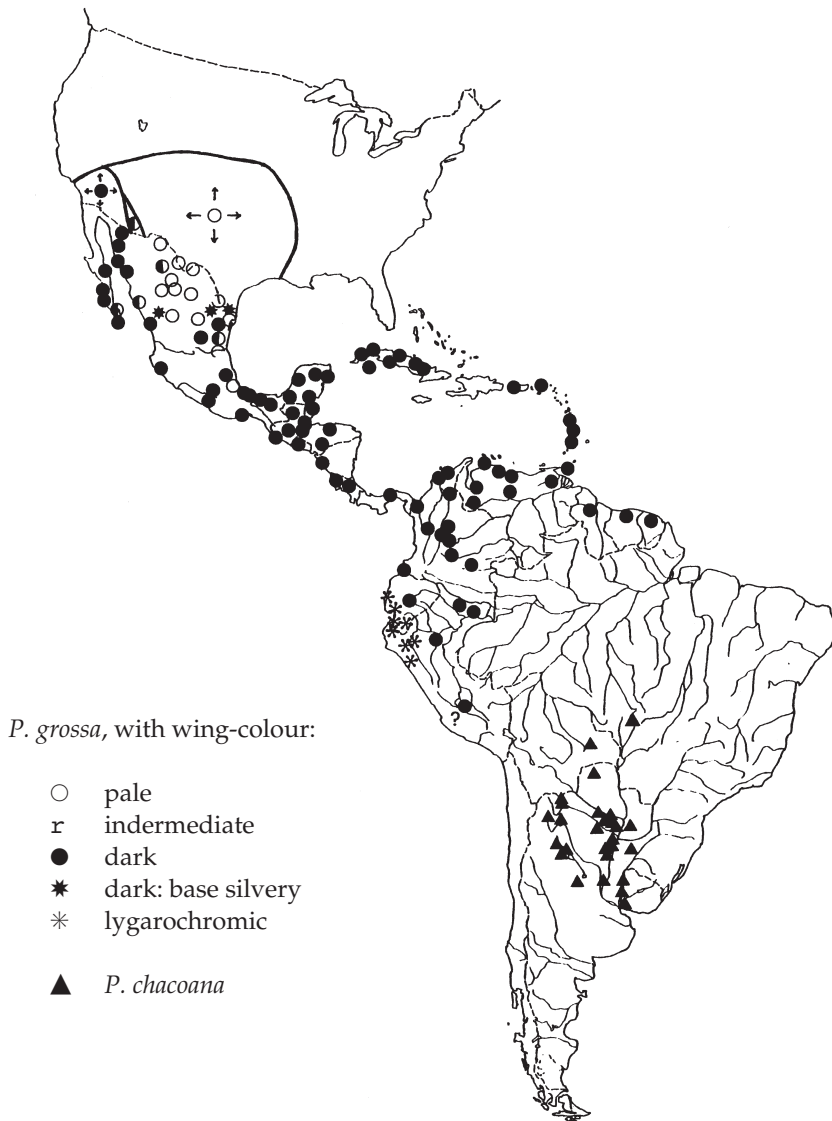


Fig. 234. Collection localities of *Pepsis grossa* (Fabricius) and *P. chacoana* Brèthes.

orange. Wings normally black with quite strong blue-violet reflections, sometimes infuscate-amber or orange, often with a dark border; base always more-or-less infuscate and apices white, the latter broader and more distinct in the male (see Variation). Antenna with only 12 segments (unique for the genus). S.5 with slightly denser hair than preceding sternites, that on S.6 denser still but shorter. SGP (figs 69,70) elongate, gradually narrower and quite strongly upturned apicad; side with a very weak, obtuse angle just before middle; expanded slightly just before the apex; with a median keel which is sharp basally, flattens out apicad and forms a pre-apical, depressed, polished area irregularly delimited distally by a raised margin; apex rounded, centrally notched and with the apex very narrowly translucent; many long, coarse hairs are present, concentrated in the median line and apically; paramere (fig. 71) about twice as long as rest of genitalia, with an obtuse angle on the inner side. Digitus as in fig. 72.

♀. BL (20-)30-51. AE index 83-101 (antenna with the normal female complement of 12 segments). Otherwise as male, except: extreme apices of antennal segments 3 onwards often dull orange. White apical margin of wings less well-defined. Head (figs 187,188) with temple and vertex very strongly swollen. MT weak. Forewing with PPV rather long, almost axial. MPN slightly to distinctly shorter than PST, its furrow broad, more or less expanded posterad; carinae: a few coarse, the rest extremely fine. Propodeum: MG usually rather weakly indicated anteriorly and posteriorly. APT very weak, PPT rather small but usually sharp. DTC fairly strong and dense (but see Variation). PTC narrow but very high, more-or-less flat-topped. Propodeal hair about as long as PST. Posterior face: VR absent, PFC covering entire face but often weaker and denser in lower half. Anterior femur with much, long, coarse hair below (sometimes very abraded). Hind tibia (fig. 186): teeth rather narrow and distant, subtending spines 1.5-2.0 times as high; inner spur reaching to 0.25-0.35 basitarsus length (about equal to tarsal segment 2 or slightly shorter) and 1.2-1.5 times as long as outer spur.

Variation.— The apices of the antennal segments are more often orange in specimens from the USA, central America and the West Indies than in the rest of the species' range. The wings are normally black, but in specimens from the southeastern USA. and northern Mexico they are orange with a fairly broad, dark border which often enters the outer cells in the forewing, and the white apex is obscure in both sexes.

Another pale form, quite distinct from the nearctic one, is found in a small area of north-west Perú and adjacent Ecuador (lygarochromic form). Both wings are heavily infuscate basally; beyond this, the forewing has a variably-sized dark amber patch, becoming more heavily infuscate until giving way to the pale apex; the rest of the hind wing is pale amber until the pale apex, which is sometimes preceded by a narrow band of weak infuscation. An interesting structural variation found mainly in males of this form is that the apical half of T.1 has a short, median groove; this is apparently a character-reversal, being a normal character of the distantly related *P. chiliensis*- and *brevicornis*-groups. The character is weaker and less frequent in females, and virtually absent from other colour forms of *P. grossa*.

Another curious feature of structural variation, found only in this species, is that females from Yucatán, Panamá, the West Indies and Trinidad display a strong tendency for the DTC to be obliquely or even longitudinally oriented (*P. obliquerugosa* Lucas). Although I have seen such specimens from Yucatán, Panamá, Cuba, Puerto Rico, St Thomas, Dominica, Martinique, St. Lucia, St. Vincent and Trinidad, this peculiarity has

not been observed in any other populations of this wide-ranging, common species.

Biology.—Cazier & Mortenson (1964: 533-541) give details of nesting behaviour of this species [as *P. formosa*]; the prey is stated to be *Aphonopelma chalcodes* Chamberlin. Cooke (1985) gives colour photographs of a *Pepsis* wasp attacking a tarantula spider, which he names as *Aphonopelma* sp. The wasp appears to be the nearctic pale form of *Pepsis grossa*, to judge by the strongly swollen vertex, and the infuscation entering the second discoidal cell of the forewing.

Punzo & Garman (1989) treated hunting behaviour of *Pepsis grossa* [as *P. formosa*] in the USA. (Texas, Brewster Co.). Their main conclusion was that "The time required to complete the hunting sequence [of behaviours] significantly decreased with increasing numbers of encounters between the wasp and its tarantula host, *Rhechostica echina* (Simon)". Punzo & Garman (1989: 513) found that *P. grossa* [as *P. formosa*] usually preyed on *Rhechostica echina* Simon, but (Punzo, 1994a, b) found that it could use *Aphonopelma echina* Chamberlin (the prey of *P. thisbe*) where it occurred sympatrically with *P. thisbe* in Trans Pecos, Texas. [This needs further investigation; it is the opposite of what would be expected if competition were to be minimized where the two wasp species occur sympatrically.] However, *P. grossa* [as *P. formosa*] females required a longer period of time to complete the hunting sequence in initial encounters.

A female from Ecuador, Llanos (TMB) has a cocoon without a label pinned beside it. The cocoon is approximately 55 mm long, and consists of two completely separated layers; nearly half of the outer one has been cut away. Both are made of a thin, extremely tough but flexible reddish-brown material, with a superficial, apparently less dense, yellowish layer which is partly rubbed away.

Distinctions.—The male has a very distinctive SGP and a 12-segmented antenna, which is unique in the genus. In the female, the head is very strongly swollen, the anterior femur has much long, coarse hair below, and the wing apices are white (when both are abraded, at least the hair insertion pits are visible). Both sexes are distinguished from their counterparts of *P. chacoana* on the basis of wing colour and distant allopatry. Caution is needed to separate females from those of *P. inbio* and *assimilis* (both in Part 1) where sympatric with them; the latter two never have coarse hair below the front femur (sometimes abaded in *P. grossa*!); neither do they have such a strongly swollen head.

Distribution.—Found from the southern USA and the West Indies to north-central Perú and the Guianas, ascending to 2,000 m in Mexico (Durango) (map fig. 234).

Material.—481 ♂♂, 318 ♀♀; AMNH, ANSP, BMNH, BPBM, BRIO, CAS, CMNH, COOPER, CSU, CUNY, EMMSU, ETHZ, FDA, FRITZ, FSAG, GILLASPY, INBIO, LACM, MACN, MCZ, MEM, MHNGV, MHNLM, MHNNEU, MICR, MIZAM, MLUH, MNCSJ, MNHNPS, MNHU, MNRJ, MZEL, NHMBAS, NMV, NMWC, NRS, OSUC, PORTER, PUCEQ, RMNH, SEMKU, SMF, TEXAMU, TMB, UCALB, UCALD, UCMB, UMBREM, UMOX, UNALM, UNCBG, UNLAMB, UNPBOG, UPAN, USNM, USU, UZMC, WAHIS, WASBAUER, WILLIAMS, ZMMICH, ZSM.

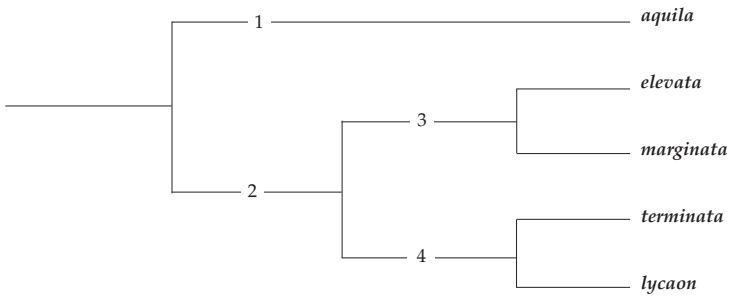
The *P. elevata*-group

Definition.—Male SGP with more or less sharp median carina. Female with lateral extension of S.2 groove absent (fig. 203) or very weak.

Description.— Medium to large species (BL males 12-37, females 17-55). Wing colour orange-amber to crimson with variably wide black border; or entirely black, sometimes with white apex, occasionally also white sub-basal band. Body black, antennae black with apex more or less orange.

Distribution.— This group is found in Mexico and Central America, the West Indies, and the whole of South America except Chile; it just reaches the USA and Argentina.

Cladogram for the *P. elevata*-group



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

1. SGP apex strongly rounded; inner, apical projection of digitus pointed.
2. SGP apex emarginate; basal half with lateral hair fringe.
3. SGP keel partly blade-like.
4. Body size small; forewing white-banded.

Phylogenetics.— Although this group consists of only 5 species, like other, larger groups it has an isolated species (*P. aquila*), but which may not be the oldest one; the rest show the usual bifurcation. However, this group differs in that it lacks a species-pair as its sister-group; instead, the *P. rubra*- and *grossa*-groups are together its sister-group. The reasons for this conclusion are that the *P. grossa*-group, although showing strong resemblance to the *P. elevata*-group (especially in the SGP structure) shares two strong synapomorphies with the *P. rubra*-group but not with the *P. elevata*-group; these are the female forewing venation character (see Cladogram), and the well-developed lateral extension of the female S.2 groove. Therefore the *P. grossa*-group is not considered to be the sister-group of the *P. elevata*-group (if it were, then the *P. rubra*-group would instead lack a species-pair sister-group). The *P. terminata-lycaon* pair display characters not shared with the rest of the *P. elevata*-group, but they are not particularly unusual. Thus the characters which distinguish this pair from the remaining species of the *P. elevata*-group do not appear to parallel those of other species-pairs, inasmuch as this pair possesses no apomorphy which is both unique in the genus and which distinguishes it from the remainder of the *P. elevata*-group. Further concordant evidence is that the species appear less closely related than do other species-pairs; neither do their distribution patterns parallel them.

Biogeography.— The composition and distribution of this group do not closely resemble those of any other group so far treated, and are doubtless a reflection of its phylogenetic position, which suggests an earlier origin. Its range shows a northern

bias: out of only five species comprising the group, two have reached the USA and two the West Indies, while only one species has scarcely reached Argentina. One species is the most widespread in the genus, including reaching the High Andes – a feat accomplished by very few other species. Although lacking a species-pair as sister-group, the *P. elevata*-group is comparable with other larger groups in that it has a single, isolated species (*P. aquila*); however, this species is the only one of comparable phylogenetic position to occupy an area north of South America (i.e. Mexico and Central America); it is also a small species, unlike the oldest species of most other multiple groups. This group's very wide distributional range, especially in the north, and considerable degree of altitude adaptation, contrast strongly with its paucity of numbers; these facts suggest an early expansion of the group followed by much extinction. The *P. elevata*-group must have existed at the time of the vicariance event which split off the ancestors of the species-pairs (i.e. the sister-groups of all the other main groups so far treated), yet appears not to have been subject to it, perhaps because it was literally not in a position to be.

Pepsis aquila Lucas, 1895
(figs 144-146, 235)

Pepsis pyramus Lucas, 1895: 742, no. 141. Lectotype ♂ (MNHU), here designated [examined]. **Syn. nov.** [*Pepsis bonariensis* Lepeletier; Lucas, 1895: 760. Misidentification].

Pepsis aquila Lucas, 1895: 797, no. 173. Lectotype ♂ (TMB), here designated [examined].

Pepsis linsleyi Hurd, 1950: 132. [Replacement name for *bonariensis* Lepeletier; Lucas, 1895, not Lepeletier].

Pepsis praetexta Haupt, 1952: 362. [Replacement name for *bonariensis* Lepeletier; Lucas, 1895, not Lepeletier].

Pepsis pallidipennis Haupt, 1952: 363, no. 10. Holotype ♀ (MLU) [examined]. **Syn. nov.**

Note.— The name *aquila* is retained because it is in current usage and is shorter than the first available name.

Type-material.— *P. aquila*: I have seen a single type-material ♂ and labelled it lectotype. *P. pyramus*: I have seen only a syntype ♂, and labelled it lectotype.

Description.— ♂. BL 21-32. Body and legs black with blue to blue-violet or blue-green sheen. Antenna mostly orange or entirely black. Wings orange, sometimes slightly infuscate; the bases scarcely infuscate, the apex with a dark band. Sternal hairs essentially unmodified; hairs on S.5, and especially S.6, denser than on preceding sternites. SGP (figs 145, 146) with a strong, central, basal, pointed tubercle; from this a keel runs apicad, very sharp at first but rapidly obsolescent; the tubercle is also transversely extended by a very weak keel; SGP slightly expanded laterally apicad and the edge is most strongly raised opposite the point where the median keel becomes obsolete; the apex is strongly rounded. Thus the SGP is strongly convex in the basal half and strongly concave in the apical. Paramere about twice as long as rest of genitalia, rounded apically. Digitus fig. 144.

♀. BL 30-37. AE index (88-)101-117. Colour as in male. Head in dorsal view with vertex (but not temples) quite strongly swollen, forming a more or less distinct ridge; in fresh specimens basal half of AS3 usually with a few bristles. Forewing with PPV almost axial. MT weak to absent. MPN usually distinctly shorter than PST, its furrow

broad; one or two carinae very strong, the rest extremely fine. Propodeum: MG replaced by a broad, flat-topped ridge. APT weak to moderate, PPT small but transversely quite sharp. DTC moderately strong anteriorly, becoming stronger and more distant apicad; with more or less distinct interstitial punctures, especially anteriorly. PTC broad, very strong, usually flat-topped. Propodeal hair about as long as PST + 1/2 MPN. Posterior face: VR absent, PFC weak above, weaker still medially, but usually stronger below, where the general surface also becomes more shiny. Lateral extension of S.2 groove absent, occasionally vestigial. Anterior femur with abundant coarse hair of varied length below; middle femur with sparser hair, posterior with very few. Hind tibia: teeth rather small and distant, the subtending spines 1.5-2.5 times as high; inner spur reaching to 0.35-0.4 basitarsus length (about equal to tarsal segment 2) and 1.3-1.5 times as long as outer spur (but see Variation).

Variation.— The antenna in both sexes is usually orange from segment 3 onwards, occasionally entirely black (when this is the case in females, the apices of the segments are narrowly orange); no intermediates have been seen. This situation, together with some unusual variation in the male SGP structure (see figs 145, 146), suggested the possible existence of more than a single species but further investigation failed to substantiate this. The apical wing-band usually covers most of the area outside of the cells, but is quite variable in width and definition. Two females from Mexico (Durango, 20 mi ne Durango (BRIO); and [Jalisco] Guadalajara (EMMSU)) have the inner spur of the hind tibia extremely short, as in females of the *P. sumptuosa*-group. The first-mentioned specimen has the extremely low AE index of 88; both specimens are otherwise normal. In view of the phenomenon of sympatric convergence, common in the genus, it may be significant that the southern part of the distributional range of this species overlaps that of certain *P. sumptuosa*-group species.

Distinctions.— The male is easily distinguished from those of other species by its colour and SGP structure, despite variation. The female is best distinguished by its colour, lack of lateral extensions of the S.2 groove, MPN sculpture, and distinct propodeal puncturation.

Distribution.— Southern USA. to Panamá, ascending to 2,000 m in the USA. and several parts of Mexico. A single record of a female from Chile: Santiago (MLU) (holotype of *P. pallidipennis*) appears to represent a labelling error. A record of three males from Ecuador [no further locality] (USNM) needs confirmation (map fig. 235).

Material.— 120 ♂♂, 92 ♀♀; AEIG, AMNH, ANSP, BMNH, BRIO, CAS, CUNY, EMMSU, FDA, INBIO, LACM, MCZ, MEM, MHNGV, MICR, MLU, MNHNPS, MNHU, NRS, RMNH, SEMKU, SMF, TEXAM, TMB, UCALD, UNAN, USNM, USU, WAHIS, WASBAUER, WILLIAMS, ZMMICH.

Pepsis elevata Fabricius, 1804
(figs 103-105, 205, 235)

Pepsis elevata Fabricius, 1804: 213, no. 30. Lectotype ♀ (UZMC), here designated [examined].

Pepsis elevata Fabricius; Perty, 1833: 143, pl. 28, f. 1. [A correct interpretation, despite his expressed doubts – see also *P. pertyi* Lucas under *P. albocincta* in Part 1 of this work].

Pepsis sciron Mocsáry, 1885: 250, no. 18. Lectotype ♀ (TMB), here designated [examined]. [Synonymized by Lucas, 1895: 685].

Pepsis cristata Haupt, 1952: 396. Lectotype ♂ (MLU), here designated [examined]. **Syn. nov.**

Type-material.— *P. elevata*: Petersen (pers. comm.) noted four specimens standing under *P. elevata* in UZMC: one in S. & T.L. and three in the Kiel Collection. I have seen the first-mentioned specimen, a ♀, which bears an original Fabrician type label, and labelled it lectotype. Petersen believed that the three in the Kiel Collection were probably not conspecific with the lectotype, but stated that two of them were labelled *Pepsis* sp. by Wahis. *P. sciron*. I have seen 2 ♂♂ and 3 ♀♀ standing under this name in TMB; however, only 2 of the ♀♀ qualify for syntype status. Of these, I have labelled as lectotype the larger one, which in this respect agrees better with the original description. It is also the only one bearing an original Mocsáry identification label. All 5 specimens are conspecific. *P. cristata*: I have seen a single type-material ♂ and labelled it lectotype.

Description.— ♂. BL (21-)24-33. Body and legs black with blue-green sheen. Antenna black, occasionally segments 3 onwards brown below. Wings black with blue-violet reflections. T.1 strongly transversely swollen. Hairs on S.5 slightly denser than on preceding sternites, on S.6 more so, but otherwise unmodified. SGP (figs 103, 104) elongate, very slightly narrower apicad, the apex truncate and slightly upturned with rounded corners, weakly emarginate centrally. A sharp, median keel extends from the base, ending rather abruptly a short distance from the apex. The lateral margin of the SGP has a narrow fringe of hair, fairly long and perpendicular to the edge basally, becoming shorter and more decumbent apicad. The apex itself is without hairs. Paramere about twice as long as the rest of the genitalia, rounded apically. Digitus fig. 105.

♀. BL 31-42. AE index 77-85. Colour as in male, except antennal segments 3 onwards often with extreme apices brown, sometimes also all these segments below. Head with temple slightly but vertex very strongly swollen. AS3 appearing quite short and thick. MT weak. Forewing with PPV almost axial. MPN equal to or shorter than PST, its furrow rather broad, often narrowest centrally; carinae mixed coarse and fine, matt. Propodeum: MG more or less indicated over its whole length, usually shallowest centrally. APT moderate, PPT strong, tooth- or peg-like. DTC fairly strong in anterior half, weaker or absent posteriorly; partly obscured by short pubescence. PTC very strong, emarginate, often almost bifid. Propodeal hair about as long as PST. Posterior face: VR absent, PFC a few fairly strong above but rapidly obsolescent medially and below. T.1 (fig. 205) distinctly transversely swollen (in dorsal view, slightly angulate laterally), but less so than in the male. Lateral extension of S.2 groove weak. Hind tibia: teeth rather small and sharp, the subtending spines 2.0-2.5 times as high; inner spur reaching to about 0.3-0.35 basitarsus length (between tarsal segments 2 and 3 in length), from equal to, to up to 1.2 times as long as, outer spur. Both spurs are quite strongly upcurved apicad.

Variation.— One of four males from Brazil: Pará, Jacareacanga (PAGLIANO) has AS3 onwards dull orange above.

Distinctions.— Both sexes are immediately distinguishable from all other large, dark-coloured *Pepsis* by the swollen T.1, although this character requires close observation to discern in the female. The male also has a distinctive SGP, and the female is distinguished from that of the very similar dark-winged form of *P. grossa* by the lack of pale wing-tips; that species also has subfemoral hair and much stronger lateral extension of the S.2 groove.

Distribution.— Found in the Guianas, along the Amazon and southwards to central Argentina and Uruguay; mainly a lowland species, but ascending to about 3,000 m in the western parts of its range (map fig. 235).

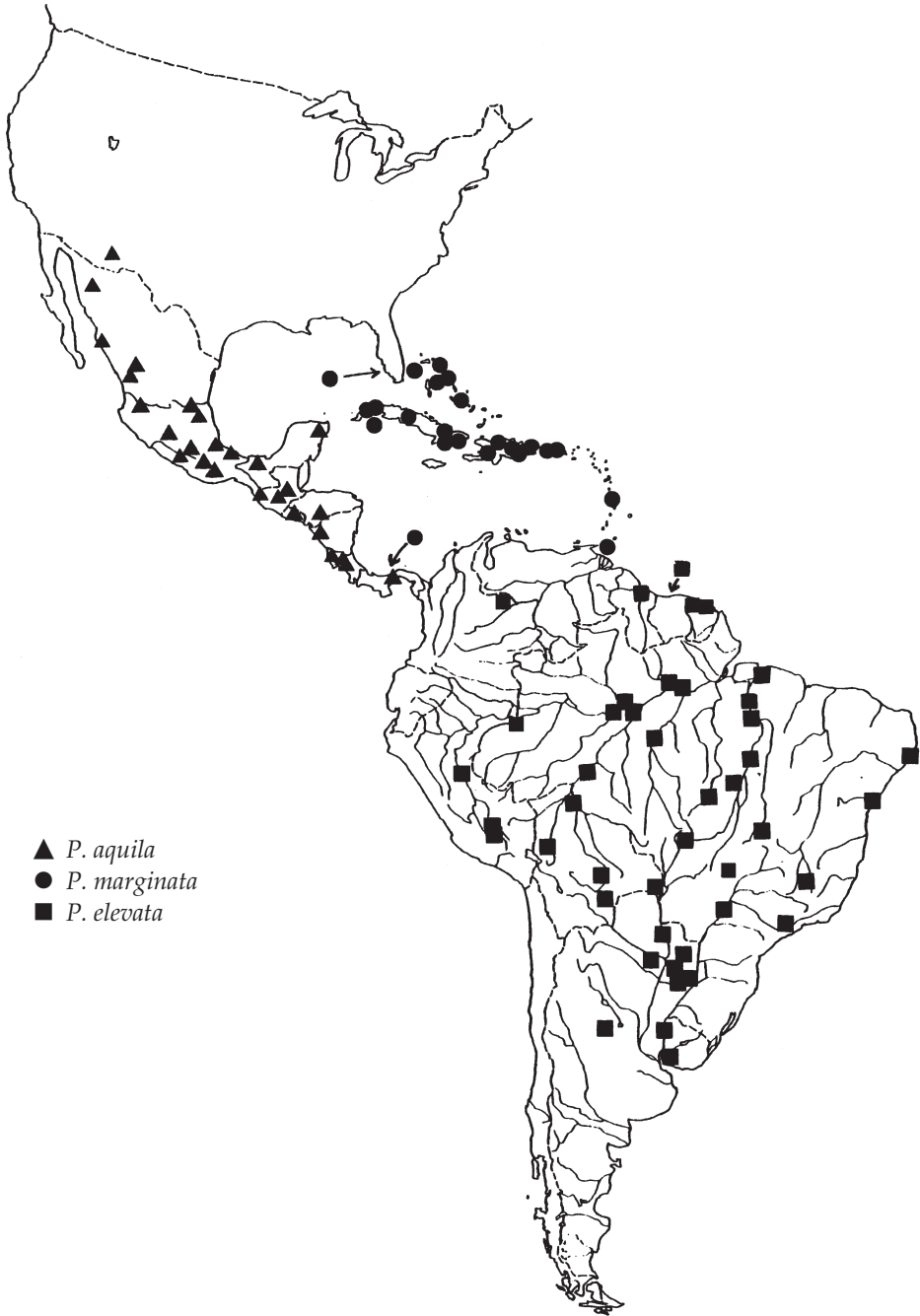


Fig. 235. Collection localities of *Pepsis aquila* Lucas, *P. marginata* Beauvois and *P. elevata* Fabricius.

Pepsis marginata Palisot de Beauvois, 1809
(figs 97-99, 235)

Pepsis marginata Palisot de Beauvois, 1809: 94, pl. 2, f. 2 & 3. Lectotype ♀ (MIZSU), here designated [examined].

Pepsis reaumuri Dahlbom, 1845: 465, no. 16. Lectotype ♀ (MZEL), here designated [examined]. **Syn. nov.** [*Pepsis heros* (Fabricius); Dahlbom, 1843: 122 (not 1845: 465). Misidentification].

Pepsis splendens Lucas, 1895: 749. [MS name cited in synonymy].

[*Pepsis nitida* Lepeletier; Lucas, 1895: 749. Misidentification].

[See also *Pepsis marginata* var. *sericata* in list of *Pepsis* species whose types are lost (in Part III).]

Type-material.— *P. marginata*: I have seen a single syntype ♀ and labelled it lectotype. It is an extremely large specimen of its species (BL 55) and is of historical interest as it is probably the sole surviving *Pepsis* type of Palisot de Beauvois. *P. reaumuri*: I have seen a single type-material ♀ and labelled it lectotype. This appears to be the specimen which Dahlbom misidentified as *P. heros* in 1843. In 1845 he misidentified a different species as *P. heros* (see under *P. frivaldszkyi* Mocs.).

Description.— ♂. BL (14-)27-37. Body and legs black with weak blue-violet sheen, pubescence dark. Antenna black. Wings bright orange to orange-brown, black at the base and with a broad, dark border covering most of the area outside the cells, sometimes just entering them. S.6 and 7 with hairs slightly denser than on preceding sternites but essentially unmodified. SGP (figs 97, 98) strongly bent up, with a median keel which is basally strongly raised into a blade; apex truncate-rounded, the outer corners thickened and polished. With lateral fringe of hair, basally rather long and perpendicular, shorter and more decumbent apicad. Paramere about twice as long as rest of genitalia, with rounded apex. Digitus fig. 99.

♀. BL 30-45(-55). AE index 100-112. Colour as in male, except: apices of antennal segments 3 onwards dull orange. Apical dark band of wings often more diffuse in larger specimens. Head with temple scarcely, but vertex very strongly swollen. MT weak or absent. Forewing covered with extremely short, dark hairs; SMC3 often short, its postero-distal angle rounded. MPN a little shorter than PST, its furrow broad; carinae few, strong. Propodeum: MG most commonly indicated anteriorly or centrally. APT weak to moderate, occasionally sharp. PPT small but usually sharp transversely. DTC quite strong, partially obscured by pilosity. Propodeal hair about as long as PST. Posterior face: VR absent, PFC covering whole face, fairly strong above but weaker medially and below (especially in smaller specimens). Lateral extension of S.2 groove extremely weak. Hind tibia: teeth rather narrow and sharp, with extremely short but dense pilosity between, the subtending spines 2.0-2.5 times as high as the teeth. Inner spur: reaching to 0.2-0.3 basitarsus length (about equal to tarsal segment 3), and equal to or scarcely shorter than outer spur.

Variation.— Only as already noted.

Distinctions.— The male has a very distinctive SGP. The female lacks the distinctive white wing apices of the sympatric *P. rubra* and *terminata*, but is similar to that of *P. sericans* (see Part I for differences). Additional characters for distinguishing female *P. marginata* are its lack of lateral extensions of the S.2 groove (a group-character) and a strong tendency for the SMC3 to be short, with its postero-distal angle rounded.

Biology.— Petrunkevitch (1926) gave an account of experiments on hunting behaviour and spider prey species.

Distribution.— Endemic to the West Indies and possibly southern Florida; up to 523 m in the Dominican Republic. A single female from an old collection (USNM) has been seen labelled "Trinidad Island" but this locality seems doubtful, as also does a single record from Panamá, Canal Zone (MCZ). Curiously, all the records from Puerto Rico pertain to the eastern half of the island (map fig. 235).

Material.— 100 ♂♂, 59 ♀♀; AFZD, AMNH, ANSP, BMNH, CMNH, CUNY, FDA, LACM, MACN, MCSNGO, MCZ, MEM, MHNGV, MHNNEU, MIZSU, MNHNPS, MZEL, NMV, NRS, PORTER, RMNH, TEXAMU, TMB, UMOX, USNM, WAHIS, ZSM.

Pepsis terminata Dahlbom, 1843
(figs 114-116, 201-204, 236)

Pepsis terminata Dahlbom, 1843: 120, no. 6. Lectotype ♀ (MZEL), here designated [examined].

Pepsis ferruginea Lepeletier, 1845: 471, ♀, Cayenne (lost). **Syn. nov.**

Pepsis ornata Lepeletier, 1845: 486. Lectotype ♂ (MIZSU), here designated [examined]. [Synonymized by Smith, 1855: 196].

Pepsis venusta Smith, 1855: 196, no. 27. Lectotype ♂ (BMNH), here designated [examined]. **Syn. nov.**

Pepsis albolimbata Mocsáry, 1885: 250, no. 17. Lectotype ♂ (TMB), here designated [examined]. **Syn. nov.**

Pepsis pulchripennis Mocsáry, 1885: 243, no. 8. Lectotype ♀ (TMB), here designated [examined]. **Syn. nov.**

Pepsis cyanosoma Lucas, 1895: 557, no. 42. Lectotype ♂ (MNHU), here designated [examined]. **Syn. nov.**

Pepsis acroleuca Lucas, 1895: 730, no. 134. Lectotype ♀ (MNHU), here designated [examined]. **Syn. nov.**

Pepsis mancoi Banks, 1946: 399. Holotype ♀ (MCZ) [examined]. **Syn. nov.**

Pepsis fuscrobura Brèthes, 1914: 321, no. 105. Lectotype ♀ (MZUSP), here designated [examined]. **Syn. nov.**

Type-material.— *P. terminata*: I have seen a single type ♀ and labelled it lectotype. *P. ornata*: I have seen two conspecific syntypes, one of each sex, and labelled the ♂ as lectotype; the ♀ is a paralectotype. *P. venusta*: I have seen a single type-material ♂ and labelled it lectotype. *P. albolimbata*: I have seen a single type-material ♂ and labelled it lectotype. *P. pulchripennis*: I have seen a single type-material ♀ and labelled it lectotype. *P. cyanosoma*: I have seen a single type-material ♂ and labelled it lectotype; the SGP and genitalia are missing. *P. acroleuca*: I have seen only a syntype ♀ which I have labelled lectotype. It bears no locality (the description gives none), but an Amazon provenance seems likely from the wing colour. Lucas, despite saying "female unknown", described both sexes. From the description, the ♂ is certainly conspecific. *P. fuscrobura*: I have seen a single type-material ♀ and labelled it lectotype.

Description.— ♂. BL 12-23(-29). Body and legs black with blue-green or blue-violet sheen. Antenna black with up to 3 apical segments orange. Wings black; forewing, sometimes also hindwing, with white apex; in the forewing usually limited to about half the area beyond the cells (but see Variation). S.6 with hairs denser than on preceding sternites but essentially unmodified. SGP (figs 114, 115) elongate, irregularly expanded to the apex, which is truncate with rounded corners and shallowly emarginate centrally. From a sharp, basal point, a strong median carina runs distad, and is obsolescent before the apex, which is concave. The sides are fringed with rather long but fine hairs, shorter and more decumbent apicad. Paramere nearly twice as long as rest of genitalia. Digitus fig. 116.

♀. BL 17-30(-40). AE index 69-98. Colour as in male except antenna entirely black. Wing colour very variable (see below), but always with at least a trace of a black border ending at a variable distance from the apex, which is white.

Head with temple and vertex slightly swollen. MT weak to moderate. Forewing (fig. 201) with SMC3 shorter than usual and with postero-distal angle rounded. MPN slightly to much shorter than PST, its furrow broad but often not reaching anterior margin (or

only in attenuated form); carinae variable, usually a few very strong, the rest extremely fine. Propodeum: MG sometimes shallowly indicated. APT moderate to strong, PPT weak to moderate. DTC quite strong but irregular, rather distant and partly obscured by pilosity. PTC weak to moderate, usually shallowly emarginate centrally. Propodeal hair about as long as PST. Posterior face: VR absent, PFC moderate above, weaker medially and below but usually covering most of face. T.1 (figs 202, 204) more or less strongly swollen. Lateral extension of S.2 groove (fig. 203) vestigial or absent. Fresh specimens have a moderate number of rather strong hairs below the femora (strongest in females from high altitude). Hind tibia: teeth smaller than usual, distant, the subtending spines 3-4 times as high; inner spur reaching to 0.25-0.35 basitarsus length (equal to tarsal segment 3 or slightly shorter), and 1.2-1.3 times as long as outer spur.

Variation.— The great diversity of colour in the genus *Pepsis* reaches its maximum in this species: not only does it display a greater than usual range of the kind of light-dark variation common in solitary wasps, in which it is rivalled only by *P. montezuma* Smith; it is also the most striking example of lygarochromic variation (see Part 1, fig. 2, p. 36 and Introduction p. 21).

Certain males have the white colour of the forewing apex more or less enlarged to include more than half the radial cell and all of SMC3; the antennal orange is also more extensive in these specimens, including up to three apical segments. These males occur mainly on or near the west coast from northern Mexico to Nicaragua, although one has been seen from northwestern Yucatán. It appears from the collecting data that these males are found together with, or at least close to, normal forms. In a few South American males, notably from the Peruvian Andes, the white apex extends a little along the costal margin. Alone in north-central Perú (the lygarochromic area), the hind wing also acquires a white apex.

The female has entirely black wings, apart from a white forewing apex, in the West Indies (with the sole exception of a red-winged female from Guadeloupe, probably mislabelled). In Mexico and Central America the wings are amber with a dark border. The wings are paler still in the higher valleys of the Peruvian Andes (upwards of c.1,000 m), where the dark border is often almost entirely lost. In the lygarochromic area of north-central Perú the forewing takes on a most beautiful, strong metallic lustre, usually golden but sometimes silver (one specimen in BMNH displays the two colours on opposite sides); the dark border often invades the second discoidal cell, and the hindwing acquires a white apex. In the remainder of the species' range, which comprises most of lowland South America except the temperate south, the forewing colour varies from amber through orange to dark crimson; the darker the general colour, the broader the dark border and the darker the hindwing.

Structural variation is of two particular kinds: some of the females from the high valleys of the Peruvian Andes exhibit a curious posterolateral, short, vertical groove on T.1 (fig. 204). The West Indian population of this species consists of larger-sized individuals on average than in any other area of its very wide range (see Introduction: "Large individuals on islands"); furthermore, in this area both sexes always have the wings entirely black except for the tips.

Distinctions.— The male is distinguished from those of other species possessing white wingtips by the SGP structure, although care is needed to separate it from the partly-sympatric *P. lycaon*, in which the median carina is continued level for a short

distance before becoming obsolescent. The female, with its many colour variations, has often been confused with those of other species. It differs from females of most other non-*P. elevata*-group species by its vestigial lateral extensions of the S.2 groove (fig. 203), and by its swollen T.1 (figs 202, 204). It differs further from other species as follows: in the West Indies, where it is parapatric with the red-winged species *P. rubra*, *P. terminata* is most easily distinguished by its black wings (a single red-winged female has been seen from Guadeloupe); but this renders it liable to be confused with *P. grossa* which also occurs there. However, apart from its larger size, the white wingtips in *P. grossa* are more obscure, it has a *P. rubra*-type radial cell, and the coarse, subfemoral hair is much reduced in *P. terminata*. In Mexico and Central America where it is sympatric with the black-winged *P. mexicana*, *P. terminata* always has amber wings with a dark border; on the other hand, because of this it resembles several other species sympatric in that area, but here as well as in the rest of its range, it is distinguished by its T.1 shape and lack of lateral extensions of the S.2 groove. Where *P. terminata* occurs within the restricted range of *P. vinipennis* (cf. fig. 236, and fig. 98 in Part I), the latter can be distinguished by its more obscure white wing apex, very short SMC3 and *rubra*-type radial cell. In the Andes *P. terminata* is difficult to distinguish from *P. tolteca* and pale forms of *P. montezuma*; a table is given below. Female *P. terminata* from the lygarochromic area of north-central Perú, because of their aberrant colour pattern, could easily be taken for a species of the *P. lampas*-group, but females of that group always have a highly-polished median area on the pygidium.

Distribution.— The most wide-ranging species of the genus, found almost everywhere from the southernmost USA southwards, from sea level to high altitudes (up to about 2,000 m in Mexico and Perú), but not known from Uruguay, Argentina or Chile. A record from Brazil, Rio Grande do Sul but without further locality (1 female, MZUSP) would be the southernmost if confirmed. In the West Indies, it appears to be absent between Cuba and Guadeloupe (map fig. 236).

Material.— 526 ♂♂, 504 ♀♀; AEIG, AMNH, ANSP, BMNH, BPBM, BRIO, CAR-RASCO, CAS, CMNH, COOPER, CSU, CUNY, EMMSU, FDA, FRITZ, GILLASPY, IMLT, INBIO, INPA, IPRI, LACM, MACN, MCSNGV, MCZ, MHNGV, MHNNEU, MNRJ, MIZAM, MICR, MIZSU, MNHNPS, MNHNPY, MNHU, MNS, MPEG, MZEL, MZUSP, NHMLIM, NMV, NRS, OCHOA, OSUC, PORTER, RIBPRET, RMNH, SEMKU, SMF, TEXAMU, TMB, UCALB, UCALD, UFPCUR, UFVIC, UMOX, UNAN, UNCUS, UNLAMB, USNM, USU, UZMC, WASBAUER, WILLIAMS, ZMMICH, ZSM.

Table for distinguishing between high-altitude forms of female *Pepsis terminata*, *montezuma* and *tolteca* with pale forewing tips. N.B. Identifications must be made on the basis of a majority of characters, because not all characters will work for every specimen.

<i>terminata</i>	<i>montezuma</i>	<i>tolteca</i>
Body sheen blue, tending to green.	Body sheen blue, tending to violet.	Body sheen blue, tending to violet.
Clypeus of normal length.	Clypeus similar to that of <i>terminata</i> .	Clypeus longer than usual.
Running forward from anterior ocellus is a broad, deep groove with a strong swelling on each side.	Frons similar to that of <i>terminata</i> .	Running forward from anterior ocellus is a narrow, shallow groove, the frons scarcely swollen beside it.

Infuscation of wingbase very narrow, extending along hind edge of forewing a shorter distance than thoracic width between tegulae.	Base of wings more broadly infuscate, extending along hind edge of forewing a much greater distance than thoracic width between tegulae.	Infuscation of wing-base rather narrow, extending along hind edge of forewing a distance equal to or less than thoracic width between tegulae.
Venation always as normal for the genus.	Venation always as normal for the genus.	PPV of SMC2 varies from normal to exceptionally long (cf. figs 181, 182). Forewing apex as in <i>montezuma</i> .
Pale forewing apex rather sharply delimited by at least a trace of black border. MT usually very weak, rarely sharp. Few hairs below anterior femur, almost none below mid or hind.	Pale forewing apex joins amber directly, junction usually blurred. MT usually strong, often sharp. Rather dense hairs below anterior femur, those on mid and hind femora progressively less dense.	MT weak to vestigial. All femora equally with dense hairs below.
Length of most hairs on side of propodeum less than maximum width of hind femur.	Length of most hairs on side of propodeum approximately equal to maximum width of hind femur.	Length of most hairs on side of propodeum approximately 1.5 times maximum width of hind femur.
T.1 swollen, its outline in dorsal view not forming an even curve with that of T.2 (fig. 202). T.1 usually with small, vertical, posterolateral groove; profile high (fig. 204). S.2 with only vestigial lateral extensions of the transverse groove (fig. 203). Hind tibial teeth very small, their vertical height scarcely exceeding basal width of the subtending spines.	T.1 more slender, its outline and that of T.2 forming an even curve. T.1 without groove; profile shallower. S.2 with the usual lateral extensions of the transverse groove. Hind tibial teeth large, their vertical height several times basal width of the subtending spines.	T.1 and T.2 as in <i>montezuma</i> . T.1 similar to that of <i>montezuma</i> . S.2 as in <i>montezuma</i> . Hind tibial teeth most often as in <i>terminata</i> , occasionally as strong as in <i>montezuma</i> .

Pepsis lycaon Banks, 1945, stat. nov.
(figs 100-102, 236; cf. 204)

Pepsis equestris var. *lycaon* Banks, 1945: 86. Lectotype ♀ (MCZ), here designated [examined].

Type-material.— I have seen two ♀ syntypes with identical collecting data and have labelled the larger one as lectotype. The other specimen is a conspecific paralectotype.

Note.— The type-locality of this species, north-west Trinidad, is almost certainly based on an error in labelling, because no other specimens have been seen from that area, despite the existence of abundant material; all other specimens are from the region described below under Distribution, which is a highly endemic area (Trinidad is not). See Mislabelling (MCZ) in Introduction, p. 8.

Description.— ♂. BL 15-25. Body and legs black with blue-green sheen. Antenna black with up to 1.5 apical segments orange. Wings black with blue-green reflections and white apices, which in the forewing covers most of the area outside the cells, just entering the radial cell anteriorly; in the hind wing covering a smaller area. Sternal

hairs denser on S.6 than on preceding sternites, but essentially unmodified. SGP (figs 100, 101) elongate, laterally expanded centrally and apically; with a sharp, strong median carina which is level in its basal part, then rapidly obsolescent apicad; at about the point where this keel becomes obsolete, a pair of weaker keels begins, each running out to its respective corner of the rounded-truncate apex, the latter slightly emarginate centrally. Lateral hair fringe fairly long and perpendicular basally, shorter and more decumbent apicad. Paramere about twice as long as rest of genitalia, apically rounded. Digitus fig. 102.

♀. BL 22-33. AE index 86-94. Colour as in male, except: antenna entirely black; forewing with narrow, sub-basal whitish-ochre band anteriorly reaching subcosta only, white colour of apex not entering radial cell. Head in dorsal view with temple scarcely swollen, the vertex only slightly more. MT small but often quite sharp. MPN slightly to markedly shorter than PST, its furrow broad; carinae moderate to fine. Propodeum: MG weak but often complete. APT and PPT both weak. DTC weak to fairly strong, a little distant, partly obscured by pilosity. PTC narrow but strong, more-or-less flat-topped. Propodeal hair equal to or slightly longer than PST. Posterior face: VR absent, PFC fairly strong above, rapidly obsolescent medially and apicad, but more-or-less covering whole face. T.1 scarcely swollen (less so than in *P. terminata*), lateral extension of S.2 groove very weak or absent. Femora, especially anterior and middle, with rather sparse but long hair below. Hind tibia: teeth very small, the subtending spines 3-5 times as high; inner spur reaching to 0.20-0.25 basitarsus length (between tarsal segments 3 and 4 in length) and equal to or scarcely longer than outer spur.

Variation.— SMC3 often rather narrow in males (anterior abscissa shorter than proximal). Females sometimes with peculiar DTC, arranged in semicircles concentric to the MPN. Fresh females have a moderate number of fairly strong hairs below the femora, strongest in specimens from very high altitudes (e.g. Perú: San Bartolomé 2,000m.) which usually also possess a postero-lateral groove on T.1 as in *P. terminata* (cf. fig. 204).

Distinctions.— The male separates from others with white wing-tips by its SGP structure, but care is needed to distinguish it from *P. terminata*, with which species it is narrowly sympatric. The female is almost identical to that of *P. equestris* (*rubra*-group) in colour, except that the sub-basal band is rarely pure silvery-white and does not reach the costa. In addition, *P. lycaon* lacks the lateral extension of the S.2 groove and typical *rubra*-group venation, and its AE index is greater.

Distribution.— Endemic in an area west of the Andes, from southern Ecuador to central Perú. A single record of a male from Perú: Loreto, Yarinacocha near Pucallpa is likely to represent a labelling error; ascending to 2,500 m (see also type-citation) (map fig. 236).

Material.— 82 ♂♂, 34 ♀♀; BMNH, CMNH, CUNY, EMMSU, FDA, FRITZ, IMLT, MACN, MCZ, NHMLIM, PORTER, PUCEQ, UNALM, USNM, ZSM.

The *P. hymenaea*-group

Definition.— Radial vein of forewing meets the costa at approximately a right angle, the junction thickened; male SGP more or less strongly 3-toothed; inhabits moderate to high altitudes.

Description.— Small and slender, to large and fairly robust species (BL males 17-25, females 20-42). Body with dense hair: either dirty-golden and short, or black, sometimes very long; femora with more or less strong hairs below. Antennae most often partly orange, the rest black. Wings amber to heavily infusate, commonly unicolorous, PPV more or less long and axial; 1r-m more-or-less straight, strongly sloping anterodistally and SMC3 with projecting but rounded posterodistal corner, so that the cell is much longer posteriorly than anteriorly. MPN often shorter in the mid-line, its furrow usually suture-like. Mesopleural and propodeal tubercles (especially APT),

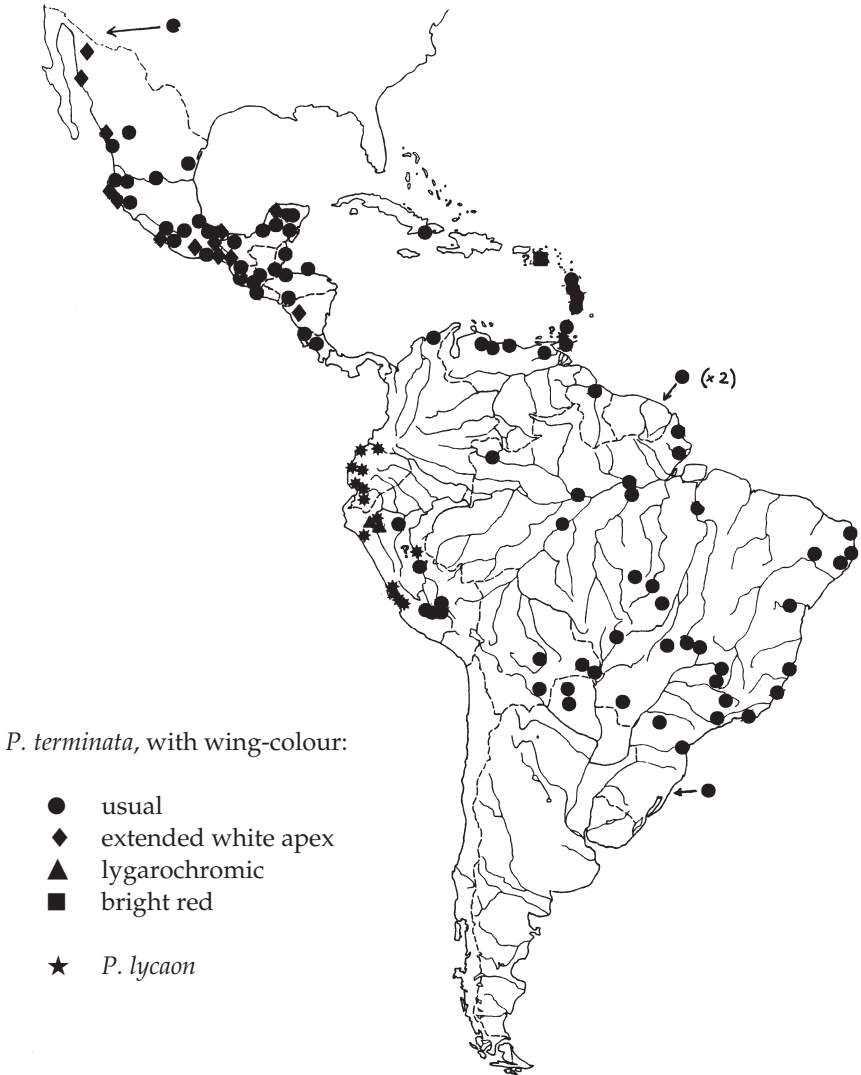


Fig. 236. Collection localities of *Pepsis terminata* Dahlbom and *P. lycaon* Banks.

and lateral projections of anal valve, often very strong. Propodeum usually strongly tapered, especially in the slender species, but despite this, PTC often strong; dorsal and posterior transverse carinae all rather weak, sometimes very irregular (but VR always absent).

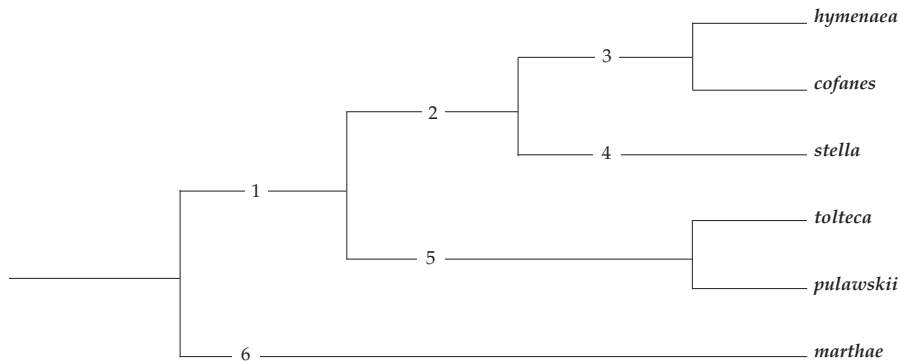
In males the SGP varies considerably in shape; in *P. marthae*, *P. pulawskii*, *P. stella* and possibly *P. tolteca* (in which the SGP is extremely thick) it possesses a pair of lacunae.

Females additionally have a long to very long AS3 (AE index 95-148), the hind tibia usually with small but sharp, distant teeth, and long inner spur (reaching to at least 1/3 basitarsus length).

Note.— Because of its slender habitus, the female of *P. gracillima* Taschenberg (see Part 3) could easily be mistaken for a member of this group; but it has the junction of radius and costa rounded, not angulate. Furthermore, its MPN furrow, although narrow, is not suture-like; the inner hind tibial spur is shorter (at most reaching about 1/4 basitarsus length) and it has little or no subfemoral hair. Its similarity to species of this group may be a reflection of its likewise predominantly montane habitat.

Distribution.— This group is restricted to the northern and central Andes, at altitudes between 500-3,000m; all have a very restricted distributional range (*P. tolteca* the least so).

Cladogram for the *P. hymenaea*-group



Characters

1. Male SGP thick, emarginate apically.
2. Male SGP bifid; with strong central elevation.
3. Small species; SGP shallowly bifid.
4. Large species; SGP very deeply bifid.
5. SGP with carinae; forewing apex pale.
6. Male SGP thin, entire; S.5 with modified hairs.

Phylogenetics.— This group of six species is the sister-group of the *P. pretiosa*-group; its wider relationships are with the *P. chiliensis*- and *P. brevicornis*-groups.

The isolated species of this group is *P. marthae*, known mainly from the Urubamba valley at Machu Picchu; however, as in the *P. elevata*-group, but unlike most other groups, it is not the largest species of its group. All the other species have their ranges further north. Despite the montane habitat, the bifurcation usual in other groups also

appears in this one, resulting in two closely related species (*P. tolteca* and *P. pulawskii*) with effectively parapatric ranges in Perú; the other branch including *P. stella* in the Colombian Andes and the extremely closely-related pair *P. hymenaea* and *P. cofanes* in Venezuela and Ecuador respectively.

Biogeography.— The ancestor of this group was surely already acclimatized to quite high altitudes before it speciated. The fact that it includes few but diverse species, suggests that much speciation and extinction has occurred. One would expect this in a montane habitat; with every climatic cycle the topography would produce new local valley weather systems, so that populations would split into numerous parts and merge again later. If the interval was long enough to allow further speciation to occur, then competition for the again-reduced number of habitats would have been considerable, resulting in multiple extinctions.

Pepsis hymenaea Mocsáry, 1885
(figs 76-83, 199, 200, 238)

Pepsis hymenaea Mocsáry, 1885: 257, no. 30. Lectotype ♂ (TMB), here designated [examined].

Type-material.— I have seen four syntypes in TMB, two of each sex. All are labelled "Venezuela, Merida". I have labelled as lectotype the ♂ in better condition; the other three specimens are paralectotypes. A further ♂ standing under this name, with locality "Bolivia", has no type status. All five specimens are conspecific.

Description.— ♂. BL 17-28. Body and legs black with blue-green sheen, occasionally tending to violet, especially on gaster. Antenna with 6-11 apical segments orange. Wings strongly infuscate with weak blue-violet reflections and occasionally a more-or-less distinct pale amber patch near the apex; this patch is anteriorly more-or-less extended into a proximal point. However, although this pattern thus resembles that in some specimens of *P. stella*, the patch is never as bright or regular as in that species. S.5 and 6 usually with hairs slightly denser than on preceding sternites (but see Variation). SGP (figs 76-79, 81, 82) laterally constricted and polished in the basal half, then the sides expanded and again narrowed to form angles with the sides of the emarginate apex. The apical half is covered with long, fairly dense hairs; in the middle of the SGP is a strong, pointed tubercle which is further emphasized by the extremely strong, dense, backward-pointing hairs at its apex. Paramere about 1.5 times as long as rest of genitalia, apex narrowly rounded. Inner projection of digitus apex (figs 80, 83) more or less broadened, ending in a blunt or acute point directed inwards.

♀. BL 22-28. AE index 123-140. Colour as in male except about 8 apical antennal segments orange. Head (fig. 200) in dorsal view transverse, with temple and vertex not swollen. AS3 very long. MT weak to moderate. Forewing fig. 199. Propodeum: MG sometimes weakly indicated anteriorly, otherwise replaced by broad, shallow ridge. APT weak to strong but usually prominent, PPT weak to strong. DTC virtually absent anteriorly, gradually becoming much stronger posterad. Propodeal hair slightly shorter than PST and MPN together. PTC weak to strong. Posterior face: VR absent, PFC very variable, but most often strong, transverse and regular, covering whole face except sometimes the lowest part, which is polished. Lateral extension of S.2 groove well developed, though often narrow. Femora with numerous but rather weak hairs

below. Hind tibia: teeth rather small, distant, the subtending spines 2-3 times as high. Inner spur reaching to 0.3-0.4 basitarsus length (about equal to tarsal segment 2 or slightly less) and 1.2-1.3 times as long as outer spur.

Variation.— In the male, occasional specimens have S.5 with an apical, transverse patch of very dense and short hairs, with a few much longer ones anteriorly and laterally. S.6 has similar but reduced hairs. The SGP varies considerably in shape; sometimes the apical points are acute, sometimes rounded; the emargination varies from shallowly U-shaped to deeply V-shaped. In one female from Venezuela: Barinas, La Chimenea (MIZAM) most of the middle PFC are directed upwards, joining the PTC, which is stronger than usual.

Distinctions.— Details of the SGP (although variable) suffice to distinguish the male (but see Discussion below); the female is distinguished from others of its group by allopatry, and further as follows: from *P. stella* by the latter's larger size and distinct wing patch (when present); from *P. pulawskii* by the latter's much larger size and deep orange-amber wings; from *P. marthae* by the latter's orange-amber wings and its distributional range; from *P. cofanes* by the latter's petiole-socket lobes (see below), orange-amber wings and antennal orange beginning sub-apically on AS3.

Discussion.— This species is very closely related to *P. cofanes* Banks; however, the male SGP, variable though it is in shape, never displays the combination of angular pre-apical expansion and shallow apical emargination as it does in that species (cf. figs 78-88); the hairs on the SGP median carina are more evenly spaced and sparser in *P. cofanes*, and the latter possesses at least weakly modified sternal hairs on S.5 (*P. hymenaea* usually has none at all). Female *P. cofanes* has a much smaller and less sharp lateral lobe beside the petiole socket and a longer AS3. Furthermore, as far as is known the two taxa are distantly allopatric. Based on the current evidence, it seems best to regard the two taxa as distinct species.

Distribution.— Found at moderate altitudes (500-1,560m) in Venezuela and northern Colombia. A single specimen (TMB) is labelled Bolivia, but this locality probably represents a labelling error (map fig. 238).

Material.— 27 ♂♂, 10 ♀♀; AEIG, AMNH, BMNH, CMNH, LACM, MCZ, MHNGV, MIZAM, MZUSP, PORTER, TMB, USNM, UZMC.

Pepsis cofanes Banks, 1946
(figs 84-89; cf. 199, 200; 238)

Pepsis cofanes Banks, 1946: 364. Holotype ♀ (MCZ) [examined].

Description.— ♂. BL 18-25. Body and legs black with very weak bluegreen sheen and patches of dark brownish-violet pubescence. Antenna black with up to 11 segments orange, extending proximad from apex. Wings light to dark amber, sometimes irregularly mottled; forewing with more or less pale extreme apex. Hindwing with margin remaining dark in paler specimens. S.5 and 6 covered by short, dense hairs, with a few long ones anteriorly and laterally. SGP (figs 84, 85, 87, 88) expanded from base, then from about mid-point very weakly convergent apicad; the apex widely, fairly deeply emarginate, joining the sides at an acute angle. Sides from midpoint, and apex, with a fringe of hairs about half as long as the apex width. In the middle of the

SGP surface is a strong median carina continued distad but rapidly obsolescent; from the highest point of the carina to the SGP apex, the whole width of the SGP is covered with rather long, dense, upright hair. Paramere about 1.5 times as long as rest of genitalia, broad, apically rounded. Inner projection of digitus apex (figs 86, 89) rather broad, ending in a slender point which is turned slightly distad.

♀. BL 20-26. AE index 142-148. Antennal colour as in male. Wings deep amber basally, gradually becoming paler apicad. Two of the five females seen also have the following wing-parts moderately infuscate: extreme bases, a rather short length of the apico-posterior margin of the forewing narrowly, and the entire apical and posterior margins of the hindwing slightly more broadly. Head (cf. fig. 200) with temple and vertex not swollen. MT moderately strong. Forewing cf. fig. 199. MPN equal in length to PST, its furrow evenly narrow, obsolete anteriorly, with a few fairly strong carinae. Propodeum: MG at most very weak, in the centre of a broad, shallow ridge. APT small but fairly prominent, PPT absent or virtually so. DTC very weak, present mainly in posterior and lateral areas, surface otherwise with fine, irregular sculpture. PTC weak, narrow. Propodeal hair about as long as PST and MPN together. Posterior face: not delimited, with irregular sculpture, shining near petiole socket. Lateral extension of S.2 groove moderately well developed. Femora with numerous but rather weak hairs below. Hind tibia: teeth distant, the subtending spines about 2.5 times as high; inner spur reaching to 0.30-0.35 basitarsus length (about equal to tarsal segment 3) and 1.1 times as long as outer spur.

Variation.— Only as noted above.

Biology.— The variation in wing colour-pattern broadly overlaps that of the partly sympatric *P. purpureipes* Packard.

Distinctions.— The male has a distinctive SGP; the female is distinguished from others in its group by its small size, pale wings and locality; but see discussion under *P. hymenaea*.

Distribution.— Known only from the upper Pastaza valley, from Baños to Mera (eastern watershed of the Ecuadorean Andes) 1,600-2,000 m (map fig. 238).

Material.— 8 ♂♂, 5 ♀♀; BMNH, COOPER, FRITZ, MHNGV, IMLT, MCZ.

Pepsis stella Montet, 1921
(figs 93-96, 195, 196, 238)

Pepsis stella Montet, 1921: 205. Holotype ♀ (MHNGV) [examined].

Description.— ♂. BL 24-25. Body and legs black with fairly strong bluegreen sheen. Antenna entirely black, or with orange beginning at any point from the end of AS4. Wings very dark brown, almost without metallic reflections; with or without a roughly circular orange-amber patch near forewing apex, sometimes anteriorly extended into a proximal point (similar to some specimens of *P. hymenaea*, but always much more distinct than in that species). S.4 (fig. 95) with slightly denser hairs than on preceding sternites, S.5 with a rather dense but narrow semicircle of long hairs, infilled centrally and behind with very dense, short hairs. S.6 with some very short, dense hair. SGP (figs 93, 94) unique, with 3 long prongs, the apical pair bent up, each with a small patch of short, dense hair on the outer side of the apex, the middle one

erect, carinate on the proximal side, and with long, dense hairs; on each side of the latter's base is an elongate lacuna (difficult to see when the chitin is very dark). Paramere about twice as long as rest of genitalia, apically curved, with a long hair fringe. Apex of digitus (fig. 96) broad, flattened, rounded.

♀. BL 27-37. AE index 114-120. Colour as in male except antenna with orange beginning at any point from mid-AS3. Head (fig. 196) in dorsal view scarcely swollen, rounded. MT moderate to strong. Forewing with PPV virtually axial; 1r-m straight; cell SMC3 very long and bulging posterodistally; junction of radial vein and costa (fig. 195) angulate. MPN much shorter than PST, its furrow narrow, more-or-less strongly expanded posteriorly; with a few strong carinae. Propodeum: MG replaced by a shallow ridge, with a short, weak groove anteriorly. APT very strongly projecting. PPT moderate to weak, PTC strong but narrow. DTC fairly strong, especially posteriorly, curved. Propodeal hair very long, as long as PST and MPN together. Posterior face: delimited only by the PTC; PFC similar to DTC but slightly weaker, more even, and covering whole of face. Postero-lateral angles of anal valve very strongly projecting. Lateral extensions of S.2 groove weak or absent. All femora with some quite long hairs below, densest on the anterior one. Hind tibia: teeth small, distant, the subtending spines 2.5-3.0 times as high; inner spur reaching to 0.35-0.4 basitarsus length (about equal to tarsal segment 3) and 1.1-1.2 times as long as outer spur.

Variation.— The orange-amber patch in the forewing is either fully present or totally absent in both sexes; no intermediates have been seen. The only other *Pepsis* seen with such patches (although much less distinct) is *P. hymenaea*.

Distinctions.— The 3-pronged male SGP is one of the most strikingly distinctive in the genus; the female is distinguished by its large size, dark wings, general sculpture and distributional range; and both sexes by the wing-patch if present.

Distribution.— Known only from the Colombian Andes, from 600-2,430 m (map fig. 238).

Material.— 4 ♂♂, 4 ♀♀; BMNH, MHNGV, MNHNPS, UNPBOG, ZSM.

Pepsis tolteca Lucas, 1895 stat. rev.
(figs 52-59, 193, 194, 238)

Pepsis tolteca Lucas, 1895: 747, no. 144. Lectotype ♂ (NMV), here designated [examined]. [Wrongly synonymized under *Pepsis petiti* Guérin by Giner Mari, 1944: 360].

Type-material.— I have seen a single type ♂ and labelled it lectotype. There is some doubt concerning the exact locality; although the general locality "Lima" may be correct, the altitude of "6,181 m" given by Lucas is excessive.

Description.— ♂. BL 17-34. Body and legs black with a weak violet-bronze to blue sheen; head, thorax, propodeum, T.1, S.1 and lower side of all femora (densest on the anterior one) with very long, dense, black hair obscuring much of body sculpture. Maxilla: cardine with dense, coarse hair; palp with segment 4 only a little longer than either 5 or 6. Antenna black. Wings pale to deep amber with narrowly infusate base and pale apex usually occupying about half the area beyond the cells, but variable. Radial vein junction with costa (fig. 193) more or less strongly angulate. PPV variable

(see below). Gastral sternites 1 and 2 with much longer hair than following sternites; 5 & 6 with slightly denser hair than 3 or 4. SGP extremely thick, with variable carinae as in figs 52, 53, 56, 57; and with elongate lacunae obscured by thickness of chitin. Paramere (figs 54, 58) about 1.5 times as long as rest of genitalia, quite sharply pointed. Digitus figs 55, 59.

♀. BL 25-39. AE index 95-125. Colour as in male. Head (fig. 194) in dorsal view rounded, with temple and vertex scarcely swollen, eyes small, antenna slender, AS3 usually long. MT weak to moderate. Forewing with junction between radius and costa (fig. 193) angulate, but less so than in the male. MPN shorter than PST, its furrow usually wide and attenuated anteriorly, but very variable; carinae very fine. Propodeum: MG sometimes complete but narrow, sometimes only partly indicated. APT strong to very strong, PPT small but quite prominent. DTC very variable in strength, very irregular, often largely obsolescent and partly obscured by hair. PTC strong to very strong, centrally flat-topped or emarginate. Propodeal hair extremely long, distinctly longer than PST & MPN together. Posterior face: VR weak or absent, PFC extremely variable, similar to DTC. Lateral extension of S.2 groove present but narrow. Base of last visible sternite with slightly raised, triangular area, tapering apicad and more or less raised into a carina, thus weakly reflecting the male SGP; the area has fine punctures and hairs, contrasting with the surrounding coarse hairs. Hind tibia: teeth vestigial to fairly large, subtending spines at least 2.5 as high, often much more; their length equal to about half the thickness of the tibia at the point where they occur; inner spur reaching to about 0.3 basitarsus length (about equal to tarsal segment 3 or slightly longer) and 1.2-1.3 times as long as outer spur.

Variation.— PPV of SMC2 more variable than in any other species of the genus except *P. chiliensis*; its extremes of length, varying from 1/5 to just over 1/3 of the total posterior cell length, overlap that of normal *Pepsis* species and that of *P. chiliensis*; the longer it is, the more axial.

Distinctions.— The male is unmistakable on account of its exceptional SGP structure, despite the variation. Many females are distinguishable by the exceptionally long PPV of SMC2 (cf. fig. 182), but those specimens in which it is shorter, i.e. normal for the genus (cf. fig. 181) strongly resemble the sympatric high-altitude forms of *P. montezuma* and *P. terminata*; a table is given under the last-named species for separating the three. Female *P. tolteca* is also almost identical to *P. pulawskii*, from which it is distinguished mainly by the latter's orange antenna.

Distribution.— The Peruvian Andes, ascending to about 3,000 m (but see note under Type-material); on the western watershed occasionally down to sea-level, but descending only to about 650 m east of the Andes; apparently becoming scarcer with decreasing altitude on both sides (map fig. 238).

Material.— 36 ♂♂, 10 ♀♀; BMNH, CARRASCO, FRITZ, IMLT, MACN, MCZ, MHNLM, NMV, OCHOA, PORTER, UNALM, UNCUS, UNLAMB, USNM, WAHIS.

Pepsis pulawskii spec. nov.
(figs 90-92, 191, 192, 238)

Type material.— Holotype ♂. Perú: 28 mi. e. Olmos, Lambayeque, 2,000 m, 19.i.1955 (Schlinger, Ross) (CAS). Paratypes. Perú: Ancash, Huaylas, 12.vi.[19]71, 1 ♀ (García 313) (MHNLM); Cajamarca, Cas-

cas, 2,390 m, 2.vi.[19]70, 1 ♀ (Haek) (García 313) (BMNH); Q[uebrada] Chinche, 14.iii.[19]75, 1 ♀ (Asencios) (UNLAMB); Pérou [N.F.L.], 1 ♀ (De Gaulle) (MNHNPS).

Etymology.— This species is named after Dr W. J. Pulawski of CAS.

Description.— ♂. BL 25. Body and legs black with blue-green sheen, blue-violet on gaster. Entire body and femora below with long, black hair (least on gaster). Antenna orange from AS3 onwards. Wings orange-amber, rather narrowly infuscate basally, forewing apically pale. S.1 and S.2 with much longer, denser hair than remaining sternites; hair of the more distal sternites not modified. SGP (figs 90-91) extremely strongly expanded and bent upwards apicad; base with an extremely strongly raised triangular tooth, with one of its angles continued apicad as a rapidly obsolescent carina; a pair of very elongate lacunae extends apicad from beside the basal tooth, ending pre-apically; apex shallowly, obtusely emarginate, with a fringe of short, dense hair. Raised basal tooth with a little short hair, SGP otherwise polished. Paramere about twice as long as rest of genitalia, apically rounded. Apex of digitus (fig. 92) very slender, evenly curved.

♀. BL 31-42. AE index 98-110. Body and legs black with a very weak violaceous sheen; most body parts with long, dense, black hair obscuring surface; antenna black basally, with orange colour beginning diffusely, sub-basally on AS3; wings orange-amber with weak, diffuse infuscation basally and (in fresh specimens) with a weak indication of a narrow apical band. Head in dorsal view (fig. 192) transverse-quadrate, eyes small. Maxillary cardine with dense hair (almost as much as in *P. tolteca*), palp with segment 4 equal in length to 6, 5 a little shorter. Forewing costa/radius junction fig. 191; PPV almost axial, as in *tolteca*. MT weak. MPN distinctly shorter than PST, its furrow deep and strongly expanded apicad, carinae difficult to see through hair cover but 2 or 3 moderately strong, especially near furrow. Propodeum: dorsal surface quadrate or slightly transverse, MG weakly indicated anteriorly narrowly, posteriorly broadly; otherwise replaced by very broad ridge; APT and PPT small but the former quite sharp; PTC high, rather narrow with weak central emargination or narrower still and arcuate in outline. DTC weak or absent anteriorly, gradually stronger apicad but matt and obscured by hair throughout. Propodeal hair a little longer than PST & MPN together. Posterior face: carinae few, strong, sometimes present only on upper part of surface (near PTC). Lateral extension of S.2 groove usually well-developed. Hind tibia: teeth usually rather small and distant, the subtending spines 2-3 times as high as the teeth; inner spur reaching to about 0.4 basitarsus length (about equal to tarsal segment 2 or slightly less) and 1.2-1.3 times as long as outer spur.

Variation.— In the female from Quebrada Chinche the lateral extension of the S.2 groove is much shorter than in the other females.

Distinctions.— Both sexes resemble only *P. tolteca*: they are most easily distinguished by their orange antennae; the male is further distinguished by its unique SGP structure, but the female is otherwise extremely similar. At first sight the female resembles that of several other species, but it is distinguished by its group-character of the angulate radial cell apex.

Distribution.— Known only from high-altitude north-western Perú, 2,000-2,400 m (map fig. 238).

Material.— 1 ♂, 4 ♀ ♀; BMNH, CAS, MNHNPS, MHNLM, UNLAMB.



Fig. 237. Collection localities of *Pepsis hymenaea* Mocsáry, *P. stella* Montet, *P. cofanes* Banks, *P. pulawskii* spec. nov., *P. tolteca* Lucas and *P. marthae* spec. nov.

Pepsis marthae spec. nov.
(figs 117-120, 197, 198, 238)

Type material.— Holotype ♂. **Perú**: Cusco, Machu Picchu, river, 2,090 m., 13.viii.1971 (Vardy) (BMNH). Paratypes. Perú: 1 ♂, Urubamba, Machu Picchu, Puente Ruinas [bridge over river] 19.i.[19]65 (Ochoa) (OCHOA); 1 ♀, Machu Picchu (Museo de Sitio, near river) 1,840 m., 19-21.iv.1983 (Vardy) (BMNH); 1 ♀, Machu Picchu, 28.xi.[19]65 (Townes) (AEIG); 1 ♀, [Junin] Chanchamayo [valley] [handwritten; correct spelling], "Chanchanzaya", H. Rolle, Berlin col. [printed], 2741, 99174 (MZUSP).

Etymology.— This species is named after my wife, Martha, who caught the first female of this species known to me.

Description.— ♂. BL 21-25. Body and legs black with weak blue-violet sheen; pubescence dark brassy with weak violet tint. Antenna orange from segment 3 onwards. Wings pale amber, forewing with orange tint. S.4 (fig. 119) just before its mid-length with a narrow, arcuate band of long but sparse, backwardly curved hairs (but scarcely stronger than those of preceding sternites); the entire area behind this with very short, dense pubescence (slightly longer apicad); S.5 also with an arcuate band of hairs, but these are longer than on S.4, basally erect then curved backwards, and behind them are very dense hairs about half as long; these latter are slightly longer towards the apex of the sternite. SGP (figs 117, 118) parallel-sided except where slightly expanded and strongly bent upwards sub-basally; at this point is a pair of lacunae. The surface is polished up to the bend, with fairly long, dense, almost erect hairs beyond. A median carina begins strong at the base, becoming obsolete preapically. Paramere narrower in apical half than basal, apex bluntly pointed. Whole of digitus apex (fig. 120) very slender and incurved.

♀. BL 25-31. AE index 122-129. Colour as in male, except antennal orange begins at mid-AS3. Head (fig. 198) with temple and vertex scarcely swollen, head quite strongly transverse. MT strong, fairly sharp. Forewing fig. 197. MPN slightly shorter than PST, its furrow narrow to rather broad, more or less obsolescent anteriorly, slightly expanded posteriorly; carinae very fine but with 1-3 stronger ones. Propodeum: MG replaced by a ridge, flatter anteriorly. APT and PPT narrow but strong and sharp. PTC strong, narrow. DTC fine, with a few stronger ones, partly obscured by fine pubescence, virtually absent in posterior 1/3 of dorsum. Propodeal hair about as long as PST + 1/2 MPN. Posterior face: VR absent, PFC very strong near PTC, continuing the same laterally only; central area sometimes with a fairly strong median longitudinal carina, and with other very irregular, obsolescent carinae. Posterolateral angles of anal valve very strongly and sharply projecting. Lateral extension of S.2 groove short and weak. A few weak hairs below front femur. Hind tibia: teeth more equal-sided than usual, i.e. scarcely backward-directed; the subtending spines about 2.0-2.5 times as high. Inner spur reaching to about 0.3 basitarsus length (equal to or slightly shorter than tarsal segment 3); 1.25-1.30 times as long as outer spur.

Variation.— Only as noted above.

Distinctions.— The male is distinguished by its SGP structure; the female by its PPT being more strongly developed than that of any other species of its group. Colour and locality also help to confirm the identity of both sexes.

Distribution.— Known mainly from the area of Machu Picchu in the Urubamba

valley, Perú between 1,800-2,100 m; its occurrence in the Chanchamayo [= Palca; = Tarma] valley [Junin department] needs confirmation (map fig. 238).

Material.— 2 ♂♂, 3 ♀♀; AEIG, BMNH, MZUSP, OCHOA.

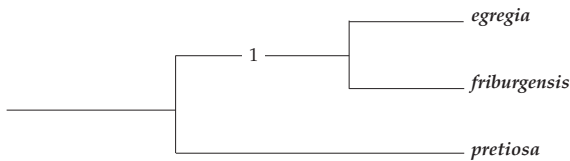
The *P. pretiosa*-group

Definition.— Forewing with very broad white apex; gaster strong metallic blue (scale-hairs extremely small); male SGP with low, median keel and lacunae.

Description.— Medium to rather large, slender wasps (BL males 14-31, females 17-43). Head transverse. Pronotal shoulders strongly prominent. Forewing with radius/costa junction angulate, the junction slightly thickened. SMC3 short to very short. Propodeum more or less strongly tapered, with strong median ridge; very strong, sharp APT and coarse DTC. Male with modified hairs on S.5, stronger on S.6. Digitus "swan-necked", i.e. narrow throughout and ?-shaped. Female antenna short, but AS3 long, with bristles. Lateral extension of S.2 groove usually short. Pygidium with very dense, brownish hair. Hind tibial teeth, small, distant; spines tiny, arising from sides of teeth; inner spur long.

Distribution.— The species of this group are found in Panamá, through the Guianas, Amazon basin, part of central Brazil, to southeast Brazil.

Cladogram for the *P. pretiosa*-group



Characters

1. Small BL; sides of SGP rounded; PPT virtually absent; PTC weak to absent.

Phylogenetics.— This species-group forms the sister-group of the *P. hymenaea*-group, and strongly resembles it in most ways except for the characters given under Definition above.

Although only three species comprise this group, their inter-relationships are difficult to assess. Despite the fact that *P. pretiosa* and *P. egregia* are quite distinct from each other, the position of *P. friburgensis* is not clear: it strongly resembles *P. egregia* in body size, and resembles it rather than *P. pretiosa* in male SGP shape, and in lacking hairs below the anterior femur, configuration of MPN furrow and carinae, and PTC development (all in the female). However, it also closely resembles *P. pretiosa* in SMC3 shape, extent of white forewing apex, APT and digitus in the male; and MT size in the female. However, the combination of white forewing apex and short SMC3 is regarded as a character reversal, as it is found also in more distantly related species of the genus (e.g. *P. vinipennis*, *P. terminata*).

Biogeography.— Two of the species of this group exhibit the north-west/trans-andean and south-eastern distribution pattern usual for a species-pair of comparable

phylogenetic position; but the third, *P. friburgensis*, is sympatric with the south-eastern one.

Pepsis egregia Mocsáry, 1885
(figs 60-62, 239)

Pepsis egregia Mocsáry, 1885: 246, no. 1. Lectotype ♀ (TMB), here designated [examined].

Type-material.— *P. egregia*: I have seen five conspecific syntypes from TMB, but there is some confusion about their provenance. Mocsáry gave Manaus and Iquitos as localities, but *teste* Dr Papp (pers. comm.) the old registration numbers given on the specimens' labels refer to "three type-specimens Brasilia, Piauhy [= Piaui]; two type-specimens Perú, Yquitos [= Iquitos]." However, the labels on the specimens are as follows:

- (1) ♂. Piauhy. 747-162. No original identification label.
- (2) ♀. Piauhy. 747-182. Mocsáry label "*P. egregia*".
- (3) ♂. Manaus. No registration label. Mocsáry label "*P. egregia*".
- (4) ♀. Yquitos. 753-45. No original identification label.
- (5) ♀. Yquitos. 753-45. Mocsáry label "*P. egregia*".

All the locality labels "Piauhy" and "Yquitos" appear to be recent. The label "Manaos" is old. Since specimen (5) is the only one complete with uncontroversial locality, original registration number and original Mocsáry identification label, I have labelled this one lectotype; the remainder are paralectotypes. All three localities mentioned are within the distributional range of the species.

Description.— ♂. BL 14-21. Head and thorax black with some short, brassy-violet pubescence. Legs black. Gaster metallic blue sometimes tending to green or violet. Antenna black, sometimes with an orange spot at the extreme apex. Wings black with strong blue-violet reflections, forewing with a broad, milky-white apex including about two-thirds of the radial cell, almost all of SMC3, and just entering SMC2 and 2nd discoidal. SGP (figs 60, 61) strongly transversely convex basally, then slightly wider and flat; this latter area, terminating in a rounded-truncate apex, is covered with moderately dense hairs of various sizes. Paramere of normal length, about 1.5 times as long as rest of genitalia, narrow but not strongly pointed. Digitus fig. 62.

♀. BL 17-29. AE index 100-108. Colour as in male, except extreme apices of antennal segments sometimes dull orange from AS3 onwards. Head with temple scarcely swollen. MT moderate to strong. MPN markedly longer than PST, its furrow fairly broad, obsolescent anteriorly, moderately expanded posteriorly; carinae many, fine, with a few much stronger ones mainly in anterior half, almost transverse. Propodeum: very strongly tapering posterad; MG replaced by a strong ridge, often sharp posteriorly; APT extremely strong, projecting sharply; PPT completely merged with the very strong lateral ridge; PTC moderate, narrow; DTC strong and distant; propodeal hair long, as long as MPN or more. Posterior face: defined above only by PTC; VR absent, PFC similar to DTC and covering whole of face. Lateral extensions of S.2 groove very short. Pygidium with long, decumbent, dark reddish hair. Hind tibia: teeth rather sharp, slightly distant; spines about the same height or slightly more; inner spur reaching to 0.4-0.45 basitarsus length (about equal to tarsal segment 2) and 1.20-1.25 as long as outer spur.

Variation.— Only as noted above.

A possible hybrid.— A small (BL 17) male from Brazil: Rio de Janeiro (SMF)

strongly resembles that of *P. egregia* in most respects, but the SMC3 shape and white forewing apex resemble those of *P. friburgensis*; it may be a hybrid between these two species. Note that *P. egregia* is rarely collected within the range of *P. friburgensis* and may only infrequently be in contact with it; these things together may constitute circumstantial evidence of their phylogenetic proximity.

Distinctions.— Closely resembles *P. pretiosa*, which see for differences; the male also resembles those of *P. vinipennis*, *P. terminata* and *P. lycaon*, but these all have totally different SGPs with very strong carinae. The white wing apex of the female is far greater in extent than in any other species of *Pepsis* except *P. pretiosa*.

Distribution.— Occurs from Panamá southwards; the entire Amazon basin including the Guianas; in the west, south to Bolivia; and in the east, south to the Ilha do Bananal on the Rio Araguaya, with a single record from Espiritu Santo; ascends to 1,200 m in eastern Ecuador (map fig. 239).

Material.— 81 ♂♂, 41 ♀♀; AEIG, AMNH, BMNH, BRIO, CAS, CDFA, CMNH, COOPER, CUNY, FDA, INPA, LACM, MACN, MCZ, MEM, MHNGV, MHNNEU, MIZAM, MLU, MNHNPS, MNRJ, MZUSP, RMNH, SMF, TMB, UFPCUR, UMOX, UNPBOG, UPAN, USNM, USU, UZMC, WAHIS, ZSM.

Pepsis friburgensis spec. nov.
(figs 63-65, 239)

Type material.— Holotype ♂, **Brazil**: Nova Friburgo, ii.1884 (Germain) (MNHNPS). Paratypes. Brazil: 1 ♂, Passa Quatro, 1898, 50 (Zikan) (ETHZ); 1 ♂, S[ão] Paulo, 3.936 (Lopes) (MNRJ); 1 ♂, XXVI [N.F.D.] (BMNH); 1 ♀, [Nova] Friburgo, ii.32, "*Pepsis (Stenopepsis) pretiosa* Dhlb." (MNRJ).

Etymology.— This species is named after Nova Friburgo, its type locality.

Description.— ♂. BL 15-20. Body and legs black, with some short, brassy-violet pubescence, especially on the MPN and propodeum; gaster with quite strong, deep blue to violet metallic sheen. Antenna entirely black. Wings very dark brown, with fairly strong blue-violet reflections; forewing with milky-white apex (see Variation). SGP (figs 63, 64) laterally slightly expanded in apical half, the apex truncate with rounded corners; the basal half is broadly rounded, flattening out apicad or changing to a weak keel; the apical half is covered with fairly dense, mainly short hair, which also forms an apical fringe. Paramere about 1.5 times as long as rest of genitalia, rather broad, not sharply pointed. Digitus fig. 65.

♀. BL 21. AEI 88. Colour as in male (see also Variation). Head in dorsal view a little swollen behind eyes, thus appearing rather transverse. MT very small but pointed. Forewing SMC3 very short (cf. fig. 201). MPN about equal in length to PST, with one very strong, transverse carina in the middle and a vestigial one behind it; before the strong carina the median furrow is very narrow, behind it very broad and shining. Propodeum: strongly tapering posterad, with a broad, median ridge slightly narrowing posterad; APT very weak, PPT virtually absent; position of PTC marked only by a few carinae being more elevated medially. DTC moderately strong, stronger in apical half. Propodeal hair (rather worn) probably as long as PST + half MPN. Posterior face: defined only by rudimentary PTC; VR absent; PFC similar to PTC and covering all but the most apical part of the face. Lateral extension of S.2 groove very short. Pygidium

covered by reddish hair, decumbent apically. Hind tibia: teeth strong, each subtended by an equal or scarcely higher spine; inner spur reaching to about 0.45 basitarsus length (slightly longer than tarsal segment 2), and about 1.30 times as long as outer spur.

Variation.— The extent of the white forewing apex in the male varies between two extremes: at one, it covers about a third of the radial cell, a small part of SMC3 and the area beyond these cells, to the posterior edge of the wing, with the boundary quite dif-

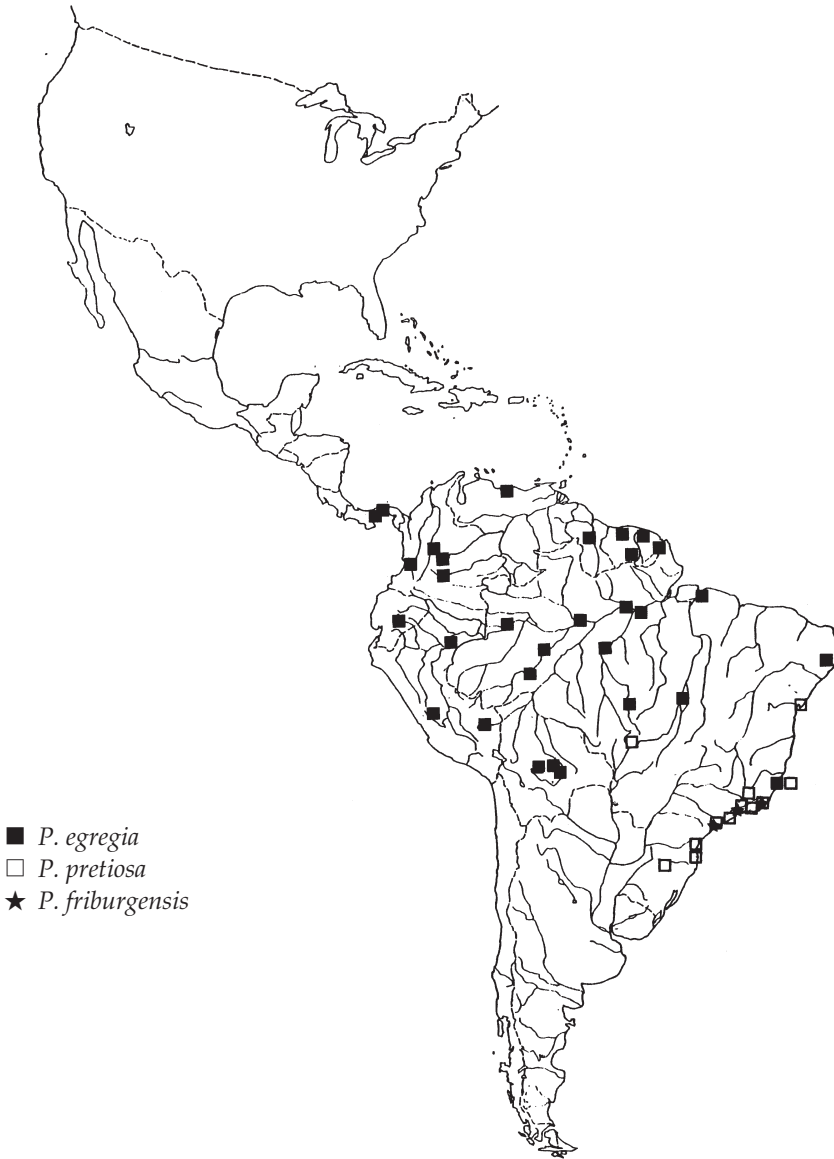


Fig. 238. Collection localities of *Pepsis egregia* Mocsáry, *P. pretiosa* Dahlbom and *P. friburgensis* spec. nov.

fuse; at the other extreme the area covers half the radial cell, most of SMC3 and most of the area beyond the cells except a small posterior part; the boundary is better defined in the latter case. The forewing of the single known female has the white apex intermediate between the extremes of variation in the males.

Distinctions.— Both sexes are distinguished from *P. egregia* by the short SMC3, smaller and less well defined white wing apex, very small APT, and distributional range; and from *P. pretiosa* by the much smaller size; the male is further distinguished from that of *P. pretiosa* by its SGP lacking the expanded, flattened, apical half of that species; while the female is further distinguished from that of *P. pretiosa* by the much smaller AEI and the very weak propodeal tubercles and PTC.

Distribution.— Known only from near the coast of south east Brazil (map fig. 239).

Material.— 4 ♂♂, 1 ♀; BMNH, ETHZ, MNHNPS, MNRJ.

Pepsis pretiosa Dahlbom, 1843
(figs 66-68, 239)

Pepsis pretiosa Dahlbom, 1843: 121, no. 7. Lectotype ♀ (MZEL), here designated [examined].

Pepsis bicolor Lepeletier, 1845: 488, no. 31. Lectotype ♂ (MIZSU), here designated [examined]. [Synonymized by Smith, 1855: 189].

Type-material.— *P. pretiosa*: I have seen a pair of conspecific syntypes, and have labelled the ♂ lectotype; the ♀ is a paralectotype. *P. bicolor*: I have seen a single type-material ♂ and labelled it lectotype.

Description.— ♂. BL (17-)24-31. Head, thorax and legs black with very weak metallic sheen; gaster with strong blue-violet sheen. Antenna black. Wings black with strong violet reflections, forewing with broad, white apex including about half the radial cell and most of SMC3. SGP (figs 66, 67) is very like that of *P. egregia* but lacks the transverse ridge, the sides are expanded more abruptly sub-basally and then taper more strongly to the apex, which is rounded. Paramere about 1.5 times as long as rest of genitalia, narrowly rounded at apex. Digitus fig. 68.

♀. BL 32-43. AE index 111-128. Colour as in male. Head in dorsal view with temple scarcely swollen. MT very strong. Forewing SMC3 very short. MPN about as long as PST; its furrow variably broad, slightly expanded posteriorly, obsolete anteriorly; carinae very strong, almost transverse. Propodeum: MG replaced by a strong (but not sharp) ridge, weaker anteriorly. APT moderate to strong, PPT fairly strong, elongate, more or less confluent with the lateral ridge anterior to them; PTC quite strong but narrow; DTC strong. Propodeal hair almost as long as PST and MPN together. Posterior face: only defined above by the PTC; VR absent, PFC similar to DTC and covering whole of face. Lateral extensions of S.2 groove very variable (short to long). Pygidium with some long, decumbent, dark reddish hair. Hind tibia: inner spur reaching to 0.35-0.4 basitarsus length (about equal to tarsal segment 3 or slightly longer) and 1.1-1.2 times as long as outer spur.

Variation.— Only as given above.

Distinctions.— The colours of forewing and gaster together separate both sexes from those of all other species except *P. egregia*, from which they are distinguished by the short SMC3, the narrower white forewing apex, less strongly tapered propodeum and much weaker APT. The males are also separated by the SGP structure. Further-

more, this species is much larger on average than *P. egregia* and they are largely allopatric (see also remarks under *P. egregia* and *P. friburgensis*).

Distribution.— Known from the Brazilian coast at low altitudes from Bahia to Santa Catharina; a record from Mato Grosso, Chapada dos Guimarães (CMNH) needs confirming (map fig. 239).

Material.— 31 ♂♂, 52 ♀♀; AEIG, AMNH, BMNH, CMNH, CUNY, ETHZ, FDA, MIZSU, MHNGV, MLU, MNHNPS, MNRJ, MZEL, MZUSP, NMW, RMNH, SMF, UFFCUR, UMOX, USNM, UZMC, ZMMICH, ZMMOSC, ZSM.

The *P. chiliensis*-group

Definition.— Entirely black species (except antenna partly orange) with extremely dense, coarse hair covering much of body. PPV extremely long for the genus, varying to just over 1/3 total posterior SMC2 length. Anterior part of gaster dorsoventrally flattened, T.1 & 2 with median groove. Male with all gastral sternites densely hairy. Female clypeus narrow and deeply, arcuately emarginate with strong ridge above emargination.

Description.— See species text.

Distribution.— See species text.

Phylogenetics.— This group is exceptional in comprising only one species; however, since its sister-group is a "normal" species-pair (*P. brevicornis*-group), this imputes to this single species a phylogenetic position comparable to that of a major species-group.

Biogeography.— Unusual facts concerning this species are:

1. It exhibits a concomitance of characters most of which are found only in isolation in other species of the genus.

2. Other phylogenetic positions comparable to that of *P. chiliensis* are always occupied by a group of multiple species; this implies that, unlike its close allies, *P. chiliensis* failed to speciate and is therefore a relict form.

3. It inhabits only the western watershed of the High Andes and adjacent desert coast (habitats which have much in common climatically).

These facts suggest that, an early stage, this species adapted to low temperatures such that it was able to maintain its preferred temperature regime (surely a high-altitude one) throughout subsequent glacial cycles simply by re-locating its range uphill or downhill, northwards or southwards, in an effectively continuous habitat. In this way it avoided the need to evolve, i.e. cope with the competition and vicariance events taking place at lower levels, which in all other cases so far studied caused the formation of groups of multiple species.

Pepsis chiliensis Lepeletier, 1845 (figs 42-46, 180-182, 237)

Pepsis chiliensis Lepeletier, 1845: 480. Lectotype ♀ (MIZSU), here designated [examined].

Abripepsis inca Banks, 1946: 314. Holotype ♀ (MCZ) [examined]. [Synonymized by Vardy, 2000: 11].

Type-material.— I have seen a single ♀ of *P. chiliensis* and labelled it lectotype.

Description.— ♂. BL 16-35. Body and legs black, gaster with blue-green sheen, legs weakly violet. Antenna mainly bright orange, beginning irregularly on AS3 and

4, slightly darker on inner side; basal segments black. Wings black with strong blue-violet reflections. Head, thorax, propodeum, T.1, all sternites and lower side of all femora with very long, dense, black hair, obscuring much of body sculpture. Maxilla: cardine with dense, coarse hair; palp segments 4-6 all short. Radial vein rounded or very weakly angulate on costa. PPV: see Variation. T.1 and 2 dorsally flattened, T.1 with a weak median groove. SGP (figs 42, 43) with sides strongly rounded, a little narrower at base than at apex; with a raised, polished median keel extending to the apex; basally, the keel is broadened into a rather large triangular area; apicad, the SGP is increasingly densely covered with hairs of two lengths: short and fairly long; the apex is weakly truncate. There is also a pair of rather broad lacunae, distinct only basally. Paramere about 1.5 times as long as rest of genitalia, broadly pointed. Inner projection of digitus apex (fig. 44) very broad, round-ended, pointing inwards.

♀. BL 22-36. AE index 118-130. Colour as in male, except antenna orange to base of AS3. Head (fig. 180) small, strongly rounded in dorsal view, temple and vertex scarcely swollen; eyes small; antenna very slender, AS3 long. Clypeus with strong, transverse, pre-apical ridge. MT weak. Forewing with PPV longer than usual, variable (see figs 181, 182). PST with a shallow median groove. MPN shorter than PST, its furrow very broad; carinae few, strong. Propodeum [all characters largely obscured by dense hair]: MG indicated anteriorly, weak or absent posteriorly. APT and PPT weak. DTC sometimes indicated irregularly posteriorly, but mainly replaced by irregular rugosity. PTC strong, broad, its centre usually shallowly emarginate. Propodeal hair: a little longer than PST and MPN together. Posterior face: VR virtually absent; PFC a few strong, irregular above, obsolescent below, the surface becoming finely striate and more shining. Lateral flaps of anal valve rather large and more-or-less pointed. Only T.1 slightly flattened and retaining traces of median groove (see male), especially basally. Lateral extension of S.2 groove well-developed, sometimes a little weak. Hind tibia: teeth tiny, the subtending spines about half as high as tibial thickness; between these is a continuous, very dense band of very short bristles; inner spur very short and thick, scarcely longer than apical thickness of tibia, reaching to only about 0.25 basitarsus length (equal to or slightly longer than tarsal segment 4) and 1.1-1.2 times as long as outer spur.

Gynandromorphs.— Two have been seen; in both cases the head (including both antennae) is male, the rest of the body female.

Variation.— In the male forewing (figs 45, 46), the PPV of SMC2 occupies from just under 1/3 to about 2/5 of the posterior length of the cell (a little longer on average in females – figs 181, 182).

Distinctions.— This species cannot easily be confused with any other member of the genus. The very long PPV resembles only that of some specimens of *P. tolteca* (distinct on wing-colour); the very long, black hair, the antennal and wing colour, and the clypeal ridge in the female are all distinctive. The only species of the genus which resembles *P. chiliensis* is the broadly sympatric black form of *P. montezuma*, and then only in colour. *P. chiliensis* is distinguished from species of other genera by its PPV, still usually shorter than in other genera, and the radial cell rounded on the costa (not pointed nor distinctly angulate).

Distribution.— Found in the coastal deserts and western watershed of the Andes

of Ecuador and Perú, ascending to 3,500 m. Despite the name of this species, its occurrence in Chile remains doubtful; the ship, during whose voyage the type-specimen of *P. chiliensis* was collected, called at more than one place on the South American west coast; the southernmost authenticated record is from Arequipa, well north of the Chilean border (map fig. 237).

Material.— 58 ♂♂, 80 ♀♀, 2 gynandromorphs; AEIG, AMNH, BMNH, CARRASCO, CAS, CMNH, CUNY, EMMSU, FDA, IMLT, MCZ, MIZSU, MNRJ, NHMLIM, PUCEQ, SEMKU, UNALM, UNLAMB, UNTRUJ, USNM, WAHIS.

The *P. brevicornis*-group

Definition.— Very robust wasps, most of body with strong bristles; antenna very short and thick. MT virtually absent. Costa/radius junction angulate, thickened at junction. Gaster dorsoventrally flattened, T.1 and 2 with median groove. Female with lateral extension of S.2 groove very short or absent. Male SGP almost parallel-sided with low, triangular tubercle at base, leading into a low median keel; with elongate lacunae. Female hind femur with extremely sharp inner, posterior carina, tibia with extremely long inner spur, reaching about half length of basitarsus.

Description.— Rather large wasps (BL male 24-32, female 29-41). Wing colour very variable, from orange-amber with a black border, to entirely black; often with more or less distinct pale apex. Most of body with fairly long but not very dense pilosity, much of it in the form of bristles. Head transverse, constricted behind eyes. APT absent or weak; PPT & PTC, also lateral projections of petiole socket, usually strong; DTC very coarse. Propodeum virtually parallel-sided, short.

Distribution.— Found from the USA. to Argentina.

Phylogenetics.— This pair of sister-species is the sister-group of *P. chiliensis*. In a male *P. cassiope* from USA: Arizona, Santa Cruz Co. (LACM) the PPV is not only axial but takes up almost half the total posterior length of SMC2, thus exceeding even the most extreme condition found in *P. chiliensis*. This is interpreted as a character reversal which strongly confirms the phylogenetic relationship which had already been established on the basis of other characters.

Biogeography.— This group displays the usual distribution pattern for species-pairs (see Biogeography in the Introduction), but *P. cassiope* and *P. grossa* are the only two species of the species-pairs to reach the USA. and West Indies. That *P. grossa* is much more widespread in the USA than *P. cassiope*, can be explained on the basis that, at least north of the Andes, *P. cassiope* seems to be more or less restricted to high ground; this attribute is also consistent with the fact that the sister group, *P. chiliensis*, is adapted to very high altitudes.

Pepsis brevicornis Mocsáry, 1894 (figs 128-130, 183, 237)

Pepsis brevicornis Mocsáry, 1894: 12, no. 20. Lectotype ♂ (TMB), here designated [examined].

Pepsis depressa Brèthes, 1908: 243. Lectotype ♀ (MACN), here designated [examined]. **Syn. nov.**

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

Description.— ♂. BL 30-32. Body and legs black with blue-green sheen. Antenna black. Wings orange with a narrowly black base and rather broadly infuscate apical border. This aptly-named species has the shortest antenna relative to body size in the genus; it is only about as long as head, thorax and propodeum together. All sternites except S.2 before the transverse groove with fairly dense, long hair; slightly denser

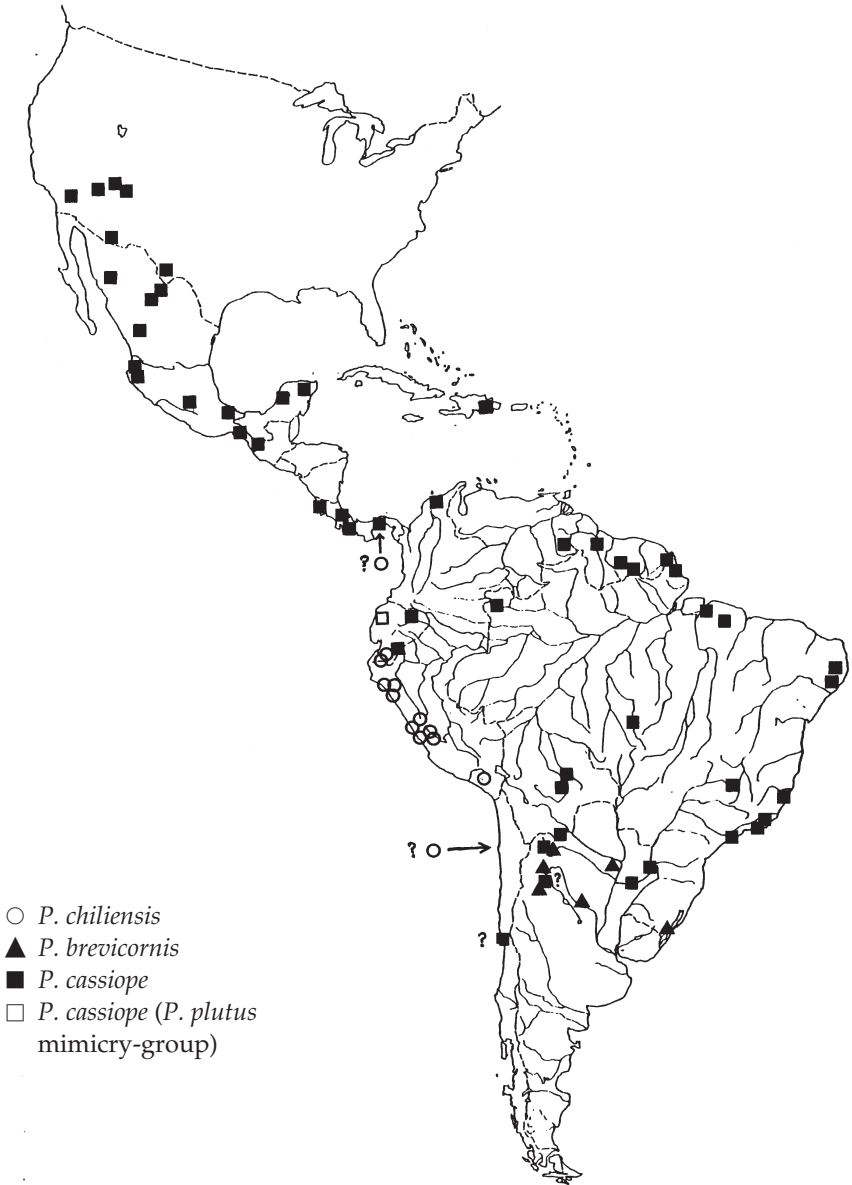


Fig. 239. Collection localities of *Pepsis chiliensis* Lepeletier, *P. brevicornis* Mocsáry and *P. cassiope* Mocsáry.

and of two sizes on S.5 and 6. SGP (figs 128, 130) with sides gradually narrowed to the truncate-rounded apex. The base is strongly convex, with an elongate lacuna on each side; this raised area narrowing apicad, ending in a rounded point; from there a broad ridge continues apicad but becomes obsolete before reaching the apex; all the lower parts are covered with rather dense hair set in irregular punctation. Paramere almost twice as long as rest of genitalia, slightly obliquely truncate, with apical hairs about 2/3 maximum paramere width; inner projection of digitus apex (fig. 129) rather slender, evenly curved, directed inwards and ending in a rounded point.

♀. BL 29-39. AE index 61-67. Colour as in male, except antenna tending to become dull orange towards apex. Head (fig. 183) in dorsal view transverse, with temple slightly and vertex more strongly swollen. AS3 even shorter than in male, only as long as thorax including propodeum. MT weak or absent. Forewing with radial vein/costa junction slightly angulate. MPN slightly shorter than PST, its furrow very broad, carinae rather coarse. Propodeum: dorsal face distinctly transverse. MG replaced by a strong, often flat-topped ridge. APT weak to strong, PPT strong, PTC moderate to strong, DTC mainly very strong, more or less distant, partly obscured by hair. Propodeal hair about as long as PST. Posterior face: VR absent, PFC quite strong above, weaker below but covering whole of face. T.1 with median groove, strongest at junction of dorsal and posterior faces. Lateral extension of S.2 groove absent to short. Hind tibia: teeth usually rather small and distant, with very short and dense hair between; the subtending spines 1.5-2.0 times as high; inner spur extremely long, reaching to 0.45-0.5 basitarsus length (about equal to tarsal segments 3 and 4 together or slightly longer) and 1.5-1.6 times as long as outer spur.

Variation.— In contrast to its close relative *P. cassiope*, this species varies but little; doubtless this is at least partly due to its considerably more restricted, mainly lowland, range. The only noticeable variation is in the width and intensity of the dark band of the forewing apex, which often enters the radial and SMC3 cells.

Distinctions.— Both sexes, especially the male, are more robust than in *P. cassiope*, and have shorter antennae. In dorsal view, the propodeum of male *P. cassiope* is virtually rectangular, that of *P. brevicornis* square; the T.1 of *P. brevicornis* is strongly swollen dorsolaterally about the middle of its length, that of *P. cassiope* much less so. The SGPs of the two species differ only in minor details. The females are also easily distinguished on the basis of the structural characters given for the males; although the proportions are different absolutely, they are similar relatively. The females are further distinguished by their different AE indexes, and the more quadrate head of *P. brevicornis*, where the vertex in particular is swollen. The two species are almost entirely allopatric.

Distribution.— Found in southern Brazil and across northern Argentina, ascending to 1,240 m in Argentina: Catamarca (map fig. 237).

Material.— 7 ♂♂, 14 ♀♀; BMNH, FRITZ, IMLT, MACN, MHNGV, MLP, MNHNPS, RMNH, TMB.

Pepsis cassiope Mocsáry, 1888
(figs 131-134, 184, 237)

Pepsis cassiope Mocsáry, 1888: 161, no. 1, ♀ (lost).

Pepsis cassandra Mocsáry, 1888: 162, no. 3. Lectotype ♀ (MNHU), here designated [examined]. **Syn. nov.**

- Pepsis lilloi* Brèthes, 1908: 241. Lectotype ♀ (MACN), here designated [examined]. **Syn. nov.**
Pepsis heterochroa Brèthes, 1914: 298, no. 61. Holotype ♀ (MZUSP) [examined]. **Syn. nov.**
Pepsis elisa Montet, 1921: 208. Holotype ♀ (MHNGV) [examined]. **Syn. nov.**
Pepsis brethesi Montet, 1921: 216. Lectotype ♂ (MHNGV), here designated [examined]. **Syn. nov.**
Pepsis arizonica Banks, 1921: 21. Lectotype ♂ (MCZ), here designated [examined]. **Syn. nov.**
Pepsis hirsuta Salman, 1933: 9. Holotype ♀ (MCZ) [examined]. **Syn. nov.**
Pepsis iolanthe Banks, 1946: 330. Holotype ♀ (MCZ) [examined]. **Syn. nov.**
Pepsis adusta Haupt, 1952: 384, no. 14. Holotype ♀ (MLU) [examined]. **Syn. nov.**

Type-material.— *P. cassiope*: Lucas' (1895: 659, no. 88) redescription of the subsequently-destroyed type enables unambiguous interpretation of the name. *P. cassandra*: I have seen a single type-material ♀ and labelled it lectotype. *P. lilloi*: I have seen a single type-material ♀ and labelled it lectotype. It bears a label "M. Lillo, Tucumán"; see comment under Distribution. *P. brethesi*: I have seen two ♂ syntypes in MHNGV, and have labelled as lectotype the specimen which is in better condition; it bears the labels "Type; Colombie; Prep. no. 38". The other specimen, a conspecific paralectotype, bears only Montet's identification label. *P. arizonica*: I have seen a single type-material ♂ and labelled it lectotype.

Description.— ♂. BL 24-32. Body and legs black with a very weak blue-violet sheen in parts; antennal colour mainly orange to entirely black; wings with various combinations of black, white and orange (see Variation). S.5 and 6 with hairs distinctly denser than on other sternites, and of two sizes. SGP (figs 131, 132) more variable in its detailed structure than that of *P. brevicornis*: in particular, it frequently possesses a median apical notch. Paramere fig. 133, digitus 134 (essentially the same as in *P. brevicornis*).

♀. BL 30-41. AE index 74-97. Colour similar to male (but see Colour variation). Head (fig. 184) in dorsal view with temple and vertex not swollen, so that the head is very strongly transverse. MT absent or very weak. Forewing with radius/costa junction usually slightly angulate. MPN usually a little shorter than PST, its furrow broad; carinae usually few and very strong, occasionally effaced. Propodeum: MG replaced by a strong ridge, narrower posterad; APT, PPT and PTC all weak to strong; DTC strong, rather distant, somewhat irregular. Propodeal hair about as long as PST and 1/2 MPN. Posterior face: VR absent, PFC usually weak and very irregular, but more or less covering whole of face. Lateral extension of S.2 groove short. Hind tibia: teeth and spur characters as in *P. brevicornis*.

Structural variation.— A male from Arizona (LACM) has a venation abnormality which is particularly interesting in view of the *P. brevicornis*-group's strong link with the putatively plesiomorphic species *P. chiliensis*. In this specimen the PPV is almost as long as the remaining abscissa of the posterior vein bordering SMC2; in this respect it thus goes even further than the most extreme specimens of *P. chiliensis* seen.

In specimens of both sexes from Venezuela to the Amazon delta, the MPN is highly polished with only traces of carinae.

Colour variation.— (See also Biology). This species exhibits several strong but complicated clines in antennal and wing colour (for example, sometimes the variation in the two organs appears to be connected, sometimes not). It would be tedious to give full details of the extremely diverse colour variation seen; furthermore, specimens of this species usually seem to be collected sporadically, leaving many gaps. In general however, forms with dark wings seem to be markedly smaller on average than those with orange wings.

Biology.— A single female from Ecuador: Los Rios, Río Palenque (FDA) has silvery-yellow body pubescence in patterns agreeing well with that of the west-Ecuadorean version of the *P. plutus* mimicry-group; in view of this, despite the fact that no other specimens of this species have been seen from the area, it is not regarded as an individual character reversal.

Distinctions.— Similar only to *P. brevicornis*, which see for differences.

Distribution.— Found from the southern USA to Bolivia, and from Colombia east through the Guianas to the Amazon delta and the south-east coast of Brazil; altitudinal distribution unusual: at some altitude in the more northern part of its range (e.g. up to about 1,800 m in Texas), but occurring at lower altitudes in South America. The single records from the West Indies (St Domingo; BMNH) and Tucumán need confirmation. In the latter case (holotype of *P. lilloi*) it is not clear whether the label signifies that the specimen was collected in Tucumán by Miguel Lillo, or whether it simply belongs to the IMLT (and could have been collected elsewhere); it is the only record of this species from within the range of its sister-species, *P. brevicornis* (map fig. 237).

Material.— 45 ♂♂, 116 ♀♀; AEIG, AMNH, BMNH, BRIO, CAS, CUNY, EMMSU, FDA, FRITZ, INBIO, LACM, MACN, MCZ, MHNGV, MLP, MLU, MNHNPS, MNHU, MNRJ, MZUSP, NMV, NRS, OSUC, RMNH, SEMKU, SMF, TMB, UMOX, UNPBOG, USNM, USU, UZMC, WASBAUER, WILLIAMS, ZSM.

The *P. sumptuosa*-group

Definition.— Males with SGP divided into polished and pilose areas (in one species entirely polished and pilose). Females with very short inner hind tibial spur, 0.10-0.20(-0.30) basitarsus length, not or scarcely longer than apex of tibia, and bearing a very strong comb-brush. AS3 long to very long (short in one species). Last segment of hind tarsus more-or-less strongly curved, claw-tooth at or beyond middle of claw.

Description.— This group includes most of the giants of the genus (BL males 18-38(-45), females 27-62) and comprises some 16 species, of which a single male (and possibly an additional species – see note under Distribution) is unknown; it may be extinct, in view of the large-scale clearance of the Ecuadorean coastal forest, its presumed habitat. Body often with abundant golden (occasionally silvery-yellow or ashy-white) vestiture forming strong patterns. The antennae display varying proportions of black and orange (occasionally entirely black). The wings are amber-orange to black (when paler, often with a dark border), often differing between sexes, sometimes with the forewing apex more-or-less pale but not strongly milky-white. Legs occasionally with bright, red-brown pubescence.

MT never very strong; APT fairly strong, PPT and PTC often very strong, especially in males where they commonly form 3 large teeth (e.g. "*P. tricuspidata*"). DTC usually very coarse, sometimes strongly curved.

Males usually with modified hairs on S.5 and 6, occasionally 7, often dense but mostly rather short, sometimes weakly curved or apically hooked. SGP very variable, broad or narrow, occasionally curved, usually with a virtually flat surface, often basally or apically constricted, more-or-less bifid apically. Base sometimes with a median tubercle, on either side of which is sometimes a lacuna. Paramere either narrow with a prominence on inner side, forming the proximal limit of a notch, or

extremely narrow and lacking these. The apex of the digitus is long and incurved.

Female AS3 long (very long in two species, where it is associated with an extremely strongly constricted temple) but very short in one; the wings are often longer in proportion to their width than in other groups; the femur, especially anterior, bears a quantity of long, coarse, sinuate hairs below; claw-tooth of hind leg overlaid by strong setae, markedly sinuate over the tooth when the latter is sub-apical.

Distribution.— The group is less widely distributed than the genus; it is absent from the USA, West Indies and the west coast of South America from Perú southwards; neither does it reach far south in Argentina.

Mr M. Cooper (pers. comm.) saw specimens of a very large wasp with strong silver-white body pubescence patterns in the Cochabamba Museum, Bolivia; they were labelled "Chaparé" and he believes the specimens probably were collected on the old road to that place. They may belong to an undescribed species of the *P. sumptuosa*-group, which is otherwise unknown from highland Bolivia. On a subsequent visit he was unable to examine the specimens further because "they had been placed in storage".

Biology.— This group forms the basis of the *plutus* mimicry-group, while specimens of *P. defecta* occurring in southeast Brazil belong to the *discolor* mimicry-group.

Phylogeny.— (See also remarks under the *P. plutus* mimicry-group).

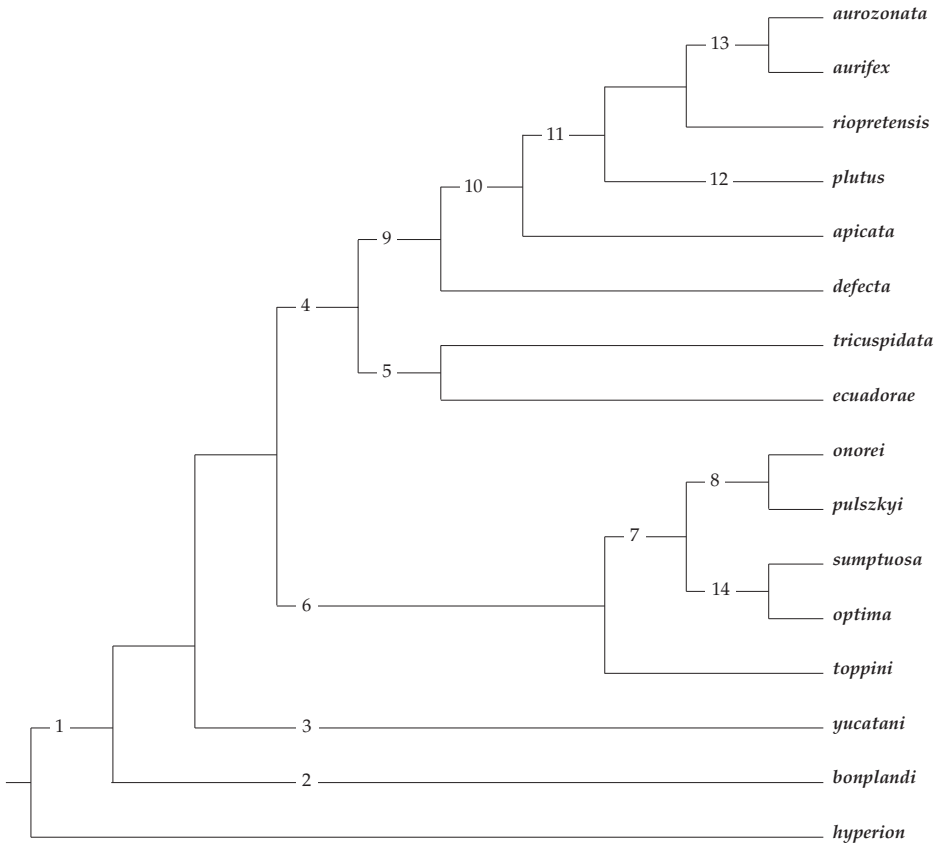
This group follows the usual pattern: it has a sister-group, the *P. deaurata* species-pair; it has a single very old species (*hyperion*); and it exhibits the major bifurcation with subsequent diversification of both branches. On one of the latter, *P. onorei*, *P. pulszkyi*, *P. sumptuosa*, *P. optima* and *P. toppini* form an especially closely-related sub-group.

The main apomorphy of this group is the division of the male SGP surface into polished and pilose areas. The extremely short inner spur, with very long, dense comb, of the female hind tibia is best exhibited in this group and found in virtually all species; however, in a less extreme form it is also found sporadically in other groups: *P. elevata* (3 of 5 species) and *P. sommeri* (5 of 9 species). The strongly curved last segment of the female hind tarsus is found in weaker form sporadically in several other species belonging to various groups, as is the medial position of the hind claw-tooth; but the sub-apical position of the hind claw-tooth, with its sinuate subtending setae, are apomorphies unique to only 4 of the more recent species on one branch of the *P. sumptuosa*-group. The male of the oldest species of the group (*P. hyperion*) has a slightly flattened T.1 with a weak median groove, as in the *P. chiliensis*- and *P. brevicornis*-groups; very weak traces of this condition are found also in a few other species of the present group. The slightly angulate, thickened radius/costa junction, characteristic of several other groups (see main cladogram), is found as a character-reversal in the male of *P. yucatani*. The very short AS3 in the female of one species is another character-reversal in this group. In three species, the lateral extension of the female S.2 groove is weak on average, but it is a very variable character in this group, and is also found in several other groups.

Biogeography.— Since only younger species of this group are found at high altitudes, this strongly suggests that it underwent much of its early proliferation exclusively at very low altitudes in the Amazon basin, only adapting to higher altitudes much later than, for example, the *P. rubra*-group. In contrast to the *P. rubra*-group, it is absent from North America and the West Indies, and is absent from Argentine Patagonia and Chile. This is what would be expected of a group which was slower to adapt

Cladogram for the *P. sumptuosa*-group

Note.— Although the male of *P. ecuadorae* is unknown, the species appears to be most closely related to *P. tricuspidata* on the basis of its subapical claw-tooth, AE index, propodeal sculpture & hair-length, hind tibial teeth and very large BL.



Characters

1. SGP with distinctly separated pilose and polished areas; apical projection of digitus directed obliquely.
2. SGP quadrate, its apex strongly truncate, and hairs directed proximad; paramere with inwardly-directed hairs.
3. Base of SGP pilose area broad and diffuse; extremely strongly constricted temples.
4. Female claw-tooth sub-apical.
5. Extremely large BL.
6. SGP elongate, with transverse basal ridge and lateral margins raised & polished; species occur at moderate to high altitudes.
7. SGP with apical lobes projecting far beyond ends of lateral margins.
8. SGP hairs short, very fine and dense; apical projection of digitus strongly expanded pre-apically.
9. SGP with lacunae.
10. SGP elongate.
11. SGP with very strong, semicircular basal carina; female subapical claw-tooth position lost; abrupt decrease in body size.
12. Lacunae lost.
13. SGP strongly bent; with basal carina extremely strong and sharp.
14. SGP with lateral shoulders strongly differentiated.

to the lower temperatures necessary to cross the Andes and Brazilian Highlands. The *P. sumptuosa*-group also differs in that it has two species whose range is exclusively eastern lowland, whereas no species of the *P. rubra*-group exhibits this type of distribution; again, an eastern distributional range could be expected in some species of a group which began its proliferation at very low altitudes in Amazonia. In accord with this, most species partake in the Amazon-based mimicry group; indeed, the *P. sumptuosa*-group can be said to form the basis of it, since very few species of other taxonomic groups are members. In the normally dark-coloured Central American species *P. tricuspidata*, several males from Costa Rica exhibit abundant, bright golden body hair, a pattern otherwise known only from the Amazon basin. This is surely a character-reversal which, because it is common, strongly suggests relatively recent spread from the ancestral area of Amazonia. Two species, rather distantly related within the group, occur in the western Andes of Ecuador; both exhibit transmuted forms of the usual golden pubescence, one silvery-white, the other ashy-grey.

A puzzling situation came to light after the phylogeny of this group had been worked out: *P. yucatani* is an old species, today restricted to Yucatán. But since it evolved before the group as a whole had adapted to higher altitudes and was thus unable to cross the Andes, how did it get there from Amazonia? There is no evidence that it took a coastal route like, for example, *P. frivaldskyi* (a member of the closely-related *P. deaurata*-group). It is planned to treat this fascinating subject in another paper; for the moment, it can be said that evidence exists of early reciprocal movement between Amazonia and Central America in other taxa.

Another interesting aspect of the *P. sumptuosa*-group, shared with its sister-group, the *P. deaurata*-group, is the extremely large size of most species. Since almost all other groups in the genus appear to reflect evolutionary pressure towards small-sized species, this suggests that the *P. sumptuosa*-group first proliferated in isolation from potential competitors, and that their ranges did not merge until such time as the large species of those other groups had mostly become extinct, thereby minimizing competition. Those very few large species of other taxonomic groups which did survive, had by this time probably adapted to unique niches safe from competition.

Pepsis aurozonata Smith, 1855
(figs 106-109, 220-224, 240)

Pepsis apicalis Lepeletier, 1845: 472 [not Gray, 1832]. Lectotype ♀ (MIZSU), here designated [examined]. **Syn. nov.**

Pepsis aurozonata Smith, 1855: 191, no. 10. Lectotype ♂ (BMNH), here designated [examined].

Pepsis somatochlora Hurd, 1950: 133. [Replacement name for *P. apicalis* Lepeletier not Gray].

Type-material.— *P. apicalis*: I have seen a single type-material ♀ and labelled it lectotype. *P. aurozonata*: I have seen four conspecific ♂ syntypes: one labelled "Pará" and one "Ega" [now = Teffé] in BMNH and two, both labelled "Pará", in UMOX. I have labelled as lectotype the BMNH specimen from Pará; the remaining three are paralectotypes.

Description.— ♂. BL 18-32. Body and legs black, with extensive short, golden pubescence forming patterns on head, thorax and propodeum; on gaster, covering T.1

and forming broad, apical bands on remaining tergites. Antenna orange, beginning almost at base of AS3, sometimes then shading gradually into black apicad, or entirely black. Wings dull infuscate-amber, forewing with extreme apex more or less distinctly pale. S.4 (fig. 109) with a few long hairs laterally; S.5 with a fairly dense, transverse, pre-apical band of long hairs, sparser centrally, with apices broadly hooked, pointing backwards, and a narrow band of shorter, straight, dense hairs on apical margin; S.6 with a dense band of straight hairs almost reaching the height (not length) of those on S.5. SGP (figs 106, 107) very narrow and strongly upcurved, with sides weakly expanded at the sharpest point of the bend; otherwise parallel-sided to the apex, which has a V-shaped emargination, the two resulting lobes rounded; the SGP also has a very strong, semicircular, basal tubercle and a weak, median keel gradually obsolescent apicad; just beyond the tubercle, on each side of the median keel, is an elongate lacuna; apex of SGP with hairs about as long as 3/4 SGP width. Paramere very narrow, with apical hairs as long as double its maximum width. Inner projection of digitus apex (fig. 108) slightly broadened.

♀. BL 28-41. AE index 109-119. Colour as in male except antennal colour: continuous orange starts at or very near base of AS5; frequently an apical ring on AS3 and irregular patches on AS4 are also orange; pronotum always black above; wings deep orange, pale forewing apex scarcely or not evident; less golden pubescence on gaster. Head (fig. 220) with temple and vertex slightly swollen; MT weak to moderate. SMC3 of forewing (fig. 221) rather long; MPN much shorter than PST, its furrow very narrow; with a single very strong carina, obsolescent mediad or obsolete medially, and a few fine ones. Propodeum: MG replaced by broad, shallow ridge. APT weak, PPT and PTC moderate to strong. DTC fairly strong, often wavy but otherwise regular; often a stronger one some distance before the PTC. Propodeal hair about 3/4 PST length. Posterior face: VR very weak or absent; PFC as strong as DTC and covering virtually the whole surface. Lateral extension of S.2 groove fairly well developed. Hind tibia (figs 222-224): teeth very small, often distant, the subtending spines 2.5-3.0 times as high. Inner spur reaching to only 0.15-0.2 basitarsus length (about equal to tarsal segment 4) and 1.0-1.1 times as long as outer spur. Claw-tooth of all tarsi about 2/3 from claw base.

Variation.— In two males from Bolivia, Quatro Ojos (CMNH) the pubescence is deep reddish-golden, almost copper-coloured.

Biology.— All specimens of this species belong to the *P. plutus* mimicry-group.

Distinctions.— The male is immediately distinguished by its unique SGP shape; the female strongly resembles that of *P. plutus*, but differs from it as in the accompanying table. None of the females of the larger lowland species of this group have such extensive gastral pubescence as in these two species.

Distribution.— Known from French Guiana, with a single record from Venezuela; the entire Amazon mainstream, in the east extending very little southwards, but in the west southwards to Bolivia; always at low altitudes (map fig. 240).

Material.— 80 ♂♂, 62 ♀♀; AMNH, BMNH, CMNH, EMMSU, FDA, FSAG, INPA, LACM, MCZ, MHNGV, MHNNEU, MIZAM, MIZSU, MNHNPS, MNHU, MNRJ, MPEG, MZUSP, NMV, RIBPRET, RMNH, TMB, UBRAS, UMBREM, UMOX, USNM, UZMC, WAHIS, WILLIAMS, ZSM.

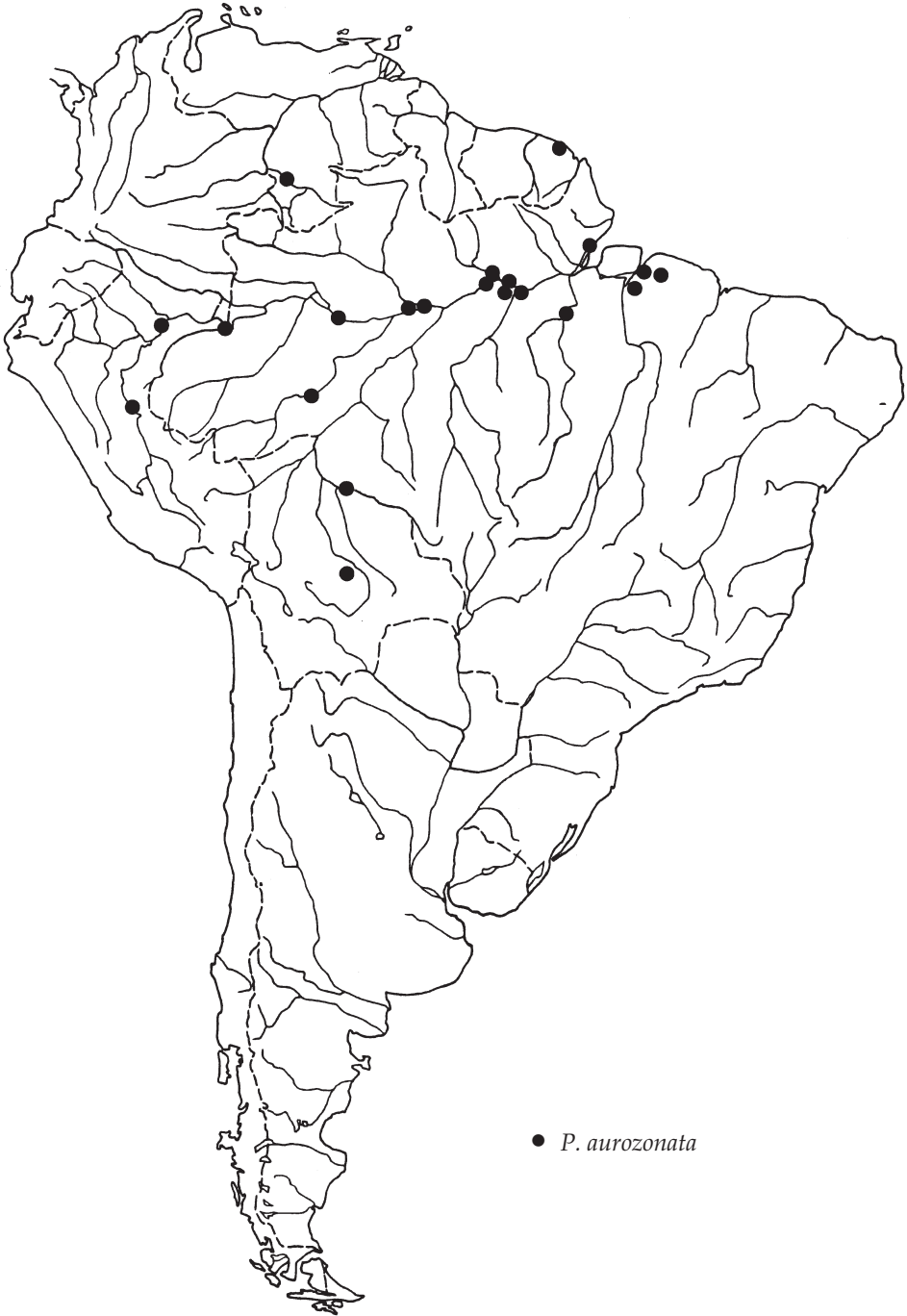


Fig. 240. Collection localities of *Pepsis aurozonata* Smith.

Table for distinguishing between females of *P. aurozonata* and *P. plutus*

<i>P. aurozonata</i>	<i>P. plutus</i>
Temple more-or-less swollen in dorsal view (fig. 220).	Temple very strongly constricted in dorsal view (fig. 227).
SMC3 shorter; anterior veinlet about equal in length to posterodistal veinlet (fig. 221).	SMC3 longer; anterior veinlet distinctly longer than postero-distal veinlet (fig. 228).
MPN furrow narrow posteriorly.	MPN furrow expanded posteriorly.
Posterior face of propodeum more or less flat, with transverse carinae of even strength over most of surface.	Posterior face of propodeum with two strong, vertical ridges; with carinae across uppermost part, rapidly decreasing in strength below.
Hind tibial teeth usually small and distant (figs 222-224).	Hind tibial teeth usually fairly large and close together (figs 229, 230).

Pepsis aurifex Smith, 1855
(figs 110-113, 216, 241)

Pepsis aurifex Smith, 1855: 191, no. 11. Lectotype ♂ (BMNH), here designated [examined].
Pepsis niphe Mocsáry, 1885: 260, no. 36. Lectotype ♀ (TMB), here designated [examined]. **Syn. nov.**

Type-material.— *P. aurifex*: I have seen three syntype ♂♂, two in BMNH and one in UMOX. I have labelled the smaller specimen in BMNH (locality "Santarem") as lectotype; the remaining two are paralectotypes. The specimen in UMOX (also "Santarem") is conspecific with the lectotype, but the second BMNH ♂ is a specimen of *P. apicata* Taschenberg. *P. niphe*: I have seen a single type-material ♀ and labelled it lectotype.

Description.— ♂. BL 26-32. Body and most of all femora black, with dense golden pubescence (darker basally on T.2-5); remainder of legs bright red-brown with paler hair. Antennal segments 1-2 dark red-brown with extremely short golden pubescence; remainder mostly dark orange-infusate, often paler apically. Wings dull yellowish-amber with the extreme apex of the forewing pale. S.5 (fig. 113) with a broad, apical band of short, very dense, golden hairs, with a few longer, slightly curved hairs amongst them; S.6 with similar hairs but the short ones are less dense and the long ones slightly shorter and straight, but denser. SGP (figs 110, 111) yellow-brown, its sides weakly convergent apicad in basal half, then strongly constricted about the middle, then expanded again to form the irregularly rounded apex; with a very strong, arcuate basal ridge directed proximad (sometimes partly hidden under edge of preceding sternite); SGP bent strongly upwards at the middle, at which point a pair of lacunae is clearly visible; apical half very broadly rounded with a shallow depression in the median line, extending right to the apex. Hairs about as long as half minimum SGP width cover a band before the apex and project beyond it. Paramere about twice as long as rest of genitalia, very narrow and parallel-sided, pointed, with apical hairs about 1.5 times its width; at about the mid-point of its inner edge is a tiny but sharp tooth. Inner projection of digitus apex (fig. 112) slender, evenly rounded, directed inwards and with a tiny point directed proximad.

♀. BL 33-38. AE index 125-137. Colour as in male, except body without golden pubescence, thoracic and propodeal short hair with weak violaceous or yellowish tint; legs dark with longitudinal band of short, dull golden-brown pubescence on inner side of hind tibia (view from below); antenna with dull orange apical rings on

all segments from AS3 onwards; the same colour beginning very diffusely on mid-AS3 to AS9, extending to apex of antenna, or only the last 3 segments dull orange; forewing apex more distinctly pale. Head in dorsal view (fig. 216) with temple only slightly swollen, rather strongly constricted behind. MT weak to moderate. MPN a little shorter than PST, its furrow narrow and deep, anteriorly flattened-out; carinae extremely fine. Propodeum: MG replaced by broad ridge; APT strong to very strong, PPT and PTC moderate to strong. DTC rather strong, often slightly curved, slightly stronger and more distant posteriorly. Propodeal hair very short, only about half MPN length. Posterior face: VR weak, divergent apicad; PFC a few strong above, rapidly obsolescent below, broadly interrupted in median line throughout. Lateral extension of S.2 groove very weak. Hind tibia: teeth rather small but not distant, the subtending spines about 1.5 times as high; inner spur extremely short, reaching only to 0.15 basitarsus length (about equal to tarsal segment 4) and 0.9-1.1 times as long as outer spur. Claw-tooth of tarsi at about the following distances from claw base: anterior 1/2-2/3; mid 2/3; posterior 2/3-4/5).

Variation.— As detailed above.

Biology.— All males belong to the *P. plutus* mimicry-group.

Distinctions.— The male SGP resembles only that of *P. riopretensis*, but is strongly bent; the female is best distinguished from others of its group by its rather small size, details of MPN and propodeal sculpture, pale forewing apex and total lack of bright body pubescence. It can be separated from small specimens of *P. defecta* by its long AS3; furthermore, its distributional range is very restricted.

Distribution.— Known only from a very short stretch of the Lower Amazon, at low altitudes (map fig. 241).

Material.— 4 ♂♂, 6 ♀♀; AEIG, BMNH, CMNH, MNRJ, NMV, UMOX, TMB, WILLIAMS, ZSM.

Pepsis riopretensis spec. nov.
(figs 175-177, 217, 241)

Type material.— Holotype ♂, **Brazil**: Rio Preto, 1927 (Richter) (SMF). Paratypes: 1♂, Brazil: Goyaz, Viannopolis, xi.1931 (Spitz) (MZUSP); 1♀, Brazil: Goyaz, Campinas, xii.1935 (Borgmeier & Lopez) (MNRJ).

Note.— There is doubt about which Rio Preto is the provenance of the holotype. There is a town of this name about 100 km north-west of Rio de Janeiro which one might assume is the one, but there is another Rio Preto which flows south-east from near Brasilia; since this river is only about 85 km from a paratype locality, there is a chance that the specimen came from that Rio Preto. I did not succeed in finding any relevant manuscript or publication by or about the collector.

Etymology.— This species is named after its type-locality.

Description.— ♂. BL 22-23. Body and legs black; head, thorax, propodeum and T.1 with dense, pale golden pubescence. Antenna bright orange from AS3 onwards. Wings pale orange-amber with extreme apex of forewing pale. S.5 and 6 with rather sparse, short black hairs. SGP (figs 175, 176) dark brown; base with an arcuate but not very sharp basal ridge directed proximad, ending in lateral "shoulders"; immediately beyond this the sides of the SGP are strongly but briefly constricted; the expansion beyond this gradually narrows to the rounded apex; the basal ridge can create the illu-

sion that the SGP is slightly bent up; between the lateral constrictions is a pair of small lacunae (visible only by back light); rather short hairs form a fringe around the narrowed, apical part. Paramere extending to about twice the length of the rest of the genitalia, very narrow; a tiny, sharp tooth is situated at about the mid-point of the inner edge, beyond which the paramere gradually narrows to the bluntly-pointed apex. Apical hairs a little longer than maximum paramere width. Inner projection of digitus apex (fig. 177) apically broadened like a cobra's head, extreme apex with a small, blunt hook directed proximad.

♀. BL 29. AEI 109. Body and legs black with weak, blue-green metallic sheen and very short, brown to violet-blue pubescence on the scutellum to propodeum inclusive. Antenna with last four segments orange-brown, the preceding one very dark brown. Wings infusate-amber, a little darker than those of the male and with the pale apex slightly more extensive. Face and especially clypeus with fine but strong, raised reticulation; head (fig. 217) in dorsal view a little swollen behind eyes, thus appearing rather transverse. MT small, blunt. MPN scarcely shorter than PST, its furrow narrow anteriorly but irregularly expanded posterad; carinae very fine, with two stronger ones showing through pubescence near furrow. Propodeum: with a broad, median ridge narrower and obsolescent apicad; APT quite strong, tooth-like; PPT smaller, pointed; PTC strong, scarcely emarginate medially; DTC rather weak, visible mainly along the ridge. Propodeal hair slightly shorter than MPN length. Posterior face: VR strong, strongly divergent apicad, PFC only strong where they cross the VR. Lateral extension of S.2 groove quite well developed. Hind tibia: teeth fairly strong but rather blunt, each subtended by a spine 2.0-2.5 times as high; inner spur reaching to about 0.20 length of basitarsus (about equal to tarsal segment 4), scarcely longer than outer spur. Tooth of anterior claw about half-way from the base, those of mid and hind claws about two-thirds from the base; the setae of the hind claw slightly sinuate where they pass over the tooth.

Variation.— None observed.

Distinctions.— The male is very similar to that of *P. aurifex*, but is smaller; it also differs in lacking golden bands on T.2 onwards and in the entirely black hind legs; the SGP is darker in colour (obscuring the lacunae), not strongly bent up, and is much more strongly narrowed to the apex; the broadened digitus apex also differs strongly from the narrow one of *P. aurifex*. The female facial reticulation is unique in the genus; it further differs from *P. aurifex* by its darker wings, the slightly longer inner hind tibial spur, and by allopatry; from the sympatric *P. bonplandi* by its pale fore-wing apex, much stronger APT and VR, and longer hind tibial inner spur.

Distribution.— Known only from three localities in central and southeast Brazil, at low altitudes (map fig. 241).

Material.— 2 ♂♂, 1 ♀; MNRJ, MZUSP, SMF.

Pepsis plutus Erichson, 1848
(figs 171-174, 227-230, 243)

Pepsis plutus Erichson, 1848: 588, ♂, ♀, Guyana (lost).

Pepsis chrysochlamys Mocsáry, 1894: 2, no. 2, ♂, Brazil, Piauhy (lost). [Synonymized by Lucas, 1895: 479].

Pepsis opulenta Mocsáry, 1894: 3, no. 4. Lectotype ♀ (TMB), here designated [examined]. **Syn. nov.**

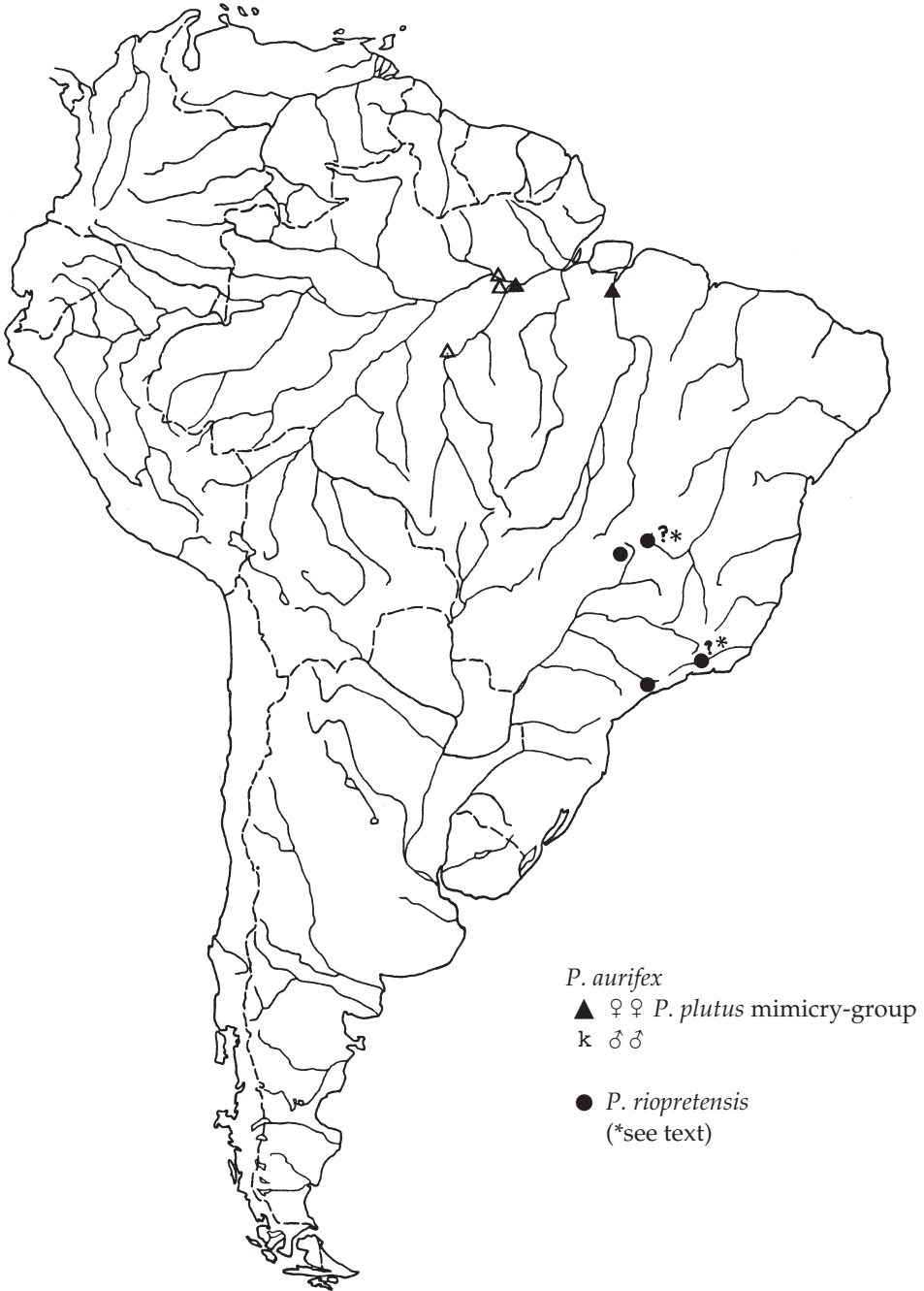


Fig. 241. Collection localities of *Pepsis aurifex* Smith and *P. riopretensis* spec. nov.

Note. *Pepsis gigas* Fabricius, 1804: 213: only the paratype ♀ belongs here; see "Excluded species" list (to be published in Part III).

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

Description.— ♂. BL 19-29. Body and legs black, mostly covered with short, golden pubescence which forms an apical band on each gastral tergite. Antenna with orange as follows: at least the apex of the last segment, often the last 2-3 segments, occasionally all except the first 2 segments. Wings dull yellowish-infusate, forewing with the extreme apex more or less distinctly pale. S.4 (fig. 174) with a few, short, weakly backwardly-curved hairs laterally; S.5 with a rather sparse, transverse band of similar but longer and more strongly-curved hairs, behind which is a dense band of short, straight ones. S.6 with a broad, dense band of hairs usually longer than the longer ones on S.5 but variable; slightly curved forwards. SGP (figs 171, 172) with sides parallel in basal half, ending in a tooth (often very sharp) on either side; suddenly constricted after the tooth, then strongly tapered to the rounded apex, which occasionally has a small emargination; a basal, semicircular ridge ends at the lateral teeth; the surface beyond the ridge is polished, and except for the lateral margins is covered with fairly long, dense hair which is longer still and sparser apicad; the apex has a fringe of much shorter hair. Paramere with apical hairs slightly longer than paramere width, its inner margin at about the middle with a strong emargination beginning proximally with a sharp tooth. Inner projection of digitus apex (fig. 173) slightly broadened, evenly tapered and narrowly truncate, with a tiny tooth directed proximad.

♀. BL 28-45. AE index 111-128. Colour as in male, except antennal orange colour starts on AS3, usually near apex; AS4 often with irregular dark patches, occasionally only apex of AS4 orange; wings frequently pale orange rather than yellowish-infusate. Head (fig. 227) in dorsal view with temple very strongly constricted, vertex scarcely swollen. MT weak to moderate. Forewing (fig. 228) with SMC3 very long. MPN slightly shorter than PST, its furrow broad; carinae very fine, sometimes slightly stronger near midline, matt, partly obscured by pilosity. Propodeum: MG replaced by broad ridge. APT weak to strong, PPT and PTC moderate to strong; DTC quite strong but obscured by pilosity; sometimes curved, often unevenly spaced. Propodeal hair slightly shorter than PST. Posterior face: VR strong, slightly divergent apicad; PFC strong only on VR above, rapidly obsolescent on rest of face, which is covered by pilosity. Lateral extension of S.2 groove usually well-developed, occasionally vestigial. Hind tibia (figs 229, 230): teeth often broader and slightly lower than usual (hence closer together), the subtending spines 2.0-2.5 times as high. Inner spur reaching to 0.2-0.25 basitarsus length (about equal to tarsal segment 4) and 1.0-1.1 times as long as outer spur. All tarsi with claw-tooth about 1/2-2/3 from claw base.

Variation.— Female pronotum black in Guianas, golden on Lower Amazon, and black with a variable admixture of golden hair on Upper Amazon and headwaters.

Biology.— The name of this species is used for a mimicry-group.

Distinctions.— The male SGP is like no other; the female most resembles that of *P. aurozonata*, under which species a table is given for their separation; however, abraded females, in which the pubescence remains only weakly on T.1, resemble small specimens of *P. sumptuosa*; antennal colour and provenance suffice to separate these.

Distribution.— Venezuela, the Guianas, entire Amazon and headwaters; in the

east, south only to Pauí; in the west, southwards to south-east Perú; the maximum altitude reached is 500m, in Venezuela: Bolivar (map fig. 243).

Material.— 36 ♂♂, 47 ♀♀; AMNH, BMNH, CMNH, INPA, MCZ, MHNGV, MIZAM, MNHNPS, MNHU, MNRJ, MPEG, MZFIR, MZUSP, NHMLIM, NMV, NRS, RMNH, TMB, UPAN, USNM, UZMC, ZMMICH, ZSM.

Pepsis apicata Taschenberg, 1869
(figs 135-139, 210, 242)

Pepsis apicata Taschenberg, 1869: 28, no. 2. Lectotype ♀ (MLU), here designated [examined].

Pepsis alcimeda Banks, 1946: 318. Holotype ♀ (MCZ) [examined]. **Syn. nov.**

Pepsis amalthea Banks, 1946: 319. Lectotype ♀ (MCZ), here designated [examined]. **Syn. nov.**

Type-material.— *P. apicata*: I have seen a single type-material ♀ and labelled it lectotype. *P. amalthea*: I have seen three syntype ♀♀, one from Bolivia: Santa Cruz (MCZ) which I have labelled lectotype, and one each from Brazil: Urucum, Corumbá and "Amazonas" (CUNY) which are paralectotypes; both are conspecific with the lectotype.

Description.— ♂. BL 28-45. Body and all femora black, with abundant golden hair or none (see Variation), but always dense reddish hair on T.7 and some on T.6; SGP bright red-brown; remainder of legs always bright redbrown, with the hair slightly paler. Antenna deep orange or dark brown from base of AS3, with paler apical rings on most segments; last 1-2 segments sometimes paler orange. Wings more or less infusate, forewing often with a trace of a pale extreme apex. S.4 (fig. 139) with a few, long hairs scattered across it, and a dense, apical band of very short, semi-erect ones; S.5 hairs similar but the longer ones denser and apically curved, and the rest more upright, forming a wider band; S.6 covered with very dense hair similar to the longer hair of S.5. SGP (figs 135, 136) essentially parallel-sided, with a strong, slightly transverse, sub-basal tubercle; on each side of this is a strong, oval lacuna; the apex is abruptly narrowed and narrowly emarginate centrally and has a fringe composed of short, dense hairs and rather sparse, very long, curved ones; immediately following the tubercle is a well-defined, slightly depressed area covered with long, dense hairs; this area expands laterad and apicad until it occupies the entire width of the SGP from the point where the latter begins to narrow to the apex; the lateral, polished areas thus remaining become thicker apicad, especially where they end at the sides. Paramere (fig. 138) rather narrow, about 1.5 times as long as rest of genitalia. Inner projection of digitus apex (fig. 137) slightly broadened.

♀. BL 28-62. AE index 113-136. Colour as in male except totally lacking the golden body hair found in Amazon males. Females from that area have only some dull brownish-violet pubescence on the thorax and propodeum; also, the legs are entirely black. The antenna is usually rather dull orange, beginning very gradually on AS3, but occasionally several segments more distally. Only occasional specimens have a faint hint of a pale forewing apex; the wings are otherwise moderately to strongly infusate, on average darker than in the male.

Head (fig. 210) with temple and vertex moderately swollen (more strongly in large specimens). MT weak to moderate. Forewing with SMC3 long. MPN slightly shorter than PST, its furrow very broad; carinae few and fine, to 2-3 very strong. Propodeum: MG replaced by broad, strong ridge. APT moderate to strong, PPT

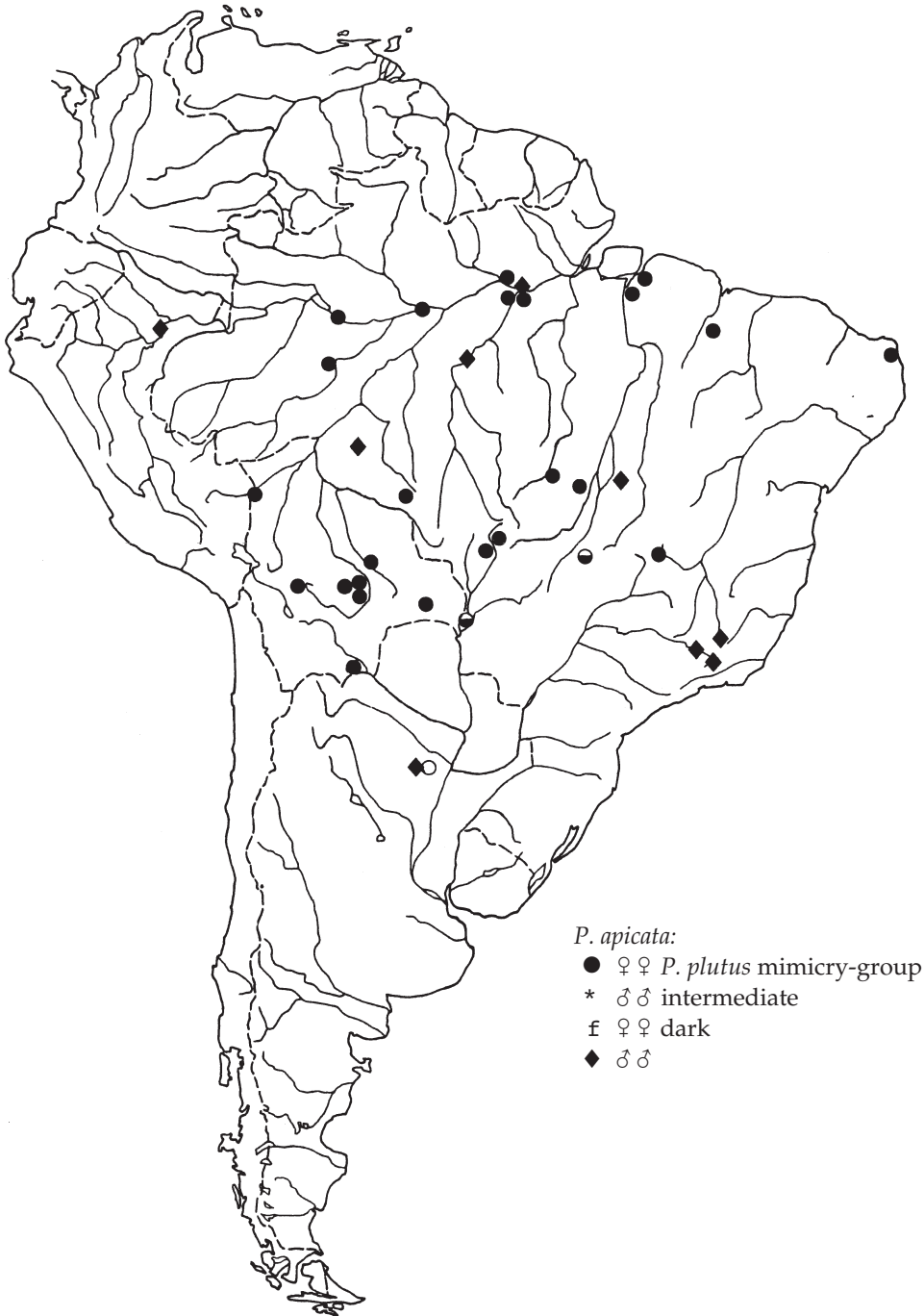


Fig. 242. Collection localities of *Pepsis apicata* Taschenberg.

strong, broad-based, PTC moderate to strong, flat topped. DTC variable (see Variation). Propodeal hair only about 3/4 PST length. Posterior face: VR at most weakly indicated near PTC; PFC rather weak but covering most of face, obsolescent medially. Lateral extension of S.2 groove well developed. Hind tibia: teeth usual for the group, occasionally rather sharp; inner spur reaching to only 0.15-0.2 basitarsus length (about equal to tarsal segment 4), and 0.9-1.1 times as long as outer spur; claw-tooth of mid and hind tarsi further from the claw-base than that of anterior tarsus (anterior just over 1/2-2/3; mid 2/3-3/4; posterior 2/3-4/5).

Variation.— Males from the Amazon belong to the major mimicry-group (*P. plutus*-group) characteristic of the area, with dense golden pubescence forming patterns on the mesoscutum (including twin median stripes) and apical bands on T.2-5. Males from the Argentine Chaco almost totally lack pale body hair, only some on the thorax and propodeum having a very weak yellowish-violet tint. However, a male from Brazil, Goiás Velho (LEBRAS) is intermediate in colour to a degree corresponding to its intermediate provenance: it mainly coincides with Amazon specimens but T.1 has only an apical band of golden hair instead of being completely covered, and the apical bands on T.2-5 are narrower. However, males from Cuiabá, Gustavo Dutra (OSUC) are similar to Amazon specimens in vestiture.

Two males from the Amazon have the SGP apically constricted and rounded like that of *P. defecta*; the hind legs have only the tarsi dull red-brown; they are otherwise normal *P. apicata*.

Specimens from the Amazon region are, on average, larger than those from further south; especially females are much larger. The DTC in females is extremely variable, from very strong to absent except usually indicated on median ridge; when strong, sometimes there is a very strong one mimicking the PTC and about 1/3 of the dorsal length in front of it; between the two is an unsculptured, shining area. This variation is not particularly size-related.

Biology.— Males occurring near the Amazon belong to the *P. plutus* mimicry-group.

Distinctions.— The male is best recognized by its SGP structure; however, the conspicuously-contrasting, bright red-brown legs are a characteristic shared only with *P. aurifex* and some specimens of *P. deaurata*. The female is best distinguished from most species of its group except *P. defecta* by the subapical claw-tooth position; it differs in having a usually much longer AS3 than *P. defecta*; however, some females of the latter are very difficult to distinguish where the two species are sympatric; further characters of use are: *P. defecta* has the head more swollen, the PPT much smaller and the forewing apex more commonly paler. *P. ecuadorae* has conspicuous whitish body pubescence, and *P. tricuspidata* has much paler wings. Both of the latter species are also allopatric from *P. apicata*.

Distribution.— Found along the Amazon mainstream west to Manaus; extending to Bolivia and southeast Brazil; not recorded from southern Brazil but occurs in Paraguay and Argentina: Chaco; a single female from Perú (MNHNPS) lacks further locality; at low altitudes, reaching only 165m, in Brazil: Rondonia (map fig. 242).

Material.— 59 ♂♂, 133 ♀♀; AEIG, BMNH, CMNH, CUNY, FRITZ, IMLT, INPA, LACM, MACN, MCZ, MHNGV, MLU, MNHNPS, MNRJ, MPEG, MZUSP, NMV, OSUC, RMNH, SMF, TMB, UBRAS, UCALB, UFPCUR, UMBREM, UMOX, WASBAUER, WILLIAMS, ZMMICH, ZSM.

Pepsis defecta Taschenberg, 1869
(figs 140-143, 214, 243)

Pepsis defecta Taschenberg, 1869: 30, no. 9. Lectotype ♂ (MLU), here designated [examined].

Pepsis fumata Enderlein, 1901: 149. Lectotype ♂ (MNHU), here designated [examined]. **Syn. nov.**

Pepsis cleanthes Banks, 1946: 320. Holotype ♀ (MCZ) [examined]. **Syn. nov.**

Type-material.— *P. defecta*: I have seen a single type-material ♂ and labelled it lectotype. *P. fumata*: I have seen all the syntypes: three ♂♂. I have labelled as lectotype the one with perfect wings (the other two have the apices slightly abraded); the remaining two specimens are paralectotypes and all three are conspecific.

Description.— ♂. BL 23-35. Body and legs black with dark blue, green or violaceous sheen. Antenna black. Wings amber to orange, more or less infuscate, usually with a more or less distinct pale, apical border, preceded by a darker band which is easier to see in the less infuscate forms. S.5 (fig. 143) often with a narrow, apical band of very short, dense hair; pre-apically is always a thin arc of rather long, straight hairs which are very sparse centrally. S.6 with hairs similar to the longer ones on S.5 but a little longer and much denser. SGP (figs 140, 141) rather short, parallel-sided or gradually narrowed towards the strongly-rounded apex which is slightly emarginate centrally; just beyond the rather weak basal tubercle, is an area moderately densely covered with long hairs and abruptly expanded at about the SGP mid-point; remainder of surface polished. Slightly distal to the tubercle on either side is an a slightly elongate lacuna. Apical hairs curved, about half as long as SGP maximum width. Paramere about 1.5 times as long as rest of genitalia; at about the middle of the inner side is a shallow emargination, at whose base is a small but sharp tooth; apical hairs a little longer than maximum paramere width. Inner projection of digitus apex (fig. 142) scarcely broadened, ending in a small tooth directed proximad.

♀. BL 32-55. AE index 94-113. Colour as in male, except antenna black but segments usually with narrow, apical orange rings becoming increasingly distinct towards the antennal apex; sometimes the last 1-2 segments dull orange. Wing-colour – see Variation. Head (fig. 214) with temple and vertex strongly swollen. MPN distinctly shorter than PST, its furrow broad; carinae none to several, moderate to strong. Propodeum: MG usually present posteriorly, otherwise replaced by a broad ridge. APT moderate to strong; PPT rather small but narrow and quite sharp (rarely very strong). DTC moderate to weak, present at least in centre-line, sometimes strongly curved; sometimes about 1/3 of the dorsal length in front of the PTC is a more or less stronger one resembling the latter. PTC moderate to very strong, broad, flat-topped, often slightly emarginate. Propodeal hair only about 1/2 PST length. Posterior face: VR absent or weak; PFC usually fairly strong, covering most of face and more or less interrupted in midline, but very variable. Lateral extension of S.2 groove well developed. Hind tibia: teeth small to medium, sharp, often more or less distant; the subtending spines 2-3 times as high. Inner spur reaching to 0.25-0.3 basitarsus length (intermediate between tarsal segments 3 and 4 in length) and 1.0-1.1 times as long as outer spur. Mid and hind tarsal claws with tooth further from claw base than that of anterior tarsus (anterior just over 1/2-3/4; mid 2/3-4/5; posterior 3/4-4/5).

Variation.— The wing-colour varies on a geographical basis in this species: in the west of Argentina, Bolivia and the Chaco it is most often deep orange-amber; becoming more strongly infusate, less orange, and acquiring pale wing-bases and a general greenish appearance in Misiones, Paraguay and south-central Brazil (in accord with the *P. discolor* mimicry-group in that area); elsewhere in Brazil the wings are rather dark infusate-orange with a broad but obscure darker border.

A female from Brazil, Ipiranga (MZUSP) has the short pubescence of the head dirty greyish-buff with a weak violet tint. The pubescence of the pronotum and mesonotum is similar but with a stronger violet tint.

Distinctions.— The male is well characterized by its SGP structure; the pale wing apex is also helpful, although sometimes evanescent. The female is well characterized by its short AS3 and subapical claw-tooth. The head is usually more strongly swollen, the AS3 shorter, and the antenna darker than in *P. apicata* (which see), with which species it shares the claw-tooth character.

Distribution.— Found from eastern Brazil, westwards to Bolivia; in the south, to Argentina: Entre Rios and La Rioja; usually at low altitudes, but reaches 1,380 m in Brazil: Minas Geraes (map fig. 243).

Material.— 198 ♂♂, 128 ♀♀; AEIG, AMNH, BMNH, BONELLI, CMNH, CUNY, EMMSU, ETHZ, FRITZ, IMLT, MACN, MCZ, MLP, MLU, MNHNPS, MNHU, MNRJ, MZUSP, NMV, RMNH, SMF, TMB, UBRAS, UCALB, UFPCUR, UMOX, USNM, UZMC, WASBAUER, ZSM.

Pepsis tricuspidata Gribodo, 1894
(figs 150-152, 208, 209, 243)

Pepsis tricuspidata Gribodo, 1894: 2, no. 2. Lectotype ♀ (MCSNGO), here designated [examined].

Pepsis lativalvis Mocsáry, 1894: 12, no. 22. Lectotype ♂ (TMB), here designated [examined]. **Syn. nov.**

Pepsis astarte Banks, 1945: 87. Holotype ♂ (MCZ) [examined]. **Syn. nov.**

Type-material.— *P. tricuspidata*: The original description refers to both sexes, but I have seen only a ♀ syntype; I have labelled this specimen lectotype. *P. lativalvis*: I have seen two specimens of each sex standing under this name in TMB, and a further two ♂♂ (one of them mislabelled "Brazil, Chiriqui") which were standing under *P. nitens* Mocs., also in TMB. The ♀♀ (one of them mislabelled "Bolivia, Chiriqui") have no type status because the original description refers only to multiple ♂♂. I have labelled as lectotype the ♂ labelled "Panamá, Chiriqui"; it also has an original Mocsáry identification label. The other ♂ lacks such a label, but is mislabelled "Bolivia, Chiriqui" (see Introduction p. 9); it is however regarded as a paralectotype, as are the two under *P. nitens*. All six specimens are conspecific.

Description.— ♂. BL 31-41. Body and legs black, short pubescence often with violaceous reflections (but see Variation). Antenna dull orange from base of AS3. Wings deep infusate-orange, often with a broad but obscure dark border (sometimes invading the outer cells), and forewing sometimes with extreme apex pale. S.4 with a few, mainly lateral, moderately long hairs; S.5 and 6 with similar hairs, progressively denser but still mainly lateral; also with apical bands of shorter, denser hairs. SGP (figs 150, 152) slightly expanded from the base to a rounded truncate apex, which has a more-or-less deep, V-shaped central notch; with a median, basal, more or less transverse tubercle, on either side of which extends a polished, lateral strip, gradually narrowing and progressively thicker apicad, ending at about two-

thirds of the SGP length; between these polished areas the surface is rather densely covered with hair, increasing in length towards the apex, the apical hairs curved and about as long as half SGP width. Paramere about 1.5 times as long as rest of genitalia, apically round, with hairs about as long as its maximum width; at the middle of its inner side is a broad, arcuate emargination whose base is angulate. Inner projection of digitus apex (fig. 151) scarcely broadened, with a narrow, rounded end and a tiny tooth directed proximad.

♀. BL 42-50. AE index 125-135. Colour as in male, except antennal orange colour begins diffusely about 1/3 from base of AS3; wings more orange, less infuscate than in male, dark border narrower when present, extreme apex not paler. Head (fig. 208) with vertex and temples more or less swollen. MT weak to moderate. Forewing with SMC3 often very long, MPN variably shorter than PST, its furrow broad, deep, more or less expanded posteriorly and often attenuate or deformed anteriorly; carinae few, strong, often curved. Propodeum: MG replaced by a broad, median ridge. PPT and PTC moderate to strong, the latter very broad; DTC coarse, especially posteriorly. Propodeal hair about as long as PST. Posterior face: VR sometimes very weakly indicated near PTC, otherwise absent; PFC usually rather weak but more-or-less covering whole face. Lateral extension of S.2 groove well developed. Hind tibia: teeth sometimes rather small and distant, the subtending spines 2.0-2.5 times as high. Inner spur reaching to 0.15-0.2 basitarsus length (about equal to tarsal segment 4 or slightly shorter) and 0.9-1.0 times as long as outer spur. Mid and hind tarsi (fig. 209) with claw-tooth further from claw base than in anterior tarsus (anterior just over 1/2, mid and posterior 3/4-4/5).

Variation.— Several males from Costa Rica have extensive bright golden pubescence patterns on the body, as in males of some S. American species (especially Amazonian). The holotype of *P. astarte*, from the Sierra Nevada de Santa Marta in northern Colombia, is intermediate in colour between these specimens and usual males; two other males from the same locality (both MCZ) are of the usual colour for this species. This is the only example in the genus of extension of range to Central America of a basically Amazonian mimicry-group, although *P. onorei* and *P. ecuadorae* are modified mimics found west of the northern Andes.

Biology.— Occasionally males of this species belong to the Amazonian *P. plutus* mimicry-group (see Variation).

Distinctions.— The male is distinguished by its SGP structure, but care is needed to separate it from *P. defecta*. The female is one of the few with the hind tarsal claw-tooth subapical; it lacks the patterned pubescence of *P. ecuadorae*; differs from *P. defecta* in that species' much shorter AS3; and from *P. apicata* in antennal colour and sculptural details. Furthermore, none of the other species with subapical claw-tooth is found in Central America; in this character it also differs from the otherwise similar but allopatric *P. toppini*.

Distribution.— Found only from Costa Rica to northern Colombia (Cauca and Magdalena valleys) and Venezuela (Maracaibo Basin), ascending to 2,600 m in Colombia: Antioquia (map fig. 243).

Material.— 24 ♂♂, 40 ♀♀; ANSP, BMNH, BPBM, CUNY, FDA, INBIO, MCSNGO, MCZ, MEM, MHNGV, MICR, MIZAM, MNHNPS, OSUC, TMB, UCALB, UMOX, UNPBOG, UPAN, USNM, UZMC, WASBAUER, ZSM.

Pepsis ecuadorae spec. nov.
(figs 206, 207, 243)

Type material.— Holotype ♀ **Ecuador**: Guayaquil, 1901 (Buchwald) (TMB). Paratypes. Ecuador: Guayaquil, 1 ♀ (Rorer) (USNM); Manabí, Palmar, 0°10'S., 79°28'W., 150m, 17.v.1941 1 ♀ (AMNH); San Rafael [west of Bucay], 2 ♀♀ (Campos) (BMNH & USNM); Ecuador [NFL], 1 ♀ (Plessen) (ZSM).

Etymology.— This species is named after its country of origin.

Description.— ♂ Unknown.

♀. BL 46-54. AE index 128-132. Body and legs black, most of body covered with pale, silvery-yellow pubescence, forming patterns as follows: large patch on mesoscutum, widening anterad and bilobed anteriorly; covering T.1 and on T.2-5 forming apical bands, broadest centrally, with diffuse anterior margins. Antenna orange from mid-AS3 onwards. Wings orange-amber with an unusual, pale sandy "bloom". Head (fig. 206) with temple scarcely and vertex a little swollen. MT weak to moderate. MPN slightly to markedly shorter than PST, its furrow narrow, slightly expanded apicad; with several strong, curved carinae, often mainly on posterior half. Propodeum: MG replaced by broad median ridge. APT weak to moderate, PPT and PTC moderate to strong, the latter usually very broad; DTC moderately fine, regular. Propodeal hair almost as long as PST. Posterior face: VR absent, PFC rather weak and somewhat irregular, but covering most of face. Lateral extension of S.2 groove well developed. Hind tibia: teeth small and more or less distant, the subtending spines 2-3 times as high. Inner spur reaching to 0.1-0.2 basitarsus length (equal to or slightly shorter than tarsal segment 4) and 0.9-1.0 times as long as outer spur. Mid and hind tarsi (fig. 207) with claw-tooth further from claw base than in anterior tarsus (anterior just over 1/2-2/3, mid & posterior 2/3-3/4).

Variation.— Only as noted above.

Biology.— At least females of this species belong to the *P. plutus* mimicry-group.

Distinctions.— Very similar to *P. onorei* but distinguished primarily by the subapical position of the claw-tooth (just beyond the mid-point of the claw in *P. onorei*); also by the very low, broad PTC (usually narrow and high in *P. onorei*); more orange, less infusate wings; and shorter SMC3. The pale "bloom" of the wings in *P. ecuadorae* can be sufficiently distinct to be helpful. The two are also allopatric, albeit closely.

Distribution.— Known only from coastal Ecuador, at low altitudes; in view of the near-total clearance of the coastal forest in Ecuador and lack of recent collecting records, this species may be extinct (map fig. 243).

Material.— 6 ♀♀; AMNH, BMNH, TMB, USNM, ZSM.

Pepsis onorei spec. nov.
(figs 156-158, 212, 213, 244)

[*Pepsis aurocincta* Mocsáry; Haupt, 1952: 401. Misidentification.]

Type material.— Holotype ♂, **Ecuador**: Los Llanos (TMB). Paratypes. Ecuador: 1♂, data as holotype (BMNH); 1♂, 3♀♀, data as holotype (TMB); 1♀, Los Llanos 295.85 (NRS); 1♂, (Ecuador only), 1♀, Los Llanos. Both with det. label "*Chrysopepsis aurocincta* Mocs. det. Haupt, 1950" (MLU); 1♀, ECUADOR occ., Balzapamba, 294.85 (NRS); 1♀, (Ecuador only), "*Pepsis sumptuosa* Sm.", 297.85 (NRS); 1♀, Guayaquil, (Goding) "*Pepsis sumptuosa* Sm. det. Sandhouse" (USNM); 1♀, Cotopaxi, Las Pampas

1,500m, Verano [Spring], [19]82 (Arregui) (MACN); 1 ♀, same data but v.1982 (Onore) (PAGLIANO); 11 ♀ ♀, same data but vi.1983 (Onore) (PUCEQ); 4 ♀ ♀, same data (BMNH); 1 ♀, same data (CMNH); 3 ♀ ♀, same data but x.1983 (Onore) (PUCEQ); 5 ♀ ♀, same data (BMNH); 1 ♀, same data (MCZ); 1 ♀, same data but xi.1983 (Onore) (MACN); 1 ♀, same data but with additional label: "*Pepsis sumptuosa* Smith, 1855. Det. A. Roig Alsina, 1984." (PUCEQ); 2 ♀ ♀, same data but x.1985 (PUCEQ). **Colombia:** 1 ♂, Bet[ween] Queremal and Buenaventura alt. 3,500-4,000 ft 1.vii.1935 (Aranibar), "Slide"[red], "*Pepsis speciosissima* Lucas, det. B[an]ks. (AMNH); 1 ♂, same data but 17.ii.1935, "Slide" [yellow], (Huntington) "*Pepsis speciosissima* Lucas, [det.] B[an]ks" (MCZ); 1 ♀, Colombia, S. Am.; Ac. 3977 [on back of label]; "*Pepsis sumptuosa* F. Sm., Det. P.P. Babiý, 1929" (CUNY). "**Brazil**": 1 ♂, Rio Pioneras 2.xii.1925" "*Pepsis auricoma* R. Luc[as]; P.P. Babiý, 1934"; added later to same label: "? - see description."; "*Pepsis aurocincta* Mocs. [det.] B[an]ks" (CUNY)

Note.— Most of the specimens with locality "Cotopaxi, Las Pampas, 1,500 m" were originally mislabelled Pichincha, Santo Domingo de Los Colorados, 400 m (*teste* Onore); this is important because of the possibility of further mislabelled specimens being discovered in future, and because the error made the species apparently sympatric with *P. ecuadorae*, which in fact occurs only at lower altitudes.

Etymology.— This species is named after Dr G. Onore.

Description.— ♂. BL 29-31. Body and legs black; with pale yellowish pubescence covering most of body, forming patterns as follows: an approximately square spot, diffuse anteriorly, on mesoscutum; covering whole of T.1 but forming narrow, apical bands on T.2-6. Antenna dull orange beginning sub-basally on AS3. Wings infuscate-amber, forewing with a pale extreme apex. S.5 with a few rather short, sparse hairs laterally, S.6 with the hairs similar but forming a dense, transverse band. SGP (figs. 156, 158) very broad, basally constricted, then weakly expanded apicad; at just over half SGP length, the sides converge to form the bilobed apex; at the base on each side begins a rather broad, polished, hairless strip which narrows and becomes thicker apicad, finishing in a point just before the sides begin to converge to the apex; the area between these lateral strips, beginning from a basal, transverse carina (half-hidden under the preceding sternite) is entirely pilose, but poorly delimited; the hairs are everywhere dense, very fine basally, becoming much longer apicad, the apicals about as long as 1/3 maximum SGP width. Paramere about 1.5 times as long as rest of genitalia, the apex roundly pointed and with hairs about as long as maximum paramere width; about the middle of its inner side is a shallow, arcuate emargination whose base is delimited by a weak angle, from which proceeds a short, transverse carina. Inner projection of digitus apex (fig. 157) strongly broadened, then abruptly tapered to a terminal hook directed proximad.

♀. BL 34-49. AE index 115-133. Otherwise as male, except body pubescence pale yellowish-grey, pale forewing apex often obscure and antenna orange from mid-AS3. Head (fig. 212) with temple and vertex slightly swollen. MT weak to moderate. Forewing with PPV very short and nearly transverse. MPN distinctly shorter than PST, its furrow rather broad; carinae few, strong, but often obscured by pilosity. Propodeum: MG replaced by broad, strong ridge. APT and PPT weak to moderate, PTC moderate to strong, DTC fine to coarse, often strongly curved. Propodeal hair about as long as PST. Posterior face: VR absent, PFC variable, often quite strong, weaker below, covering whole of face but often totally obscured by pilosity. Lateral extension of S.2 groove varying from strong to weak, occasionally vestigial. Hind tibia: teeth often rather small and distant, the subtending spines 2.0-2.5 times as high. Inner spur reaching to 0.1-0.15 basitarsus length (about equal to tarsal segment 4 or slightly

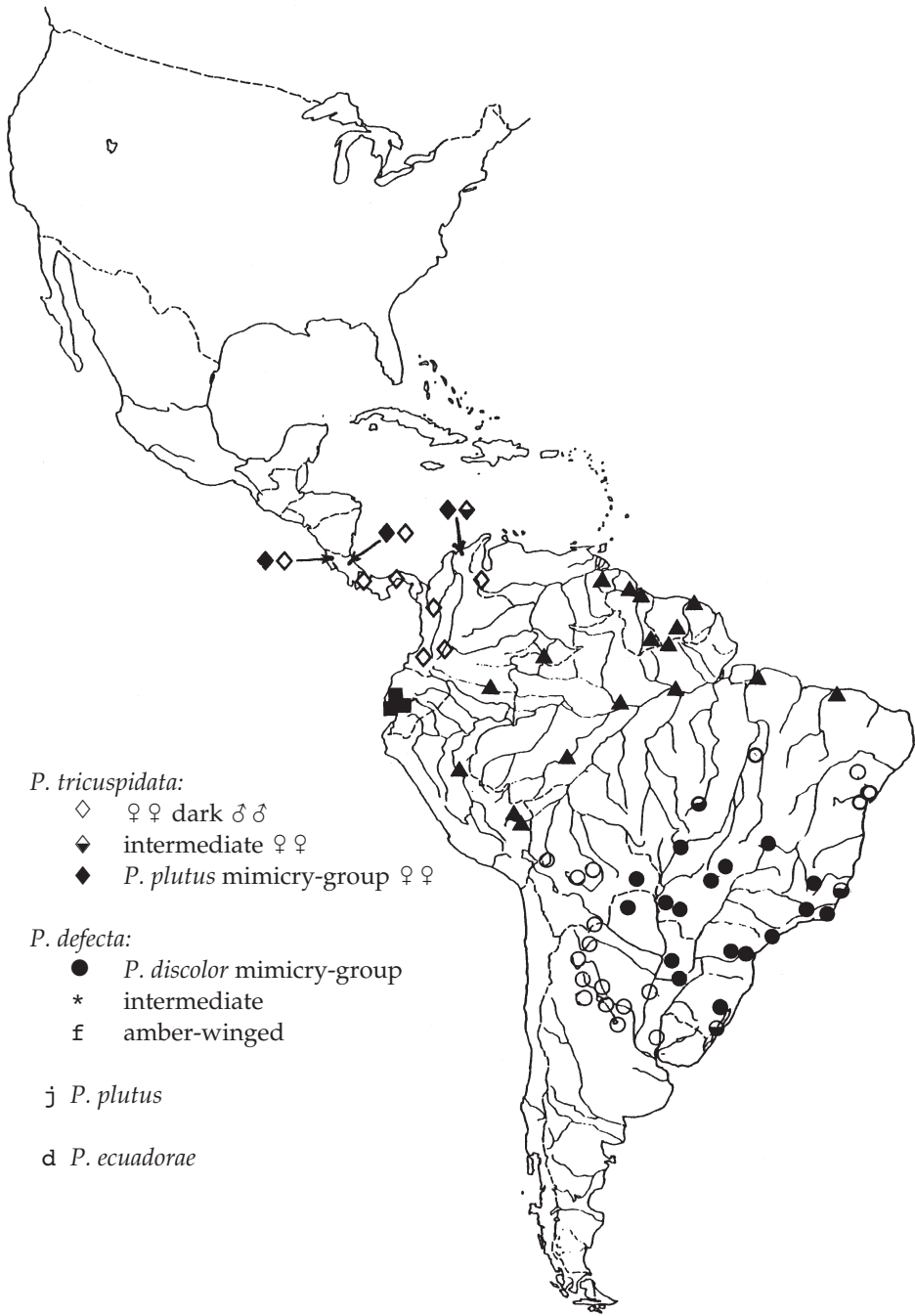


Fig. 243. Collection localities of *Pepsis tricuspidata* Gribodo, *P. defecta* Taschenberg, *P. plutus* Erichson and *P. ecuadorae* spec. nov.

shorter) and 0.9-1.0 times as long as outer spur. All tarsi with claw-tooth distant from claw base as follows: anterior and mid just over 1/2-way, posterior (fig. 213) 1/2-2/3.

Variation.— The males from Colombia have much denser propodeal pilosity and much darker wings than do the other males; on the other hand the pilosity, especially of the propodeum, is much denser in the Ecuadorean females from Las Pampas than in any others.

Biology.— This species belongs to the *P. plutus* mimicry-group.

Distinctions.— The male is distinguished from others of its group by the SGP structure, and by the combination of pubescence colour and patterns; the female pubescence colour and pattern is similar only to that of *P. ecuadorae*.

Distribution.— Found only in the western watershed of the Andes of Colombia and Ecuador, between about 1,000-1,500 m. The Brazilian record is almost certainly due to a labelling error (map fig. 244).

Material.— 7 ♂♂, 40 ♀♀; AMNH, BMNH, CUNY, MACN, MCZ, NRS, PAGLIANO, PUCEQ, TMB, USNM.

Pepsis pulszkyi Mocsáry, 1885
(figs 159-161, 226, 244)

Pepsis pulszkyi Mocsáry, 1885: 261, no. 37. Lectotype ♀ (TMB), here designated [examined].

Pepsis aurocincta Mocsáry, 1894: 1, no. 1. Lectotype ♂ (TMB), here designated [examined]. **Syn. nov.**

Type-material.— *P. pulszkyi*: I have seen 2 ♀ syntypes, from Tefé and Fonteboa; I have labelled as lectotype the smaller specimen (Fonteboa), which is in better condition. The paralectotype is a specimen of *P. apicata* Tasch. A further ♀ in the André collection (MHNNEU) is labelled as "type" but has no such status; it is a specimen of *P. frivaldszkyi* Mocsáry. *P. aurocincta*: I have seen a single type-material ♂ and labelled it lectotype.

Description.— ♂. BL 30-37. Body and legs black, mostly covered with short, golden hair, forming twin median stripes on mesoscutum and apical bands on T.2-6. T.7 has entirely dark hairs. Antenna dull orange to infuscate-orange, paler beneath. Wings dull infuscate-amber. S.4 effectively without modified hair; S.5 with some short, sparse hair, denser laterally, and an apical band of very short and very dense hair; S.6 covered with hairs a little longer than the longer ones of S.5 and very dense. SGP (figs 159, 161) sides expanded slightly from the base, then parallel to about half-way, then narrowed again to the pair of rounded lobes forming the apex; a transverse basal ridge is sharp centrally but almost hidden under the preceding sternite; from the base, on either side extends apicad a polished lateral strip, broad at the base, gradually narrowing, terminating where the sides begin to narrow to form the apex; the remaining surface is covered with rather long and very dense hair, the lateral ones incurved. Paramere rather narrow, about twice as long as rest of genitalia, rounded-ended with apical hairs about 1.5 times maximum paramere width. The middle of the inner side has a semicircular emargination with a tiny but sharp tooth at its base. Inner projection of digitus apex (fig. 160) strongly broadened and flattened, ending in a square truncation with a tiny tooth directed proximad.

♀. BL 40-55. AE index 143-162. Colour as in male, except body and legs black with dark pubescence, often with weak yellowish to violet reflections on thorax and

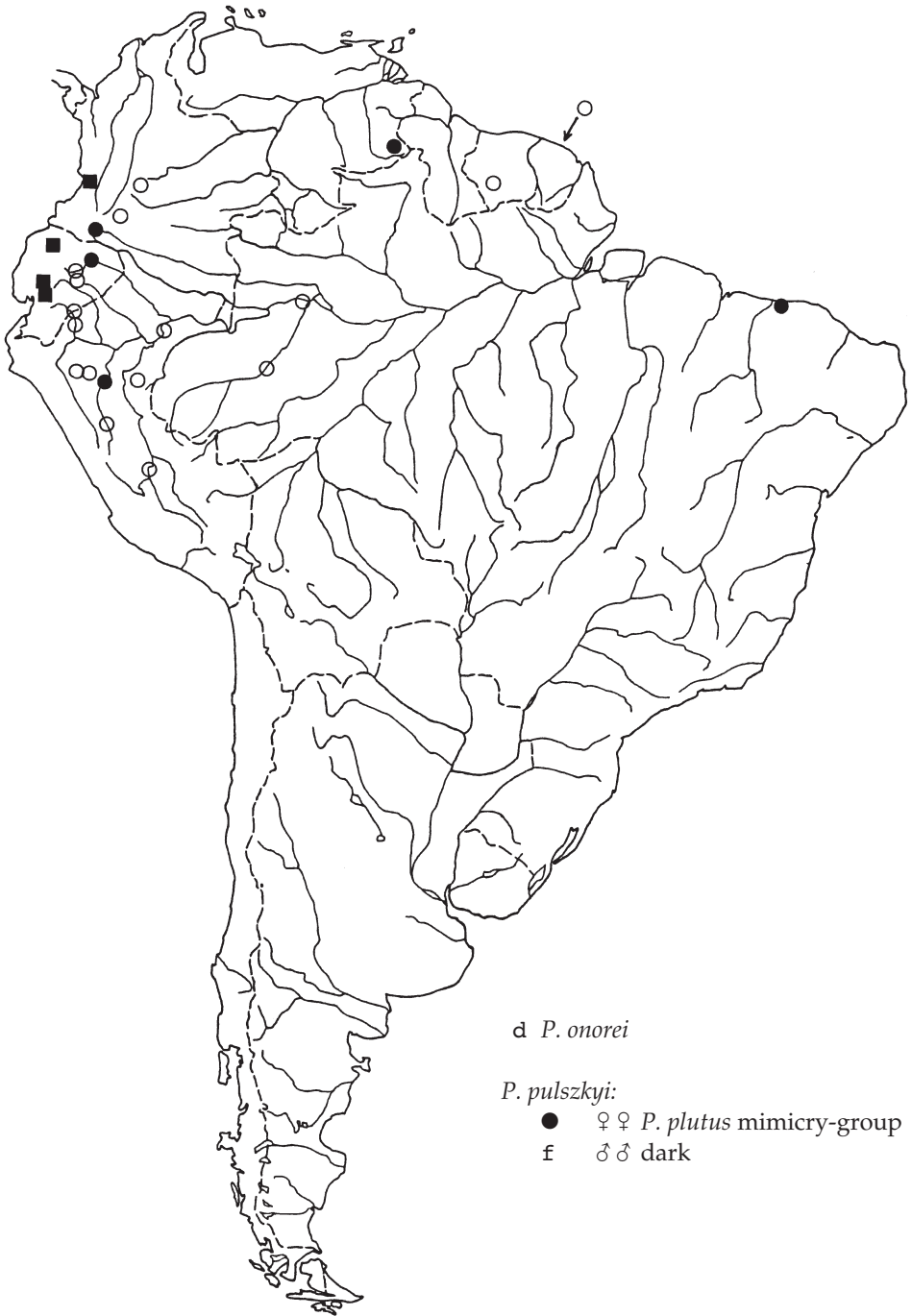


Fig. 244. Collection localities of *Pepsis onorei* spec. nov. and *P. pulszkyi* Mocsáry.

propodeum. Antenna: AS3-5 always with orange apical rings and AS6 onwards entirely orange; usually AS4 has irregular patches, often AS4 and 5 darker in specimens from the Guianas; a specimen labelled only "Colombia" (FRITZ) has continuous orange beginning diffusely just beyond the middle of AS3, thus resembling *P. toppini* in colour (but not in structure). Head (fig. 226) in dorsal view very strongly transverse, with temple and vertex scarcely swollen. The wings, especially the forewing, usually appear a little narrower and longer than in other species of the *P. sumptuosa*-group. MPN slightly shorter than PST, its furrow broad, often obsolescent anteriorly, expanded posterad, with a highly-polished transverse area posteriorly; with usually two strong, arcuate carinae. Propodeum: MG replaced by a very broad, rounded ridge. APT and PPT moderate to strong, PTC weak to moderate, sometimes double. DTC moderately coarse but irregular, often strongly V-shaped, pointing posterad; often more distant or absent in apical 1/3 before PTC. Propodeal hair equal to or slightly longer than PST. Posterior face: VR broad but weak to absent near PTC, absent below; PFC very weak near PTC, rapidly obsolescent apicad especially in centre-line. Lateral extension of S.2 groove well-developed. Hind tibia: teeth usually small and rather distant, the subtending spines 2.5-3.0 times as high. Inner spur reaching to 0.10-0.15 basitarsus length (slightly shorter than tarsal segment 4) and 0.9-1.1 times as long as outer spur. All tarsi with claw-tooth about 2/3 from claw base (anterior 1/2-just over 1/2; mid and posterior just over 1/2-2/3).

Variation.— A male from Venezuela: Bolivar (MIZAM) has the antenna black dorsally except for the apical segment, while the underside is bright orange.

Biology.— Martin Cooper, who has personally collected both sexes of this species, told me that it inhabits mainly the canopy of primary forest. Males belong to the *P. plutus* mimicry-group.

Distinctions.— The male SGP resembles that of *P. sumptuosa* but is broader and much less abruptly narrowed apically; the apical part of the digitus is much broader; and *P. sumptuosa* has no golden pubescence on the gaster after T.2. The female is distinguished from most others of its group except *P. yucatanii* (which see) by its strongly transverse head and extremely long AS3; further from the similar *P. tricuspidata* by its MPN sculpture, antennal colour, very large size and allopatric distributional range. In most females, the forewing is narrower than in other, similar species but this is easier to see than to measure.

Distribution.— Inhabits eastern Venezuela, the Guianas and western Amazon basin from Colombia to Perú. A single record from Piauí, eastern Brazil (the lectotype of *P. aurocincta*) needs confirmation; at low altitudes, reaching 650 m in eastern Ecuador (map fig. 244).

Material.— 5 ♂♂, 22 ♀♀; AMNH, BMNH, FRITZ, HENSEN, IMLT, INPA, MCZ, MIZAM, PUCEQ, RMNH, SEMKU, TMB, UNALM, UNPBOG, USNM.

Pepsis sumptuosa Smith, 1855
(figs 153-155, 211, 245)

Pepsis sumptuosa Smith, 1855: 197, no. 33. Lectotype ♀ (UMOX), here designated [examined].

Pepsis colossica Stål, 1857: 64. Lectotype ♀ (NRS), here designated [examined]. **Syn. nov.**

[*Pepsis eximia* Smith; Fox, 1897: 281. Misidentification].

Brethesia apollinariii Brèthes, 1926: 9. Lectotype ♂ (MACN), here designated [examined]. **Syn. nov.**

[*Pepsis speciosa* Smith; Haupt, 1952: 402. Misidentification].

Type-material.— *P. sumptuosa*: I have seen a single type-material ♀ and labelled it lectotype. A ♀ standing under this name in BMNH is conspecific but has no type status. *P. colossica*: I have seen a single syntype ♀ and labelled it lectotype. *P. apollinarii*: I have seen two syntypes, one of each sex, and labelled the ♂ as lectotype. The ♀ is a conspecific paralectotype.

Description.— ♂. BL 30-32. Body and legs black with extensive short, bright golden pubescence on most of body including T.1 and S.1, forming patterns as follows: a large, approximately square patch on mesocutum, T.2 with a very weak, narrow apical band, but remaining tergites black. Antenna orange from base of AS3, but often becoming gradually infusate apicad. Wings strongly infusate. S.5 mostly covered with short, dense hairs; among them are a few much longer and thicker but sparse hairs, slightly curved backwards apically; S.6 with similar hairs to the long ones on S.5, but slightly longer, very dense and virtually straight. SGP (figs 153, 155) weakly constricted basally, then with parallel sides which are increasingly raised apicad, ending in an angle which begins the rather abrupt taper to the deeply emarginate apex. Basally is a fairly strong, transverse but short ridge; from each side of this extends a polished lateral area, becoming narrower apicad and ending at the pre-apical angles. The remainder of the surface is covered with long hairs, longer and more curved apicad, but the junction of the two areas is poorly-defined basally. Paramere about 1.5 times as long as the rest of the genitalia, its inner edge with a semicircular emargination, whose proximal end is marked by a tiny, sharp tooth; apex narrowly rounded, with hairs a little longer than maximum paramere width. Apex of digitus (fig. 154) turned perpendicularly inwards, slightly broadened, ending in a tiny tooth directed proximad.

♀. BL 34-56. AE index 107-121. Colour as in male, except dorsum of gaster without golden hair, or sometimes weakly present across the apex of T.1; antenna orange from mid-AS3 onwards. Head (fig. 211) with vertex and temples slightly swollen. MT weak to moderate. Forewing with SMC3 long, especially posteriorly. MPN a little to markedly longer than PST, its furrow broad; with one to several very strong carinae; between them are extremely fine ones, giving a matt surface. Propodeum: MG broad and low throughout. APT and PPT moderate to strong; PTC very variable: broad and low to narrow and high, in the latter case sometimes double, i.e. formed of two transverse carinae very close together. DTC rather coarse, often slightly U-shaped. Propodeal hair about as long as PST + 1/2 MPN. Posterior face: VR absent; PFC strong or weak (in proportion to size of insect), rather distant when strong, obsolescent medially and weaker apicad. Lateral extension of S.2 groove well-developed. Hind tibia: teeth sometimes rather small, the subtending spines 2.0-3.0 times as high. Inner spur reaching to 0.15-0.20 basitarsis length (about equal to tarsal segment 4 or slightly longer) and 0.8-1.1 times as long as outer spur. All tarsi with claw-tooth more or less just beyond mid-point of claw (anterior 1/2; mid 1/2-just over 1/2; posterior just over 1/2-2/3).

Variation.— Only as described above.

Biology.— This species belongs to the *P. plutus* mimicry-group.

Distinctions.— The male is readily distinguishable by its SGP structure and unique gastral pubescence pattern; the female pubescence colour and pattern is diagnostic; however, small females resemble abraded specimens of *P. plutus*, which see for differences.

Distribution.— Known only from the Colombian Andes, from 1,200 to at least 2,000 m; there is a single, doubtful record from the coast north-east of the Sierra Nevada de Santa Marta (map fig. 245).

Material.— 7 ♂♂, 41 ♀♀; AMNH, BMNH, CUNY, ETHZ, FRITZ, FSAG, LACM, MACN, MCZ, MHNGV, MIZAM, MNHNPS, MNS, MLU, MZUSP, NRS, OSUC, SMF, UMOX, UNPBOG, ZSM.

Pepsis optima Smith, 1879
(figs 165-170, 215, 245)

Pepsis optimus Smith, 1879: 157. Lectotype ♀ (BMNH), here designated [examined].

Pepsis andrei Mocsáry, 1885: 267, no. 47. Lectotype ♀ (TMB), here designated [examined]. **Syn. nov.**

Type-material.— *P. optimus*: I have seen two ♀ and five ♂ syntypes. I have labelled the larger ♀ ("Rio Susio") as lectotype; the smaller one ("Irazu") is a conspecific paralectotype. Although the five ♂♂ are also paralectotypes, they are specimens of *Hemipepsis*, probably *H. rogersii* Cameron (*teste* M.C. Day). *P. andrei*: I have seen two ♀ syntypes: one in TMB, one in MHNNEU; and labelled the first as lectotype. The specimen in MHNNEU is a conspecific paralectotype.

Description.— ♂. BL 26-31. Body and legs black, body pubescence with weak violaceous sheen. Antenna with at least AS1-2 black, and any number from none to all of the remainder orange, the colour advancing from the antennal apex. Wings dark infusate-orange, more heavily infusate basally and with a more-or-less broad, irregular, infusate apical border, often invading the outer cells. S.5 (fig. 170) with a fairly dense, transverse, pre-apical band of rather long hairs, slightly curved apically (see Variation); along the apical margin is a narrow band of short, dense hairs. S.6 with similar long hairs over the whole sternite, but denser, longer and decumbent but with recurved apices. SGP (figs 165-168) with the sides almost parallel from sub-basally to just over half the SGP length and increasingly thick and raised up to that point; the base is abruptly constricted, the apex more gradually, the latter with two rounded to pointed lobes (see Variation). Just beyond the basal, transverse tubercle begins a long-pilose area which broadens apicad, meeting the sides at the point where the SGP begins to converge to the apex; apical hairs a little longer than the rest, equal to about 3/4 maximum SGP width; the remaining surface is highly polished. Paramere about 1.5 times as long as rest of genitalia, apex with hairs a little longer than maximum paramere width. Inner margin with strong emargination at mid-point, its proximal end marked by a sharp tooth (see Variation). Inner projection of digitus apex (fig. 169) slightly broadened, evenly tapered, ending in a rounded tip with a tiny tooth directed proximad.

♀. BL 37-52. AE index 112-128. Colour as in male, except antennal orange colour beginning diffusely about a quarter from base of AS3; wings usually less infusate. Head (fig. 215) in dorsal view with vertex and temple more or less swollen. SMC3 long. MPN a little to markedly longer than PST, its furrow broad, often strongly expanded posterad; carinae, usually several strong. Propodeum: MG sometimes weakly indicated. APT, PPT and PTC all moderate to strong, the last narrow. DTC very variable, weak to moderate, usually present at least posteriorly; sometimes arcuate. Propodeal hair about as long as PST + 1/2 MPN. Posterior face: VR absent; PFC

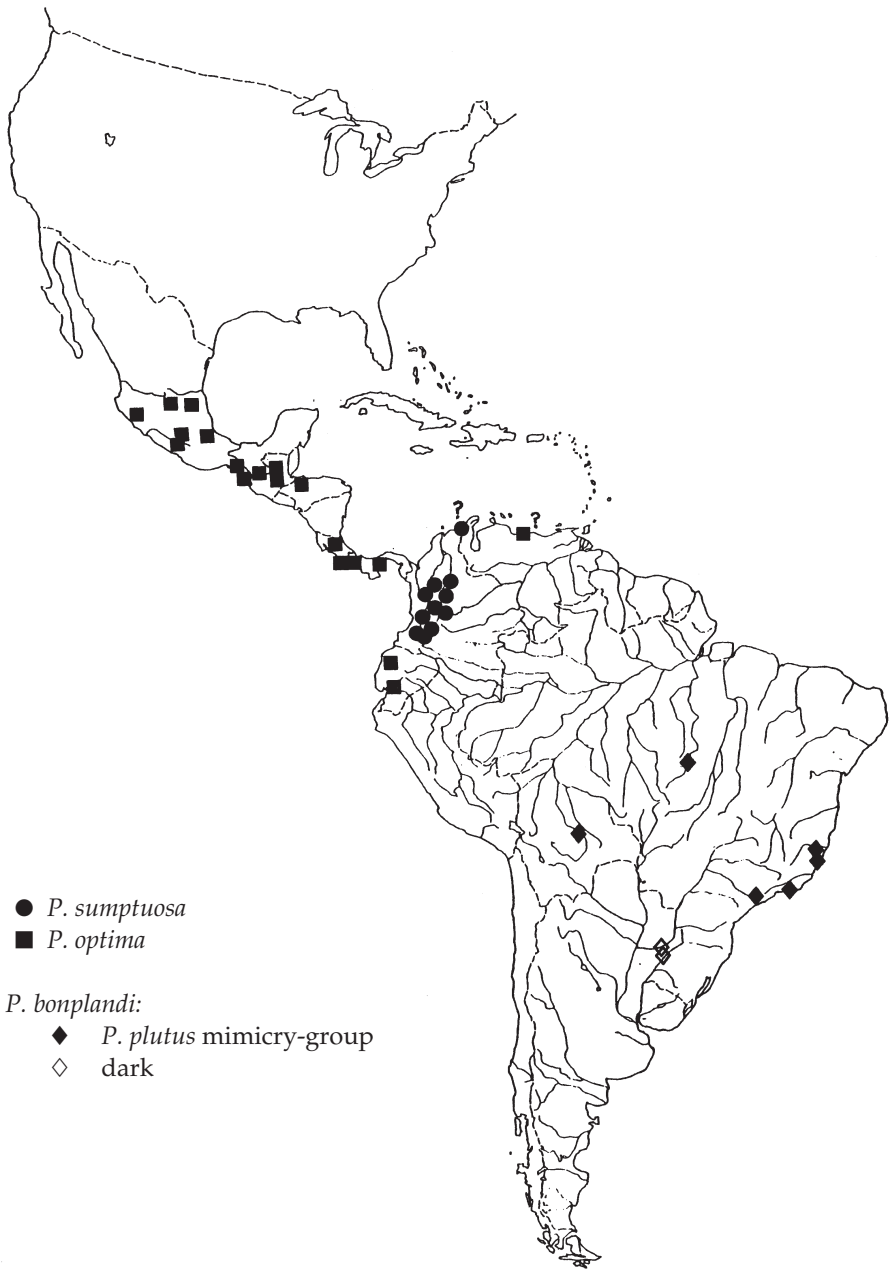


Fig. 245. Collection localities of *Pepsis sumptuosa* Smith, *P. optima* Smith and *P. bonplandi* Brèthes.

usually moderately strong and covering the whole face but sometimes absent except laterally above. Lateral extension of S.2 groove well-developed. Hind tibia: teeth sometimes rather weak, the subtending spines 2.0-3.0 times as high. Inner spur reaching to about 0.15-0.2 basitarsus length (about equal to tarsal segment 4) and 0.9-1.1 times as long as outer spur. All tarsi with claw tooth just beyond mid-point of claw (anterior 1/2-2/3 from base; mid just over 1/2; posterior just over 1/2-2/3).

Variation.— A female from Mexico: Chiapas (USNM) has the wings entirely heavily infusate; the antenna, however, is normally coloured.

The male SGP structure (figs 165-167) varies in a north-south cline: the apical lobes gradually become longer from Mexico to Panamá. Their breadth and the depth of the emargination between them also varies, as does the length and degree of convergence of the raised sides; but these characters do not form such a clear gradient as the first-mentioned one. The tooth forming the proximal limit of the inner notch of the paramere becomes smaller but sharper southwards. Furthermore, the longer hairs of S.5 are sparser centrally in specimens from further south.

Distinctions.— The male SGP is similar to that of *P. sumptuosa*, but its body entirely lacks the bright golden pubescence of that species; it is also similar to that of *P. toppini*, but the apical lobes are longer in the latter. The female is very similar to that of *P. toppini*; however, the two are allopatric, and usually also differ as follows (characters of *P. toppini* are in parentheses): orange colour of antenna begins 1/4 from base of AS3 (about the middle of AS3); hind tarsus with tooth 3/4 from base of claw (just over half); teeth of hind tibia rather broad (small and distant).

Distribution.— Ranges southwards from Mexico to Panamá, also recorded from west coastal Ecuador and north coastal Venezuela; ascends to 2,194 m in Mexico: Chiapas (map fig. 245).

Material.— 45 ♂♂, 76 ♀♀; AMNH, ANSP, BMNH, BRIO, CAS, CUNY, EMMSU, FDA, INBIO, LACM, MCZ, MHNNEU, MICR, MLU, MHNGV, MNHNPS, NMV, OSUC, PORTER, PUCEQ, RMNH, SEMKU, TMB, USU, WAHIS, WASBAUER, UCALD, UPAN, USNM, UZMC, ZMMICH.

Pepsis toppini Turner, 1915
(figs 162-164, 233, 246)

Pepsis toppini Turner, 1915: 413. Lectotype ♀ (BMNH), here designated [examined].

Brethesia selvatica Brèthes, 1920: 49. Lectotype ♀ (MACN), here designated [examined]. **Syn. nov.**

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

Description.— ♂. BL 27. Entire insect black except for weak brownish-violet sheen of body pubescence and faint orange apices of the antennal segments beneath. S.5 with some rather short, straight hairs, especially laterally; S.6 with similar but much denser hairs. SGP (figs 162, 164) very short; constricted basally, then almost parallel-sided with thickened margins, the latter forming "shoulders" immediately before the SGP is abruptly narrowed to the broadly bilobed apex; the transverse basal ridge is half-hidden under the preceding sternite; the base and sides are polished; the central area has some short, rather sparse hair and expands apicad, occupying the whole

width of the SGP beyond the shoulders. Hairs increasing in length apicad, those on the apical lobes almost as long as 1/2 maximum SGP width. Paramere about 1.5 times as long as rest of genitalia, with apical hairs slightly longer than maximum paramere width; middle of inner margin with a rather large semicircular emargination which is delimited basally by a small but sharp tooth. Inner projection of digitus apex (fig. 163) moderately broadened, the end rounded and with a small tooth directed proximad.

♀. BL 42-57. AE index 119-136. Colour as in male, except antennal orange which begins diffusely about the middle of AS3. Wings pale amber to deep orange, usually with a dark apical border of variable width. Head (fig. 233) in dorsal view with temples and vertex more or less strongly swollen. MT weak to moderate. MPN slightly to markedly shorter than PST, its furrow broad, often further expanded apicad; carinae very variable, from moderate to coarse and fine mixed. Propodeum: MG replaced by a strong ridge, but sometimes flattened in posterior 1/3 (before PTC). APT and PPT moderate to strong, the latter usually small and more-or-less pointed, but variable; PTC weak to moderate, narrow and strongly rounded (but see Variation). DTC sometimes coarser and less regular, sometimes U-shaped. Propodeal hair varying from slightly shorter than PST to slightly longer. Posterior face: VR absent, PFC variable but usually rather weak and more or less obsolescent in median line above. Lateral extension of S.2 groove well developed. Hind tibia: teeth usually small and rather distant, the subtending spines about twice as high. Inner spur reaching to 0.15-0.2 basitarsus length (about equal to tarsal segment 4) and 0.9-1.2 times as long as outer spur. All tarsi with claw-tooth more-or-less just beyond half-way from claw base (anterior half to just over half; mid and posterior just over half).

Variation.— The female lectotype of *P. toppini* is exceptional in having the PTC low and flat-topped, with the depression in front of it stronger than in any other specimen seen; it appears to be a slight deformity.

Distinctions.— The male is well distinguished by the shape of its SGP. However, the female is one of the least well-characterized of the group. The rather limited distributional range is helpful in identification. The small size and usually strongly-rounded shape of the PTC, and position of the hind tarsal claw-tooth (placed just beyond the mid-point of the claw) are helpful, but it needs experience to assess the degree of claw abrasion (and hence the tooth position) and the PTC is occasionally aberrant. The antennal colour is almost always constant. See also *P. optima* and *P. tricuspidata*.

Distribution.— Known only from the eastern watershed of the Ecuadorean and Peruvian Andes, from 800-1,600 m (map fig. 246).

Material.— 1 ♂, 20 ♀♀; BMNH, CUNY, IMLT, MACN, MCZ, MIZAM, MNHNPS, NHMLIM, PUCEQ, UNALM, UNLAMB, USNM (including the male), WAHIS.

Pepsis yucatani spec. nov.
(figs 147-149, 225, 246)

Type-material.— Holotype ♂, **Mexico**: Chiapas, 34k e Tuxtla Gutierrez, El Mirador for Chicoasen Dam, 823m, 15.xi.1976 (Breedlove) (CAS). Paratypes. Mexico: Chiapas: El Sumidero, 1♂, 14.ix.1974 (Hanson & Bohart) (USU); Municipio Chiapa de Corzo, El Chorreadero, 670m, 1♀, 16.viii.1976 (Breedlove) (CAS); Tuxtla Gutierrez, 308m, 2♂♂, 24.iv.1959 & 3.v.1959 (Evans) (BMNH, CUNY); near Tuxtla Gutierrez, 1♀, 29.iii-5.iv.[19]59 (Emmel) (LACM); Yucatan: Chichen Itza Hacienda, 1♀, 9.vi.1932 (Creaser) (ZMMICH); Piste, 1♀, 23.vi.1967, 1♂, 1♀, 14.vii.1967, 1♀, viii.1967 (Welling)

(BMNH, LACM); Xcan, Quintana Roo, 2♂♂, 1♀, v.1963, 7♀♀, vii.1963, 1♀, viii.1963, 1♀, x.1963, 1♀, xi.1963, 1♀, iv.1964 (Welling) (BMNH, OSUC); Nuevo Xcan, Quintana Roo, 1♂, 18.vii.1983, 1♂, 7.x.1983, 1♀, 3.vi.1984, 1♀, 16.vi.1984, 1♀, 18.ix.1985, 1♀, 22.x.1985 [all 6: either (Welling) or no collector given] (BMNH, WILLIAMS); [NFL] 1♂ (Gaumer) (SEMKU); [No data] 1♀ (ANSP).

Etymology.— This species is named after the Yucatán peninsula.

Description.— ♂. BL 32-34. Body and legs black with long, dark, rather dense hair, with a weak violaceous sheen in parts. Antenna bright orange from base of AS3. Wings rather pale infuscate-orange, forewing with pale extreme apex. S.5 with a few fairly long and dense, mainly lateral, hairs and a very narrow, apical band of very short, dense hairs. S.6 with similar hairs, but the longer ones are denser and the short ones more extensive. SGP (figs 147, 149) near the base bent upwards but thicker centrally, with sides weakly expanded apicad, apex strongly rounded with a V-shaped central notch; a transverse basal ridge is present at the overlapping edge of the preceding sternite; a lateral, polished strip gradually narrows from the base, finishing in a point about 2/3 towards the apex; the area between the strips is entirely pilose; near the base the area is poorly delimited laterally and has very short hairs; they are much longer apicad, the apicals about as long as half maximum SGP width. Paramere about twice as long as rest of genitalia, apex rounded, with hairs a little longer than maximum paramere width; at about the middle of the inner margin is a very shallow, arcuate emargination, whose base is scarcely angulate and lacks a tooth. Inner projection of digitus apex (fig. 148) scarcely broadened, rounded-ended with a minute tooth directed proximad.

♀. BL 33-47. AE index 148-158. Otherwise as male, except: antennal orange colour begins diffusely 1/3 from base of AS3. Wings paler than in male, and partly because of this the pale forewing apex is less apparent. Head (fig. 225) with temple and vertex not or scarcely swollen, but the head is long, so that the overall outline in dorsal view is more or less triangular. MT weak to moderate. MPN distinctly shorter than, to equal to, PST; its furrow broad and with a few, strong, often curved carinae. Propodeum: MG present in larger specimens, replaced by a ridge in smaller ones. APT weak to strong, PPT weak to moderate, PTC moderate to strong. DTC very fine to rather coarse, stronger posterad. Propodeal hair longer than PST in larger specimens, equal in smaller ones. Posterior face: VR absent; PFC fairly strong, sometimes irregular, more-or-less covering whole of face. Lateral extension of S.2 groove well developed. Hind tibia: teeth tiny, the subtending spines 3-4 times as high; on the inner side of the teeth is a row of strong, backwardly-directed bristles. Inner spur reaching to 0.1-0.15 basitarsus length (equal to or shorter than tarsal segment 4) and 0.9-1.1 times as long as outer spur. All tarsi with claw-tooth more or less just over 1/2-way from claw base (anterior and mid 1/2-just over 1/2, posterior 1/2-2/3).

Variation.— Specimens from higher altitudes (in Chiapas state) have the wings orange rather than amber, and the extreme apex of the forewing is often dark.

Sometimes the male has a slightly angulate costa/radius junction.

Distinctions.— The male SGP structure is distinctive, especially in the lack of a well-defined boundary between polished and pilose areas. The female is best characterized by its pale wings, strongly transverse head, tiny hind tibial teeth and distribution (but see *P. pulszkyi*).

Distribution.— Known only from the southern Mexican state of Yucatán, with a few records from adjacent Chiapas, where it ascends to 823 m (map fig. 246).

Material.— 10 ♂♂, 23 ♀♀; ANSP, BMNH, CAS, CUNY, LACM, OSUC, SEMKU, USU, WILLIAMS, ZMMICH.

Pepsis bonplandi Brèthes, 1914
(figs 121-123, 218, 219, 245)

Pepsis bonplandi Brèthes, 1914: 282. Holotype ♂ (MACN) [examined].
Pepsis eubule Banks, 1946: 321. Holotype ♂ (MCZ) [examined]. **Syn. nov.**

Description.— ♂. BL 19-28. Body and legs black; antenna usually black, but any number of antennal segments dull orange except AS1-2; head, and especially thorax and propodeum, with much short, pale yellowish or weakly violaceous hair. Wings dull infusate-orange to heavily infusate, forewing usually with a small white apex. S.4 with a very sparse patch of rather long hairs laterally (sometimes all broken off); S.5 with long, moderately dense, mainly lateral hairs, the apices slightly curved inwards and backwards; S.6 with similar but denser hairs. SGP (figs 121, 123) virtually square; a large but poorly-defined, medio-basal area has a patch of coarse, rather long, weakly recurved hairs; remainder polished. From about the mid-point of its length, the SGP becomes thinner apicad, ending in a straight or slightly arcuate, sharp blade with raised lateral shoulders. Paramere with apical hairs a little longer than its maximum width. Inner projection of digitus apex (fig. 122) slightly broadened, very sharply and evenly pointed, directed inwards, with a small, pre-apical barb on its proximal side.

♀. BL 27-41. AE index (105)-110-118(-126). Colour as in male, except: some antennal segments with narrow, obscure, apical orange rings, apex of last segment orange. Pale hair less evident on head and pronotum. Head (fig. 218) with temple and vertex slightly swollen. Forewing with SMC3 rather long. MT moderate to strong. MPN a little shorter than PST, its furrow narrow anteriorly but strongly expanded apicad; the carinae usually moderate and fine mixed, sometimes one strong sub-basal and the rest fine. Propodeum: MG replaced by a broad ridge, often flat-topped, usually higher about the middle. APT very weak, PPT moderate, PTC strong, apex strongly rounded. DTC moderate to fine, sometimes a little stronger and more distant apicad. Propodeal hair about as long as PST + 1/2 MPN. Posterior face: VR absent or very weak, close together, sometimes slightly divergent apicad. PFC fairly strong, slightly weaker below and in median line but covering most of the face except apico-posteriorly, where the surface is polished. Lateral extension of S.2 groove absent or almost so. Hind tibia: teeth rather small, distant, the subtending spines 2.0-2.5 times as high. Inner spur reaching to 0.15 basitarsus length (about equal to tarsal segment 4) and 1.0-1.1 times as long as outer spur. Claw-tooth of all tarsi (fig. 219) about half-way from claw base.

Variation.— In the males from Argentina: Misiones, the wings are very heavily infusate, whereas in the Brazilian ones they are infusate-orange. The colour of the body pubescence varies concomitantly: it is violaceous in the former, yellowish in the latter.

Biology.— Both sexes of this species belong to the *P. plutus* mimicry-group in the more northern part of their range.

Distinctions.— The male SGP is like no other. The female is similar to small specimens of *P. hyperion* but is readily distinguished by the sculpture of the posterior face

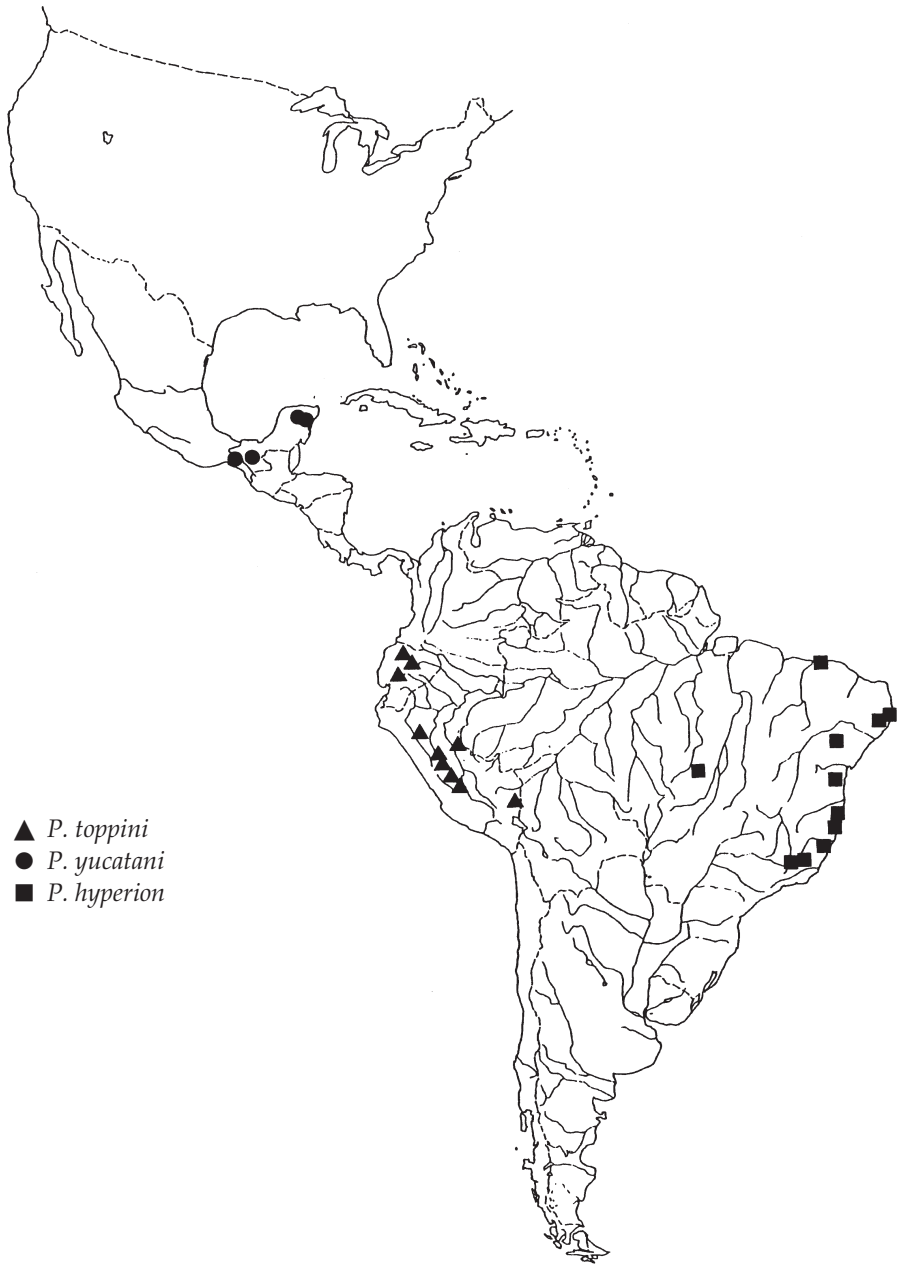


Fig. 246. Collection localities of *Pepsis toppini* Turner, *P. yucatani* spec. nov. and *P. hyperion* Mocsáry.

of the propodeum: the carinae rapidly decrease in strength posterad, and are obsolete above the anal valve, so leaving a rectangular, shining area almost as high as the MPN length; in *P. hyperion* the carinae are finer and denser posterad but remain matt; they are also obsolete medially. *P. bonplandi* is further distinguished by its pale body hair, and by the propodeum which is more strongly tapered posterad and more rounded in profile; seen from in front, the PTC is very similar in shape to the PPT but larger (in *P. hyperion* the two structures are not similar); lastly, female *P. hyperion* usually has the hind tibial teeth much larger, albeit rounded.

Distribution.— Known only from eastern Brazil to north-eastern Argentina, at low altitudes (map fig. 245).

Material.— 16 ♂♂, 30 ♀♀; BMNH, CMNH, FRITZ, IMLT, MACN, MCZ, MHNGV, MLP, MLU, MNHNPS, MNRJ, MZUSP, RSM, SMF, TMB, UCALB, UMOX, USNM, UZMC, ZMMOSC.

Pepsis hyperion Mocsáry, 1894
(figs 124-127, 231, 232, 246)

Pepsis hyperion Mocsáry, 1894: 11, no. 18. Lectotype ♀ (TMB), here designated [examined].

Pepsis gigantea Lucas, 1895: 575, pl. 32, f. 129. Lectotype ♀ (MNHU), here designated [examined]. **Syn. nov.**

Pepsis altitarsus Enderlein, 1901: 147. Holotype ♂ (MNHU) [examined]. **Syn. nov.**

Type-material.— *P. hyperion*: I have seen two ♀ syntypes with identical original labels, and have labelled the larger one as lectotype. The paralectotype is a specimen of *P. inclyta*. *P. gigantea*: I have seen a single type-material ♀ and labelled it lectotype.

Description.— ♂. BL 22-37. Body and legs black with dark blue-green sheen. Antenna black with the extreme apex orange. Wings dark infusate-amber with weakly pale apices; anterior half of radial cell black. S.5 and 6 (fig. 126) with transverse, anterior bands of long, rather dense, more-or-less straight hairs, weaker centrally; S.5 also has fairly dense, shorter hairs behind the others. SGP (figs 124, 125) parallel-sided for basal two-thirds then narrowed to a rounded-truncate apex, which is slightly emarginate centrally; SGP curved upwards where it begins to narrow; with a weak, basal, central tubercle which has a pair of ridges extending from it, forming an obtuse angle and joining the lateral margins, which are narrowly raised to the point where the SGP narrows to form the apex; entire surface polished, with moderately dense, coarse punctures bearing hairs the longest of which are nearly equal to SGP width. Paramere bluntly pointed, apex with hairs about 1.5 times as long as maximum paramere width; inner margin with a small emargination at about the middle, beginning with a distinct angle. Inner projection of digitus apex (fig. 127) evenly tapered, directed inwards-apically, its extreme apex truncate and with a tiny tooth pointing proximad.

♀. BL 38-58. AE index 113-118. Colour as in male, except a few, apical antennal segments sometimes with very narrow, obscure orange, apical rings; up to half the last segment apically dull orange. Sometimes only a broad border of the wings remains heavily infusate, when the remainder is dark orange-brown. Head (fig. 231) with vertex and temple very strongly swollen. MT weak to moderate. Forewing with 1r-m usually abruptly curved inwards anteriorly, often also outwards posteriorly.

MPN slightly to markedly shorter than PST, its furrow narrow, slightly obsolescent anteriorly, usually slightly expanded posteriorly (sometimes strongly in small specimens); the carinae are very fine, occasionally a few stronger, mostly in the anterior half. Propodeum: MG often present only posteriorly, flattened-out anterad. APT and PPT weak to strong, PTC moderate to very strong, usually rather narrow, strongly rounded, occasionally slightly emarginate centrally (rarely double and flat-topped). DTC moderate to coarse, coarser posterad, rather irregular. Propodeal hair about 3/4 PST length. Posterior face: VR usually weak, but variable; PFC most often moderately strong, interrupted medially, and weaker below, but variable. Lateral extension of S.2 groove varying from rather short to totally absent. Hind tibia (fig. 232): teeth usually low, broad and strongly rounded, occasionally sharper; the subtending spines 1.5-2.5 times as high; inner spur reaching to 0.15-0.2 basitarsus length (about equal to or shorter than tarsal segment 4) and 0.9-1.1 times as long as outer spur. All tarsi with claw-tooth just beyond half-way from base of claw.

Variation.— The wing-colour varies from wholly heavily infusate to infusate-amber with only a broad border remaining darker.

Distinctions.— The male is absolutely distinct on its SGP structure. The female is distinguished from those of *P. apicata* and *P. defecta* by its more centrally placed hind tarsal claw-tooth; and from other species by its large, rounded hind tibial teeth, very strongly swollen temples and vertex, usually rounded PTC and entirely black antenna. Also its distributional area is helpful in recognition, but see also the very similar *P. bonplandi*.

Distribution.— Found in central and eastern Brazil, at low altitudes (map fig. 246).

Material.— 18 ♂♂, 44 ♀♀; BMNH, MHNGV, MNHNPS, MNHU, MNRJ, MNS, MZEL, MZLAU, MZUSP, NMV, NRS, RSM, TMB, UFPVIC, UMOX, UZMC, WILLIAMS, ZSM.

The *P. deaurata*-group

Definition.— Both sexes with temple and vertex strongly swollen, female extremely so; the latter sex also with a very strongly, rectangularly emarginate clypeus, ending in a tooth on either side. Males with strongly modified hairs on S.4 & 5.

Description.— Large, robust species (BL males 25-35, females 34-47). Body with either dull, slightly violaceous pubescence, or bright golden which forms patterns; wings moderately infusate or orange-amber; antenna black basally, becoming orange apicad. Since the two species comprising this group are virtually identical in structure (differing only on average in various structural respects; constantly only in colour), the specific description of *P. deaurata* will suffice to represent the group also.

Distribution.— Found in Panamá, Venezuela, the Guianas, and the entire Amazon and its western headwaters south to central Perú.

Cladistics.— Although this species-pair differs strongly from the *P. sumptuosa*-group in the detailed structural characters of both sexes, its general habitus, size and vestiture are virtually identical to those of many species in that group; they are therefore regarded as sister-groups.

The modified sternal hairs in the males of the *P. deaurata*-group do not resemble those of the latter group, nor indeed of any other group with strongly modified SGP. However, they are similar (at least regarding the sternites on which they occur –

regarded as more important than the form they take) to those generally found in the remainder of the genus. This suggests that the *P. sumptuosa*- and *P. deaurata*-groups together are part of the link between those groups whose males possess strongly modified SGPs and those possessing strongly modified sternal hairs instead. This, taken together with the pattern of incidence of the lacuna and other characters in groups with modified SGPs, again suggests that the *P. sumptuosa*- and *P. deaurata*-groups together are not so closely related to the *P. hymenaea*- and *P. chiliensis*-groups (and their sister-groups) as the two latter are to each other.

Biogeography.— This species-pair has a rather unusual distributional pattern compared with other pairs, although the general geographical bias is still discernible. Although one species is indeed transandean, it is indirectly so via the Guianas between Panamá and the Lower Amazon, i.e. a lowland route; the other is found from French Guiana, along the entire Amazon, then southwards beside the eastern Andes to Perú. These patterns are interesting in that they are consistent with the putative lowland habitat during the early evolution of its closest relative, the *P. sumptuosa*-group. Furthermore, both sexes of the mainly Amazonian species (*P. deaurata*) are members of the Amazonian *P. plutus* mimicry-group, most of which is comprised of species of the *P. sumptuosa*-group.

Pepsis deaurata Mocsáry
(figs 47-51; cf. 178, 179; 247)

Pepsis speciosa Smith, 1855: 195. [not Fabricius, 1793]. Lectotype ♂ (BMNH), here designated [examined]. **Syn. nov.**

Pepsis deaurata Mocsáry, 1894: 2, no. 3. Lectotype ♀ (TMB), here designated [examined].

Pepsis auricoma Lucas, 1895: 489, no. 6, ♂, Brazil (lost). **Syn. nov.**

Pepsis speciosissima Schulz, 1906: 167-168. (New name for *P. speciosa* Smith not Fabricius).

[*Pepsis sumptuosa* Smith; Haupt, 1952: 402. Misidentification].

Type-material.— *P. speciosa*: I have seen two ♂ syntypes and have labelled the one in BMNH as lectotype. The one in UMOX is a conspecific paralectotype. *P. deaurata*: I have seen a single type-material ♀ and labelled it lectotype.

Description.— ♂. BL 25-35. Body black with extensive areas of dense, mostly short, conspicuous, golden pubescence; on the gastral tergites usually forming broad, apical bands but occasionally covering whole of dorsal surface. All femora, and anterior and mid tibiae black; in Lower Amazon only, remainder of legs almost always brown with bright reddish pubescence; in specimens from elsewhere, the legs are entirely black. Antenna rather dull orange from base of AS3 onwards (brighter orange in forms which have the hind tibia appearing red). Wings infuscate-amber (more reddish in Lower Amazon specimens), darker pre-apically; apices, especially of forewing, more-or-less distinctly paler. Head (fig. 48) with temples strongly swollen; clypeus strongly arcuately emarginate. S.3 (fig. 47) with hairs denser than on preceding sternites, especially laterally; S.4 laterally with a dense brush of long, golden hair, the apices weakly incurved; also a few similar but straighter hairs across the centre anteriorly; between the lateral brushes is a patch of shorter, inwardly-directed hairs; S.5 has identical long hairs but the central ones are shorter, straight and less dense; S.6 with a few weak, lateral hairs, essentially unmodified. SGP (figs 49, 51) widest in the middle, where it is slightly bent up, i.e.

concave; from that point the sides gradually converge to form the strongly rounded apex; a basal tubercle, slightly transverse, is almost covered by fine but rather long hair; this hair cover splits, leaving a V-shaped clear area centrally, each band of hair tapering apicad to a point laterally where the SGP is widest; surface with dense, fine and also sparser, coarse punctures, much sparser towards the polished centre; apex with a dense fringe of hair about as long as 1/3 maximum SGP width. Paramere about 1.5 times as long as rest of genitalia, with an apical hair-fringe about as long as the SGP maximum width. Inner projection of digitus apex (fig. 50) scarcely developed, strongly rounded.

♀. BL 34-45. AE index 97-99. Colour as in male except orange antennal colour begins at about mid-point of AS3. Legs always entirely black. Golden pubescence much less conspicuous on gaster, usually forming at most very weak apical bands on tergites. Wings less infusate, apex only of forewing pale, more obscure than in male. Head (cf. fig. 178) with temple and vertex extremely strongly swollen (more so than in any other species except *P. frivaldszkyi*); clypeus (cf. fig. 179) with a strong, transverse, pre-apical ridge, with each end continued at a right angle and ending in a large tooth on the clypeal margin, altogether forming a rectangular emargination. Between the teeth the margin is sharply bent in from the ridge, its distal edge arcuately emarginate. MT very weak. Forewing with SMC3 long. MPN equal to PST (occasionally scarcely shorter), its furrow narrow; carinae extremely fine, sometimes slightly stronger centrally. Propodeum: MG replaced by strong, broad ridge, highest and narrowest centrally. APT weak, PPT moderate. DTC moderate to strong, fairly regular but often effaced laterally, especially in smaller specimens. Propodeal hair about as long as PST. PTC weak or absent. Posterior face: not delimited from dorsal face; VR absent; PFC, usually a few weak ones above, the lower face flat but covered by very dense, short hair obscuring the surface. Lateral extension of S.2 groove rather narrow but very long. Fore femur lacking hairs below. Hind tibia: teeth rather small and distant, the subtending spines about 1.5 times as high. On their inner side is a sparse line of backward-curving bristles. Inner spur reaching to only 0.2-0.25 of basitarsus length (about equal to tarsal segment 4) and 1.3-1.5 times as long as outer spur.

Variation.— Only as noted above.

Biology.— This species belongs to the *P. plutus* mimicry-group.

Distinctions.— See under *P. frivaldszkyi*.

Distribution.— Occurs along the entire Amazon mainstream and its western headwaters from southern Colombia to southern Perú; also occurs in French Guiana; the maximum altitude recorded is 600 m in Colombia: Putumayo (map fig. 247).

Material.— 40 ♂♂, 17 ♀♀; AMNH, BMNH, CMNH, LACM, MLU, MNHNPS, MNHU, MNRJ, MNS, MPEG, MZUSP, NMV, PMA, SMF, TMB, UMBREM, UMOX, USNM, WILLIAMS, ZSM.

Pepsis frivaldszkyi Mocsáry, 1885
(figs: cf.47-51, 178, 179; 247)

Pepsis frivaldszkyi Mocsáry, 1885: 259, no. 34. Lectotype ♀ (TMB), here designated [examined].

[*Pepsis heros* Fabricius; Dahlbom, 1845: 465 (not 1843: 122). Misidentification].

Type-material.— *P. frivaldszkyi*: I have seen two conspecific ♀ syntypes. I have labelled as lectotype the smaller one, which bears the locality "Obidos, Brasil". It is in better condition than the larger one, a

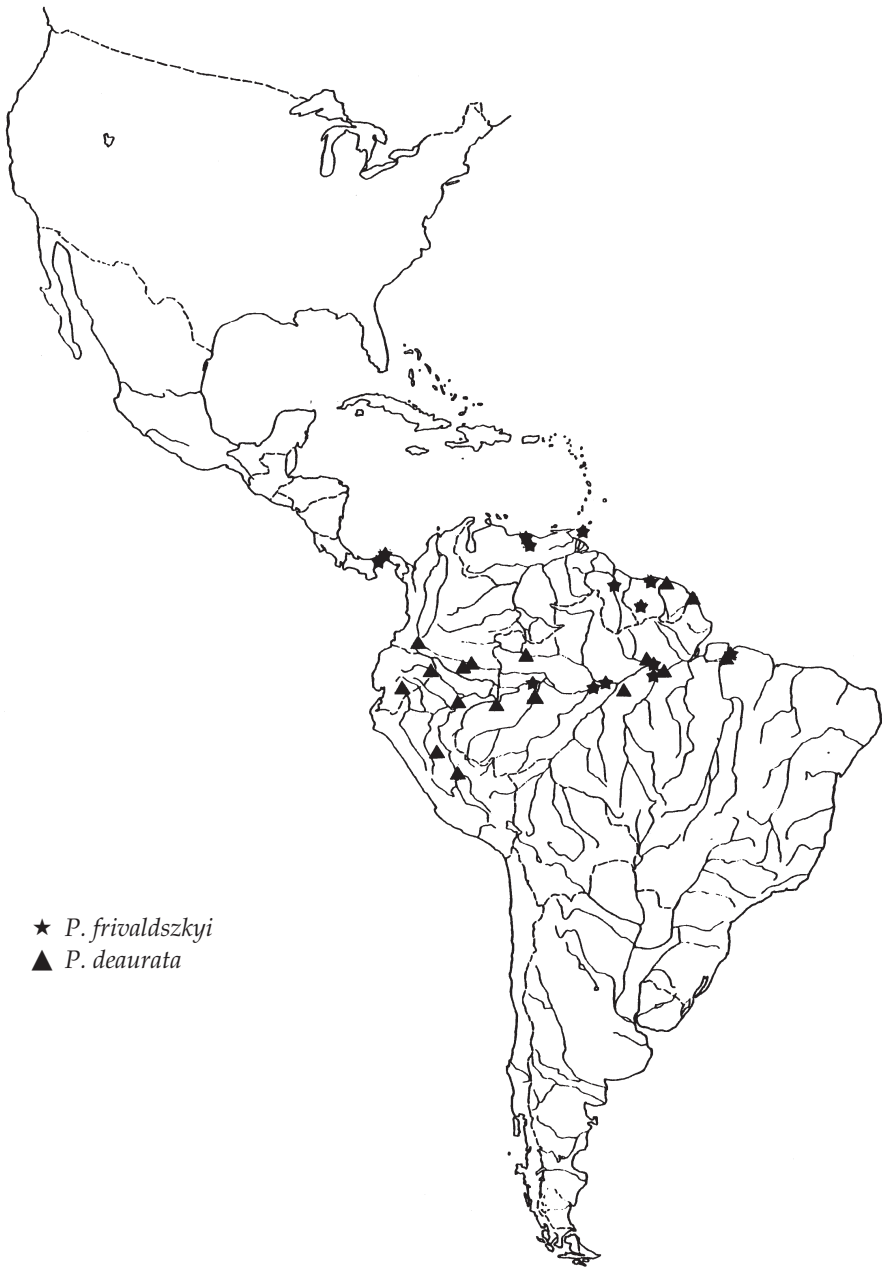


Fig. 247. Collection localities of *Pepsis frivaldszkyi* Mocsáry and *P. deaurata* Mocsáry.

paralectotype, which bears the locality "Massauary" [= Maçauari]. "*P. heros*": two ♀ specimens still exist (MZEL), bearing Dahlbom's [mis]identification labels (see also under *P. marginata*).

Description.— ♂. BL 33-34. Body and legs black with blue-green sheen; body also with sparse, long, black hair and short brownish-violet pubescence. Antenna bright orange from base of segment 3 onwards. Wing colour varying from pale amber or orange-amber to heavily infuscate, apex of forewing often slightly paler, sometimes also with weak pre-apical infuscation in paler wings. Head shape (cf. fig. 48) as in *P. deaurata*; modified hair of sternites (cf. fig. 47) exactly as in *P. deaurata*, but black instead of golden. SGP (cf. figs 49, 51) as in *P. deaurata* except that the widest part is a little closer to the base, the central area is less punctate and more polished, and the basal part has denser, black hairs at the edges. Paramere structure similar, but with dark brown hairs. Inner projection of digitus apex (cf. fig. 50) larger, but still with a very rounded point.

♀. BL 38-47. AE index 95-100. Colour as in male, except antennal orange colour begins at base or one-third from base of AS3. Head (fig. 178) and clypeal shape (fig. 179) as in *P. deaurata*, as are all other structural details.

Variation.— Wing-colour is more variable in this species than in *P. deaurata*; this may be a result of the more diverse habitats occupied by the present species. A male from Venezuela (BMNH) has the legs entirely dark red-brown; the specimen is probably teneral. A female from Brazil, Manacapurú (CMNH) has the pubescence dull copper-golden rather than brown; but still not nearly as bright as the brassy pubescence of *P. deaurata*; since the two species are parapatric along the Lower Amazon, this specimen may be a hybrid between them.

Biology.— A female from "Chagueramas" [= Venezuela: Chaguaramas] (BMNH) was apparently killed by an entomophagous fungus; most of its intersegmental junctions are covered with a dense white substance.

Distinctions.— The unusual clypeal and vertex shapes at once distinguish both sexes from those of all other species except *P. deaurata*. The conspicuous bright golden pubescence of that species is lacking in *P. frivaldszkyi*. See above (Description) for main structural distinctions; although other structural differences exist, they are only on average and therefore difficult to define. This applies especially to the females, which are essentially distinguishable only by colour and often also by distribution.

Distribution.— Found in Panamá, along the entire Caribbean coast and west along the Amazon mainstream only, as far as Fonte Boa (66°W.); in the latter area and French Guiana only, it is sympatric with *P. deaurata*; at low altitudes (map fig. 247).

Material.— 5 ♂♂, 52 ♀♀; BMNH, CMNH, INPA, LACM, MCZ, MHNGV, MHN-NEU, MLU, MNRJ, MPEG, MZEL, NRS, RMNH, RSM, TMB, UMOX, USNM, USU, UZMC, WILLIAMS, ZSM.

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Notes on priority of publication: (i) 1845: Dahlbom, manuscript finished 12th. June, probably published later than Lepeletier; Lepeletier, must have been published shortly before 12th. July (teste Verhoeff, 1948: 183); (ii) 1894: Gribodo, 1st. January; Mocsáry, 30th. June (both printed on the journal-part covers); (iii) 1921: Montet, February; Banks, April (both printed on the journal-part covers); (iv) 1952: Hurd and Haupt (no clash of priorities, as no new species were described in the former).

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Junior synonyms and other invalid names are given in italics.

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Addendum to Part I

The following points have kindly been notified by the persons indicated:

Dr P. D'Angello:

The colloquial name "San Jorge" is also used for *Pepsis* everywhere in Chile, supposedly recalling the fight between St George and the dragon. Another colloquial name is used in Chile: "arañuelo" ("little spider"); D'Angello supposes that it refers to the slow, spider-like movement of, for example, the pompilid wasp *Chirodamus kingi* on cold mornings, which he has personally observed. [It would be worth investigating the cold-adapted physiology of these wasps].

Ruiz (1937) gives a list of species, including *Pepsis limbata* Guerin and *P. caridei* Brethes (as *reaumuri* Dahlbom); the latter visits the flowers of *Escallonia alba*.

Claude-Joseph (1930) treats the natural history of *Pepsis limbata* Guerin: it preys on the Mygale spider *Phryxotrichus roseus*; occurs in hills; and visits flowers of *Ammi visnaga* and others. He also describes hunting and nesting behaviour.

De Santis & Esquivel (1966: 94) give the names of six *Pepsis* species which are ostensibly predators on Blattariae; but as far as is known, all species of the genus prey on mygalomorph spiders, none on cockroaches.

Dr A.S. Menke:

"Distinctions" should be more explicit.

These are intended to draw attention to the more important points in the descriptions, not to repeat them. Of course, the keys and figures should also be used! However, the more difficult the species are to distinguish, the more detailed the Distinctions.

Dr D. Quintero A.:

UPAN (University of Panamá) is omitted from Depositories.

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