

SYSTEMATIC STATUS AND DISTRIBUTION OF THE
LITTLE-KNOWN CHARAXINE *PREPONA WERNERI*
HERING & HOPP

KURT JOHNSON

Department of Entomology, American Museum of Natural History,
Central Park West at 79th Street, New York, New York 10024

AND

HENRI DESCIMON

Laboratoire de Systématique évolutive, Université de Provence,
3 Place Victor Hugo, F-13331, Marseille, Cedex 3, France

ABSTRACT. *Prepona weneri*, hitherto of uncertain systematic status, and since 1925 recorded from only the holotype male, is authenticated from eight additional specimens. Genitalia dissection and review of characters defining *Archaeoprepona* Fruhstorfer and *Prepona* Boisduval indicates *weneri* belongs in *Prepona sensu stricto*. Most specimens are from hydric forest habitat in the Chocó and Cauca areas of endemism, Colombia, but one has data indicating occurrence southward in the upper Rio Putumayo region. The disjunct distribution is probably relict, reflecting former wider occurrence of per-humid biomes.

Additional key words: Apaturidae, *Archaeoprepona*, Neotropics, biogeography.

Of all "Prepona" butterflies, *P. weneri* Hering & Hopp (1925) has been the most problematical. Previously recorded only from the holotype male (Hering & Hopp 1925, Le Moults 1932-33), its melanic appearance, unusual under-surface wing pattern, and hitherto unexamined genitalia have made it a taxon of uncertain status. The most recent treatment of Neotropical Nymphalidae (D'Abrera 1987) does not mention the species. From fieldwork and survey of public and private collections, we recently located eight additional specimens of *P. weneri*. Only two of these were collected since 1929, and it appears unlikely that more specimens will soon be available for study. We therefore summarize below our current determinations of the taxonomic status, biology, and biogeography of this seldom-collected charaxine butterfly.

Taxonomy of "Prepona" Butterflies

Despite accumulation of specimens in private and public collections, there has not been wide agreement on the systematics of "Prepona" butterflies. Because of overall similarity in the striking blue and black markings of the wing upper surfaces, many authors have treated "Prepona" as a monophyletic group (Comstock 1944, Barcant 1970, Brown & Heinemann 1972, Riley 1975). However, as early as 1915, Fruhstorfer defined two subgroups of "Prepona". One he described as genus *Ar-*

chaeprepona (type species *demophon* Linnaeus) (Fig. 2C), which he regarded as "primitive" (Fruhstorfer 1915). The other, including taxa placed with Boisduval's (1836) *Prepona* (type species *demodice* Boisduval) (Fig. 2D), he noted as sharing all morphological characters with *Agrias* Doubleday, from which it differed only in wing pattern. Le Moulton (1932–33) also noted the heterogeneity of the group and proposed *Pseudoprepona* (type species *demophon* L., a junior objective synonym of *Archaeoprepona*). The above distinctions were followed by a number of authors (Orfila 1950, Rydon 1971, Descimon et al. 1973–74, Johnson & Quinter 1982).

As defined hitherto in the literature, some obvious phenetic differences separate *Archaeoprepona* from *Prepona* (Table 1). Authors recognizing these differences have considered both groups as genera (Stichel 1939, Papworth 1982) and even tribes (Rydon 1971) (Table 1). Our concern when considering the taxonomic status of *weneri* has been whether *Prepona* and *Archaeoprepona* are monophyletic groups. Our unpublished numerical cladistic analyses on taxa placed in these groups (Table 1), including outgroups *Charaxes*, *Polyura*, *Palla*, *Euxanthe* and Comstock's (1961) *Anaea sensu lato*, do not conflict with generic usage of *Prepona* and *Archaeoprepona* as reviewed in Table 1. Therefore, based on male genitalia (Fig. 2A, B) and historical usage, *P. weneri* can be reliably placed in *Prepona sensu stricto*.

Prepona weneri Hering & Hopp
(Figs. 1A, B, C, 2A)

Diagnosis. Male. Upper surface of wings: ground darker black-brown than congeners, with blue stripes of deeper azure color (not silverish or blue-green) restricted thinly caudad the forewing discal cell and in a median arc across hindwing. Under surface of wings: hindwing with variably suffused median band, area basad discal band variously marked with dark blotches, two large eyespots each submarginal in cells RS and CuA1 (or a third in cell M3), forewing with disjunct or continuous apical and postmedian lines. **Genitalia** (Fig. 2A). Typical of general configuration of *Prepona sensu stricto* (Fig. 2D).

Female. Unknown.

Distribution. Principally Chocó and Cauca regions (region names follow areas of endemism postulated by Brown 1976, 1982), Colombia, with a single specimen having data indicating upper Putumayo region.

Known specimens. In addition to the type male (Zoologisches Museum der Humboldt Universität zu Berlin, ZMH), labelled "Origin, *Prepona weneri* Hering & Hopp, Rio Micay, Columbien, Februar 1925, 1000m" (Fig. 1A, B, C), eight male specimens are reported here for the first time: (1) Rio Guayabal, Colombia, February 1929, anonymous private collection (examined by first author); (2) Rio Bravo, Prov. Valle, Colombia, March 1985, anonymous private collection (noted by collector as only specimen taken at locality in many years of collecting, examined by David Matusik, Field Museum of Natural History, FMNH, photograph examined by us); (3) Frontino, Colombia, no other data, anonymous private collection (photograph furnished to first author), one male; (4) Cisneros, Colombia, 6 May 1928 (purchased from Le Moulton collection February 1968 from Niedhoffer collection), Milwaukee Public Museum (MPM) (photograph examined; genitalia dissected, illustrated in Fig. 2D); (5) Rio Micay, Cordillera Occidentale, Colombia,

TABLE 1. Main characters in literature differentiating *Archaeoprepona* and *Prepona*.

Character location (authors)	<i>Prepona</i>	<i>Archaeoprepona</i>
Wing upper surface (1-6)	Androconia well-defined, brush-like, with rigid setae	Androconia diffuse, softly hairy
Hindwing under surface (1-6)	Eyespots large, usually two, postmedian to marginal, cells RS and CuA1	Eyespots small, undifferentiated, marginal, cells RS to CuA2
Male genitalia (1, 3-5)	Slender in all parts (especially uncus and valvae); gnathos rod-like, with prominent radial spines	Stout in all parts; gnathos flat, without spines
Female genitalia (3, 7)	Sterigma Y-shaped	Sterigma circular

Taxa included: *Prepona amesia* Fruhstorfer, *brookstana* Godman & Salvin, *deiphile* Godart, *demodice* Godart, *dexamenes* Herbst, *eugenes* Bates, *garleppiana* Staudinger, *gnorima* Bates, *laertes* Hübner, *omphale* Hübner, *pheridamas* Cramer, *praeneste* Hewitson, *pylene* Hewitson, *neoterpe* Hewitson, *xenagoras* Hewitson, *Archaeoprepona amphimachus* Fabricius, *camilla* Godman & Salvin, *chalciope* Hübner, *demophon* Linnaeus, *demophoon* Hübner, *lcomedes* Cramer, *phaedra* Godman & Salvin, *meander* Cramer (Rydon 1971 included *chromus* Guérin-Méneville and *priene* Hewitson in his genus *Noreppa* and treated genera as tribes).

Authors: (1) Fruhstorfer (1915, 1916)*; (2) Stichel (1939)*; (3) Orfila (1950)*; (4) Rydon (1971)*; (5) Descimon et al. (1973-74)*; (6) Papworth (1982)*; (7) Johnson and Quinter (1982)*. * Emphasized certain characters, ** grouped taxa based on these characters.

February-April 1928, collector Kruger, sold by Niepelt 31 May 1928, in Biedermann Collection, Zurich, Switzerland (examined by second author); (6) Cisneros, Rio Dagua valley, 1000 m, 28 February 1928, collector Hopp, sold by Staudinger 15 May 1928, in Biedermann Collection (examined by second author); (7) Queremal, Colombia, November 1986, collector Julian Salazar, Manizales Museum (K. S. Brown Jr. pers. comm., sole South American deposition known to him); (8) Upper Rio Putumayo valley, 1981, local collectors, obtained by David Matusik (FMNH), deposited in American Museum of Natural History (AMNH) (Fig. 1D).

No specimens were located at Allyn Museum of Entomology (AME), British Museum (Natural History) (BMNH), Carnegie Museum of Natural History (CMNH), Field Museum of Natural History, Rijkmuseum van Natuurlijke Historie (Leiden, Netherlands) (RMNH), Museum National d'Histoire Naturelle (Paris), National Museum of Natural History (Smithsonian Institution).

Variation. Variation in the Chocó and Cauca samples appears slight (Fig. 1C), but the single Putumayo specimen (Fig. 1D) is distinctive, as follows: hindwing with emphatic medial band, area basad discal band with heavy blotched markings, three large submarginal eyespots (cells RS, M3, CuA1), and forewing with subapical stripe connected to postmedian stripe across vein M3.

Biology. The few acquirers of *P. weneri* provide the only sources of information about the butterfly's biology. Most specimens now in public (6) or private (3) collections derive from the pre-World War II era of highly financed butterfly sampling in the Neotropics. Initially, commercial interest prompted collection of *P. weneri* at several localities on the Pacific slopes of the Colombian Cordillera (mostly Chocó region). These sites proved extremely inhospitable (Hering & Hopp 1925), being rain forest with extraordinarily high precipitation; Gentry (1982) cites Chocó as the rainiest tropical forest in the world. Consequently, commercial interest in the insect waned, and only one specimen has since been recorded from the region (specimen 6 above). Specimens are so few that most private owners, to avoid deluges of buy offers, request anonymity.

Biogeography. Most specimens of *P. weneri* are from the Chocó region, though one (Queremal, Colombia) is near its eastern margin with the Cauca region. Very likely the extremely hydric Chocó region was a "forest refugium" during Pleistocene glaciations

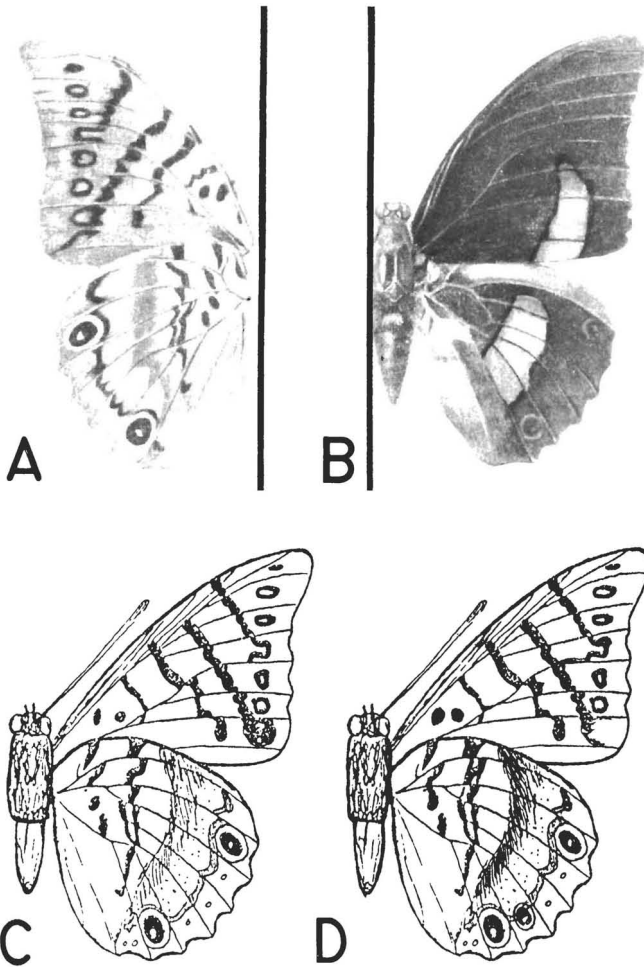


FIG. 1. *Prepona weneri*. A, B, Le Moul't's (1932-33) figure of the holotype of *P. weneri*. A, Under surface. B, Upper surface. C, Reproduction of Hering and Hopp's (1925) original figure of holotype (showing distinctive markings characterizing Chocó and Cauca specimens). D, Drawing indicating distinctive markings on divergent specimen from upper Rio Putumayo region.

(Brown 1976, 1982), explaining the occurrence of a number of highly insular and seldom collected butterflies in it and immediately adjacent areas. Brown emphasizes the close geographic proximity of the Chocó and Cauca regions, and includes them in his "North-western Region" cluster (Brown 1976). He notes zones of hybridization between their taxa. If represented only by Chocó and Cauca specimens, *P. weneri* might be characterized as a seldom collected, insular cis-Andean species, typifying limited hydric habitat. However, a larger view of its taxonomy and biogeography is necessitated by specimen 8 above from the upper Putumayo region of south-central Colombia. This collection is

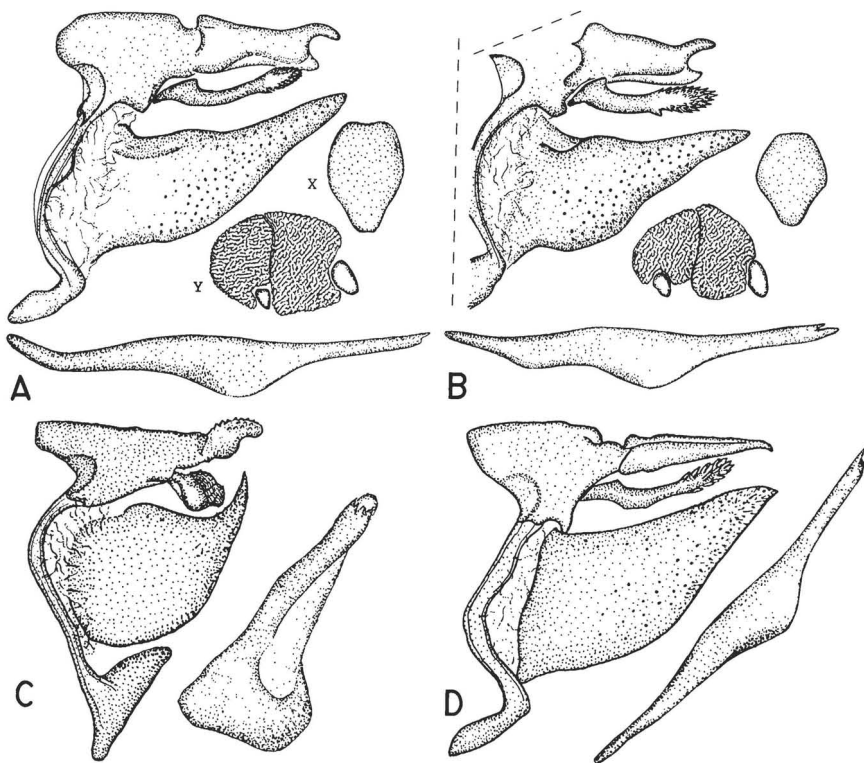


FIG. 2. Male genitalia of *Archaeoprepona* and *Prepona*, and male genitalia and abdominal androconia of *P. weneri*. A, Topotypical *P. weneri*, lateral view of genitalia with aedeagus removed (aedeagus, lateral view, beneath) and (x) ventral view, juxta, (y) lateral view, abdominal androconia at first and second abdominal spiracles. B, *P. weneri* specimen from upper Rio Putumayo region (dashed lines indicating areas of genitalia not available for study because of prior damage to abdomen). C, *Archaeoprepona*, type species *demophon*, Rio de Janeiro, Brazil, same format except for x and y. D, *Prepona* type species *demodice*, Rio de Janeiro, Brazil, same format except for x and y. Females of *Archaeoprepona* and *Prepona* are illustrated in Orfila (1950).

particularly striking, since the Andes are usually considered as a very efficient barrier against faunal exchange. The Putumayo region is located disjunctly southwest of the Chocó and Cauca regions and included in Brown's (1976) "Andean Foothills" cluster. Brown notes very little hybridization between taxa of the Putumayo and Chocó-Cauca regions. Faunal elements of the Putumayo region are mostly trans-Andean. Thus, occurrence of *P. weneri* in the Putumayo region appears biogeographically significant. It seems likely that disjunct distribution in *P. weneri* is relict, reflecting former more widespread occurrence of perhumid biomes. Compared to the rest of the Andes, uplift of its northern elements was relatively recent (Gansser 1973). Consequent separation of *P. weneri* into cis-Andean and trans-Andean nuclei associated with general climatic drying appears more likely than dispersal across the Andes in present or recent times. If further documented, the Putumayo *P. weneri* could be construed as a subspecies.

ACKNOWLEDGMENTS

Dale Jenkins (AME), K. S. Brown Jr. (Universidade Estadual de Campinas, Brazil) and two anonymous reviewers made helpful comments on the manuscript. We particularly thank David Matusik (FMNH) for obtaining the Putumayo specimen of *P. werneri* for AMNH, and A. M. Young (MPM) for providing a Chocó specimen for dissection. For location of additional material we thank David Matusik, H. J. Hannemann (ZMH), and three anonymous private collectors. The following also assisted in efforts to locate specimens: Philip Ackery (BMNH); L. D. Miller (AME); R. deJong (RMNH); J. E. Rawlins (CMNH); and K. S. Brown Jr (various South American inquiries). F. H. Rindge (AMNH) kindly facilitated assistance at AMNH including obtaining archival material. Robert Aronheim (Oakton, Virginia) generously provided an AMNH patron grant in 1981 for initial study of *Agrias* and *Prepona* butterflies which was subsequently followed by a similar grant from Joel B. Grae (Harrison, New York).

LITERATURE CITED

- BARCANT, M. 1970. Butterflies of Trinidad and Tobago. Collins, London. 314 pp.
- BOISDUVAL, J. B. A. D. 1836. Histoire naturelle des insectes. Species general de Lépidoptères. Paris, Libr. Encycl. de Roret. 690 pp.
- BROWN, F. M. & B. HEINEMANN. 1972. Jamaica and its butterflies. F. W. Classey, London. 478 pp.
- BROWN, K. S. 1976. Geographical patterns of evolution in Neotropical forest Lepidoptera (Nymphalidae: Ithomiinae and Nymphalinae—Heliconiini), pp. 118–160. In Descimon, H. (ed.), Biogeographie et Evolution en Amerique Tropicale, Laboratoire de zoologie de l'école normale supérieure, No. 9, 344 pp.
- . 1982. Paleogeology and regional patterns of evolution in Neotropical forest butterflies, pp. 255–308. In Prance, G. T. (ed.), Biological diversification in the tropics. Columbia Univ. Press, New York. 714 pp.
- COMSTOCK, W. P. 1944. Butterflies of Porto Rico. New York Acad. Sci. Scientific Survey of Porto Rico and the Virgin Islands, Insects of Porto Rico and the Virgin Islands 12(4):421–622.
- . 1961. Butterflies of the American tropics: the genus *Anaea*, Lepidoptera, Nymphalidae. American Museum of Natural History, New York. 214 pp.
- D'ABRERA, B. 1987. Butterflies of the Neotropical region. Part 4. Nymphalidae (Partim). Hill House, Victoria, Australia. Pp. 528–678.
- DESCIMON, H., J. MAST DE MAEGHT & J. R. STOFFEL. 1973–74. Contribution à l'étude des Nymphalides néotropicales. Description de trois nouveaux *Prepona* mexicains. Alexanor 8:101–105, 155–159, 235–240.
- FRUHSTORFER, H. 1915. Beitrag zur Morphologie der *Prepona* und *Agrias*. Entomol. Rundsch. 32:45–47.
- . 1916. *Prepona* Bsd., pp. 550–566. In Seitz, A. (ed.), 1910–1919. The Macrolepidoptera of the world. 5. The American Rhopalocera. Alfred Kernen, Stuttgart. Pp. 593–1139.
- GANSER, A. 1973. Facts and theories of the Andes. J. Geol. Soc. London 129:93–131.
- GENTRY, A. H. 1982. Phytogeographic patterns as evidence for a Chocó refuge, pp. 112–136. In Prance, G. T. (ed.), Biological diversification in the tropics. Columbia Univ. Press, New York. 714 pp.
- HERING, M. & H. W. HOPP. 1925. Sammelausbeute des H. Werner Hopp aus der Choco Kolumbiens. Deut. Entomol. Z. (Iris) 38:194–195.
- JOHNSON, K. & E. L. QUINTER. 1982. Commentary on Miller and Brown vs. Ehrlich and Murphy *et al.*: Pluralism in systematics and the worldwide nature of kinship groups. J. Res. Lepid. 21:255–269.
- LE MOULT, E. 1932–33. Etudes sur les *Prepona*. Nov. Entomol. II, 1, Suppl. 1: 16 pp.; III, Suppl.
- ORFILA, R. N. 1950. Las especies Argentinas de "Prepona" Boisd. (Lep. Nymph.). Cienc. Zool. I(7):273–321.

- PAPWORTH, H. 1981-82 [1982]. A review of the Trinidad butterflies hitherto placed in the genus *Prepona* (Lepidoptera: Nymphalidae). Living World, J. Trinidad and Tobago Field Naturalist's Club, unnumbered, pp. 4-8.
- RILEY, N. D. 1975. Field guide to the butterflies of the West Indies. Collins, London. 244 pp.
- RYDON, A. H. B. 1971. The systematics of the Charaxidae (Lepidoptera: Nymphaloidea). Entomol. Rec. J. Var. 83:219-233, 283-287, 310-316, 336-341, 384-388.
- STICHEL, H. 1939. Pp. 628-664. In Bryk, F., Lepidopterorum Catalogus. 93: Nymphalidae III. Subfamily Charaxinae II. 794 pp.

Received for publication 1 April 1987; accepted 27 May 1988.