

A Revision of *Pachacutia*, a New Genus of Rare Andean Ithomiine Butterflies (Nymphalidae: Ithomiinae), with the Description of Two New Species

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ABSTRACT A new genus, *Pachacutia* n. gen., of large, rare Andean ithomiine butterflies is described and characterized, containing four species. Two species and their constituent subspecies and synonyms (*Ithomia cleomella* Hewitson, *Ithomia mantura* Hewitson, *Ithomia honrathi* Srnka, and *Dircenna barrettii* Dannatt) are transferred to *Pachacutia* from *Godyrus* Boisduval (n. comb.). Two additional species are described from southern Ecuador (*Pachacutia baroni* n. sp.) and Bolivia (*Pachacutia germaini* n. sp.), and a new subspecies, *Pachacutia mantura joroni* n. ssp., is described from Peru. *Pachacutia* is a member of a clade containing otherwise small, often abundant lowland forest ithomiines, including *Mcclungia* R.M. Fox, *Brevioleria* Lamas, and some species of *Hypoleria* Godman & Salvin. A comparative phylogenetic analysis showed *Pachacutia* species to be related as follows: (*baroni* + (*mantura* + (*cleomella* + *germaini*))). A key for identification of all taxa, and illustrations of male and female genitalia for all species and adult specimens of all taxa, are presented, and the taxonomy and natural history of all taxa are discussed.

KEY WORDS Andes, Ithomiinae, taxonomy

Materials and Methods

Despite being taxonomically one of the best studied groups of Neotropical butterflies (e.g., Fox 1940, 1956, 1960, 1967; Fox and Real 1971; Brown 1977, 1980; D'Almeida 1978; Mielke and Brown 1979; Brown and Freitas 1994), a recent phylogenetic analysis of the Ithomiinae (Willmott and Freitas 2006) has uncovered a number of cases of genera that are not monophyletic, including *Godyrus* Boisduval, 1870. One exemplar species studied from that genus, *Ithomia mantura* Hewitson, proved to be more closely related to several other genera in the tribe Godyridini, particularly *Mcclungia* R.M. Fox, 1940, *Brevioleria* Lamas, 2004, and some members of *Hypoleria* Godman & Salvin, 1879. Further study found that *Ithomia cleomella* Hewitson and two additional undescribed species, also formerly placed in *Godyrus* (Mielke and Brown 1979, Lamas 2004), were morphologically similar to *I. mantura*. All four species share several synapomorphies, and they are ecologically distinct from their nearest relatives. We therefore describe a new genus for these four species and review the taxonomy of all included taxa, describing the two new species and an additional new subspecies.

Collections. Specimens were examined in major public and private collections in Europe and North and South America (listed in Willmott and Lamas 2006) to record distributional data, study morphological variation, assess taxonomic diversity, and locate type specimens. Three lectotypes are designated to ensure nomenclatural stability. The following collection codens and abbreviations are used in the text: BMNH, Natural History Museum, London, United Kingdom; CMNH, Carnegie Museum of Natural History, Pittsburgh, PA; FV, Fabio Vitale collection, Lecce, Italy; GTB, Gerrit ten Broek collection, Krommenie, Holland; KSB, Keith S. Brown, Jr. collection, Campinas, Brazil; KJWH, Keith R. Willmott & Jason P. W. Hall collection, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; MGCL, McGuire Center for Lepidoptera and Biodiversity, University of Florida, Gainesville, FL (contains former Allyn Museum of Entomology); MNRJ, Museu Nacional, Rio de Janeiro, Brazil; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; OD, Olivier Duviols collection, Provence, France; PB, Pierre Boyer collection, Le Puy, France; UFP, Universidade Federal do Paraná, Curitiba, Brazil; ZSBS, Zoologische Sammlung des Bayerischen Staates, Munich, Germany; (D)FW, (dorsal) forewing; and (V)HW, (ventral) hindwing.

Morphological Study. Morphology was studied using standard techniques, with adult abdomens being

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Table 1. Dissections of *Pachacutia* and outgroup taxa used in cladistic analysis

Genus	Species	Subspecies	Sex	Vial no.	Country	Province	Locality	Collection
<i>Godyris</i>	<i>zavaleta</i>	<i>matronalis</i>	m		Ecuador	Napo	Apuya	KWJH
<i>Godyris</i>	<i>zavaleta</i>	<i>matronalis</i>	f		Ecuador	Napo	Chichicorrumi	KWJH
<i>Godyris</i>	<i>zavaleta</i>	<i>rosata</i>	m*	BMNH-6786	Ecuador	Imbabura	Paramba	BMNH
<i>Godyris</i>	<i>zavaleta</i>	<i>telesilla</i>	f*	BMNH-6719	Ecuador	Bolívar	La Chima	BMNH
<i>Hypoleria</i>	<i>adasa</i>		m	BMNH-6790	Brazil	São Paulo	São Paulo	BMNH
<i>Hypoleria</i>	<i>adasa</i>		m	BMNH-7171	Brazil	Rio de Janeiro	Rio de Janeiro	BMNH
<i>Hypoleria</i>	<i>adasa</i>		f	BMNH-6722	Brazil	Rio de Janeiro	Rio de Janeiro	BMNH
<i>Brevioleria</i>	<i>aelia</i>	<i>plithenes</i>	m	BMNH-7163	Brazil	Distrito Federal	Belo Horizonte	BMNH
<i>Brevioleria</i>	<i>aelia</i>	<i>plithenes</i>	m*		Brazil	Goiás	Goiás Velho	UFP
<i>Brevioleria</i>	<i>aelia</i>	<i>plithenes</i>	f*		Brazil	Goiás	22 km W Ipora	UFP
<i>Pachacutia</i>	<i>baroni</i>		m*	BMNH-6793	Ecuador	Zamora-Chinchipec	Zamora	BMNH
<i>Pachacutia</i>	<i>baroni</i>		f*	BMNH-7193	Ecuador	Morona-Santiago	Macas-9 de Octubre	BMNH
<i>Pachacutia</i>	<i>mantura</i>	<i>honrathi</i>	m*	BMNH-6379	Peru	Junín	[La] Oroya	BMNH
<i>Pachacutia</i>	<i>mantura</i>	<i>honrathi</i>	f*	BMNH-6718	Peru	Junín	La Merced	BMNH
<i>Pachacutia</i>	<i>mantura</i>	<i>honrathi</i>	m	s/n	Peru	Junín	Valle Chanchamayo	MUSM
<i>Pachacutia</i>	<i>mantura</i>	<i>joroni</i>	m	s/n	Peru	San Martín	Tarapoto	MUSM
<i>Pachacutia</i>	<i>mantura</i>	<i>mantura</i>	m	s/n	Peru	Cuzco	Marcapata	MUSM
<i>Pachacutia</i>	<i>mantura</i>	<i>mantura</i>	m	BMNH-7223	Peru	Puno	Inambari	BMNH
<i>Pachacutia</i>	<i>mantura</i>	<i>mantura</i>	f	BMNH-7224	Peru	No data	No data	BMNH
<i>Pachacutia</i>	<i>cleomella</i>		m*	MNRJ-01	Peru	No data	No data	MNRJ
<i>Pachacutia</i>	<i>cleomella</i>		m	s/n	Peru	No data	No data	MUSM
<i>Pachacutia</i>	<i>cleomella</i>		f*	BMNH-7196	Bolivia	No data	No data	BMNH
<i>Pachacutia</i>	<i>germaini</i>		m*	BMNH-7195	Bolivia	La Paz	Caranavi area	BMNH
<i>Pachacutia</i>	<i>germaini</i>		m	s/n	Bolivia	La Paz	Caranavi	MUSM
<i>Pachacutia</i>	<i>germaini</i>		f*	BMNH-7194	Bolivia	No data	No data	BMNH

Asterisk (*) indicates a figured specimen.

soaked in hot 10% KOH for 10–15 min, dissected, and subsequently stored in glycerol (Table 1). Body morphology and dissections were studied using a stereomicroscope at up to 50× magnification. Wing venation was drawn from wings cleared with bleach as well as from uncleared specimens. Hindwing androconial scales and other wing scales were examined in situ, after removal of the right forewing, by using stereomicroscope at 50× magnification. Male androconial scales were further examined in *I. mantura* (and ≈80 other ithomiine species as part of the phylogenetic analysis of the Ithomiinae), by using a Hitachi S2500 scanning electron microscope, at magnifications of up to 5,000×. Wing sections for examination were mounted on stubs with polyvinyl acetate glue and coated with a 20-nm layer of gold/palladium (95%/5%) by using a Cressington sputter coater (Cressington Scientific Instruments Ltd., Watford, United Kingdom).

Phylogenetic Analysis. We investigated the relationships among *Pachacutia* species by using a cladistic analysis of characters from adult morphology of both sexes (immature stages are unknown) (Tables 2 and 3). All characters were equally weighted and multistate characters unordered. To polarize character states, we used *Godyris zavaleta* (Hewitson, [1855]) as the outgroup and included in the ingroup two members of other genera in the ithomiine clade containing *Pachacutia*, namely, *Brevioleria aelia plithenes* (D'Almeida 1958) and *Hypoleria adasa* (Hewitson, [1855]) (Willmott and Freitas 2006; also see generic diagnosis below). An exhaustive search was conducted in PAUP* 4.0b10 (Swofford 1998) with maximum parsimony as our optimality criterion. We estimated support for branches by using 1,000 bootstrap replicate exhaustive searches

and by calculating Bremer support by using constraint searches generated by hand and run in PAUP. Characters were optimized onto the cladogram with ambiguous changes placed according to the most plausible evolutionary scenario, in general favoring loss over independent gain.

Revision of *Pachacutia*

Pachacutia Willmott & Lamas, n. gen.

(Figs. 1D–G, I–L, 2A and B, F–K, 3–4, 6–9, 11–14)

Type Species. *Ithomia mantura* Hewitson, 1876.

Systematics and Diagnosis. Cladistic analysis indicates that *Pachacutia* is a member of the ithomiine tribe Godyridini, which has the following unique synapomorphy: male DHW androconial scales beneath hair pencil in cells Rs-Sc+R₁ and M₁-Rs, reaching vein M₁ (Fig. 2). Most other ithomiines have these scales confined to cell Rs-Sc+R₁ only, except the Tithoreini, in which the scales extend slightly into cell M₁-Rs, and Melinaeini, in which they extend into M₁-Rs and the anterior portion of the discal cell (Willmott and Freitas 2006).

Within the Godyridini, *Pachacutia*, *Brevioleria*, *McClungia*, *H. adasa*, *Hypoleria sarepta* (Hewitson, [1852]), *Hypoleria ocalea* (Doubleday, 1847), and *Hypoleria aureliana* (H.W. Bates, 1862) form a clade (the *McClungia* clade), with the following synapomorphies: aedeagus rotated 90° to right, opening laterally into ductus ejaculatorius on right-hand side (Figs. 5J, 6G, 7F, 8F, 9F; the aedeagus opens dorsally in all ithomiines (e.g., Fig. 5D) except *Callithomia* H.W. Bates, 1862, in which it opens ventrally); correlated with the previous character, the ductus ejaculatorius is

Table 2. Characters used in cladistic analysis

No.	Character
1	Antennal clubs: (0) black; (1) yellow
2	Forewing with cells R ₄ -R ₃ , R ₃ -R ₂ and R ₂ -R ₁ : (0) opaque; (1) translucent
3	Male VHW costa with white stripe in cell Rs-Sc+R ₁ : (0) absent; (1) present
4	Female forewing distal marginal border with inner edge: (0) straight; (1) scalloped
5	Hindwing discocellular bar: (0) absent; (1) present
6	VHW white marginal spots: (0) present; (1) absent
7	VFW costal margin: (0) dark blackish brown; (1) pale yellowish
8	Hindwing discocellular vein Cu ₁ -M ₃ : (0) longer than M ₃ -M ₂ ; (1) shorter than M ₃ -M ₂ or equal in length
9	Male hindwing with 3d pointing: (0) distal of base of vein M ₂ ; (1) basal of base of vein M ₂
10	Female with forewing Mr: (0) on 3d; (1) on 2d
11	If female with forewing Mr on 2d, male with forewing Mr on: (0) 3d; (1) 2d
12	Male DHW androconial scales under hair pencil: (0) in two isolated patches; (1) in two adjacent patches
13	Male basal DHW androconial scale patch: (0) ending basal of discocellular veins; (1) ending distal of discocellular veins
14	Male distal DHW androconial scale patch: (0) extending across area between Mr and anterior edge discal cell; (1) in anterior half only of area between Mr and anterior edge discal cell
15	Hindwing hair pencil: (0) single, complete; (1) double, complete; (2) single, basal only
16	Aedeagus in dorsal view: (0) straight; (1) curving to left
17	Aedeagus (with vesica unevverted) tip: (0) not swollen; (1) swollen
18	Saccus: (0) short (100–150% length valva); (1) long (>200% length valva)
19	Uncus and tegumen in posterior view: (0) more or less symmetrical; (1) twisted clockwise
20	Ventral medial flange on valva: (0) simple rounded point; (1) bifid plate
21	Female genitalia with dorsal eighth sternite "scoop": (0) broad; (1) narrow
22	Ductus seminalis base: (0) simple, directly on corpus bursae; (1) convoluted, at base of ductus bursae; (2) perpendicular to expanded base of ductus bursae
23	Posterior edge of seventh sternite: (0) smooth; (1) indented at ostium bursae

uniquely rotated 90° to the left to lie flat against the aedeagus so that it opens dorsally (Figs. 5I and J, 6G, 7F, 8F, 9F), rather than being perpendicular to the remainder of the aedeagus (e.g., Fig. 5D); ductus bursae portion anterior of ductus seminalis absent, so that ductus seminalis arises from corpus bursae (Figs. 10J, 11F and L, 12F and L), rather than from the middle of the ductus bursae (Fig. 10E). Only in *Methona* Doubleday, 1847 does the ductus seminalis also arise

from the corpus bursae, but this seems to be due to the great elongation of the antrum resulting in loss of the ductus bursae.

Within the *Mcclungia* clade, *Pachacutia* may be distinguished by a number of universal synapomorphies (characters have been checked in all members of the *Mcclungia* clade). 1. Male DHW androconial hair pencil complete, extending from base of cubital vein to discocellular veins (Fig. 2F–I). This state is also the same in *Godyris* (Fig. 2C). *Mcclungia cymo* (Hübner, [1806]) and *Hypoleria* have the hair pencil divided in two (Fig. 2D), whereas in *Brevioleria* the distal portion of the hair pencil is absent (Fig. 2E). 2. Basal patch of wing androconial scales beneath hair pencil in cell Rs-Sc+R₁ extending distal of discocellular veins (Fig. 2F–I). Other *Mcclungia* clade members have this patch ending basal of the discocellular veins. 3. Antennal club yellow (Figs. 3 and 4). In all other *Mcclungia* clade species the antennal club is black. It is also yellow in three *Godyris* species and two *Hypoleria* species, but otherwise black in the majority of Godyridini. 4. Basal halves of forewing cells R₄-R₃ and R₃-R₂ translucent (Figs. 3 and 4). In most other Godyridini (exceptions include *Veladyris* R. M. Fox, 1945), except those with uniform reduction of all the dark wing margins, these cells are opaque. 5. Genitalic valva with broad, slightly bifurcate postero-ventral flange (e.g., Figs. 6D and E, 7D). In all *Mcclungia* clade species this flange is a simple point (Fig. 5H). 6. Aedeagus posterior tip with a rounded bulge at base of vesica, visible when vesica not everted (e.g., Fig. 7F). In all other *Mcclungia* clade species there is no such bulge present, the base being similar in width to the remainder of the aedeagus (Fig. 5J). 7. Female FW vein Mr on discocellular vein 2d (Fig. 11). All other *Mcclungia* clade species, and Godyridini [except *Godyris duillia* (Hewitson, 1854) and certain *Veladyris*], have Mr on 3d.

Description: Male. *Wings* (Figs. 3 and 4): forewing length 34–38 mm. Similar to most Ithomiinae, relatively elongate, rounded at apex, distal margin slightly convex, anal margin concave. *Dorsal surface* (Figs. 3 and 4): Both wings largely translucent through reduction of cover scales to "pitchfork"-shaped scales, as in many more derived Ithomiinae (Willmott and Freitas 2006); translucent areas almost entirely colored pale yellow to whitish yellow, except in one species with intense orange-yellow; costal, distal and FW anal margins opaque blackish brown, HW anal margin translucent or semiopaque reddish brown (one species); FW costal margin translucent yellow postdiscally into

Table 3. Character matrix for cladistic analysis

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>zavaleta</i>	1	0	0	0	0	0	0	0	0	0	#	#	#	#	0	1	0	0	0	0	0	#	1
<i>adasa</i>	0	0	0	0	0	1	0	0	1	0	#	0	0	0	1	0	0	1	0	0	0	2	1
<i>aelia plisthenes</i>	0	0	0	0	0	1	0	0	0	0	#	0	0	0	2	1	0	1	1	0	0	0	0
<i>baroni</i>	1	1	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	0	0	1	0	0	0
<i>mantura</i>	1	1	0	0	(01)	0	0	1	0	1	1	1	1	1	0	1	1	0	0	1	0	0	1
<i>cleomella</i>	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1
<i>germaini</i>	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	1

#, not applicable.

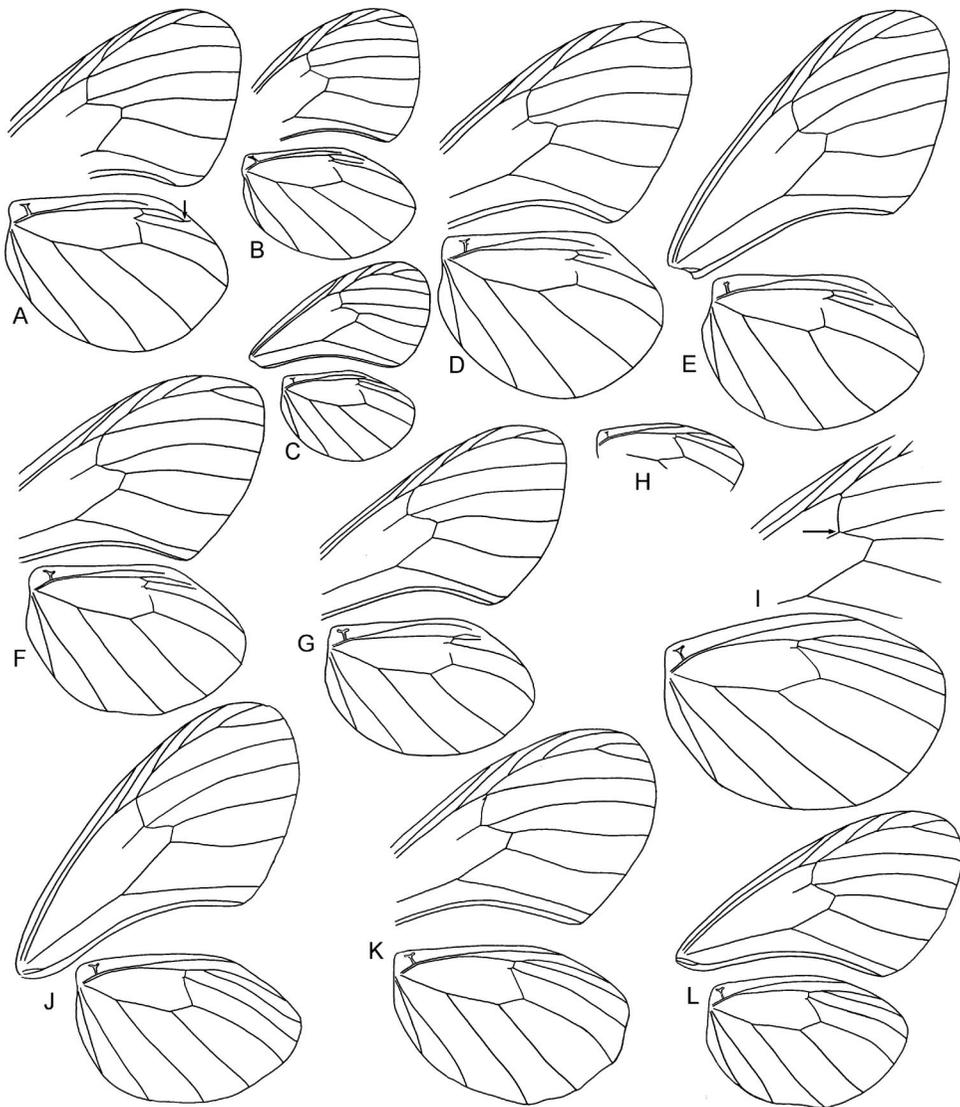


Fig. 1. Wing venation, both wings (except H), some forewings showing discal area only. (A) *Godyrus zavaleta sosunga* (Reakirt, [1866]), ♂, Costa Rica, BMNH. (B) *Hypoleria adasa*, ♂, Brazil, BMNH. (C) *Brevioleria aelia plisthenes*, ♂, Brazil, UFP. (D) *Pachacutia baroni* n. sp., ♂, holotype, Ecuador, BMNH. (E) *P. mantura honrathi*, ♂, Peru, BMNH. (F) *P. cleomella*, ♂, Peru, MNRJ. (G) *P. germaini* n. sp., ♂, paratype, Bolivia, BMNH. (H) *Brevioleria aelia plisthenes*, ♀, Brazil, UFP, hindwing only. (I) *Pachacutia baroni* n. sp., ♀, paratype, Ecuador, PB. (J) *P. mantura honrathi*, ♀, Peru, BMNH. (K) *P. cleomella*, ♀, lectotype, Peru, BMNH. (L) *P. germaini*, ♀, paratype, Bolivia, BMNH.

basal half of cells R_4-R_3 , R_3-R_2 and R_2-R_1 , yellowish anterior of discal cell in two species; inner edge of distal marginal border scalloped or straight, hindwing distal marginal border broadest in cell $2A-Cu_2$, narrowest in cell Cu_1-M_3 , with white submarginal spots variably present; FW apex with white subapical spots variably present; FW and HW (except in one species) discocellular veins with black scaling or bar, in some taxa continuing thinly along vein Cu_1 to distal margin; black, opaque FW discal cell bar present in some taxa. *Ventral surface* (Figs. 3 and 4): Similar to dorsal surface except white submarginal spots usually more numerous and prominent, some taxa with reddish

brown scaling in dark marginal borders, two species with VFW costal margin basal of discocellular veins yellowish; white HW costal streak in cell $Rs-Sc+R_1$ in two species. *Venation* (Fig. 1): All veins present and typical of Godyradini except FW medial recurrent vein (Mr) on $2d$ in three species, on $3d$ in one species, and relatively long; HW with discocellular vein Cu_1-M_3 relatively short in some species; $1d$, $2d$, $3d$ present, $3d$ incomplete anteriorly; M_1 , Rs and $Sc+R_1$ all separate, not reaching distal margin; cell $Rs-Sc+R_1$ relatively broad; humeral vein distinctly bifid with distal and basal arms of similar length. *Wing androconia* (Fig. 2): Undivided patch of hair-

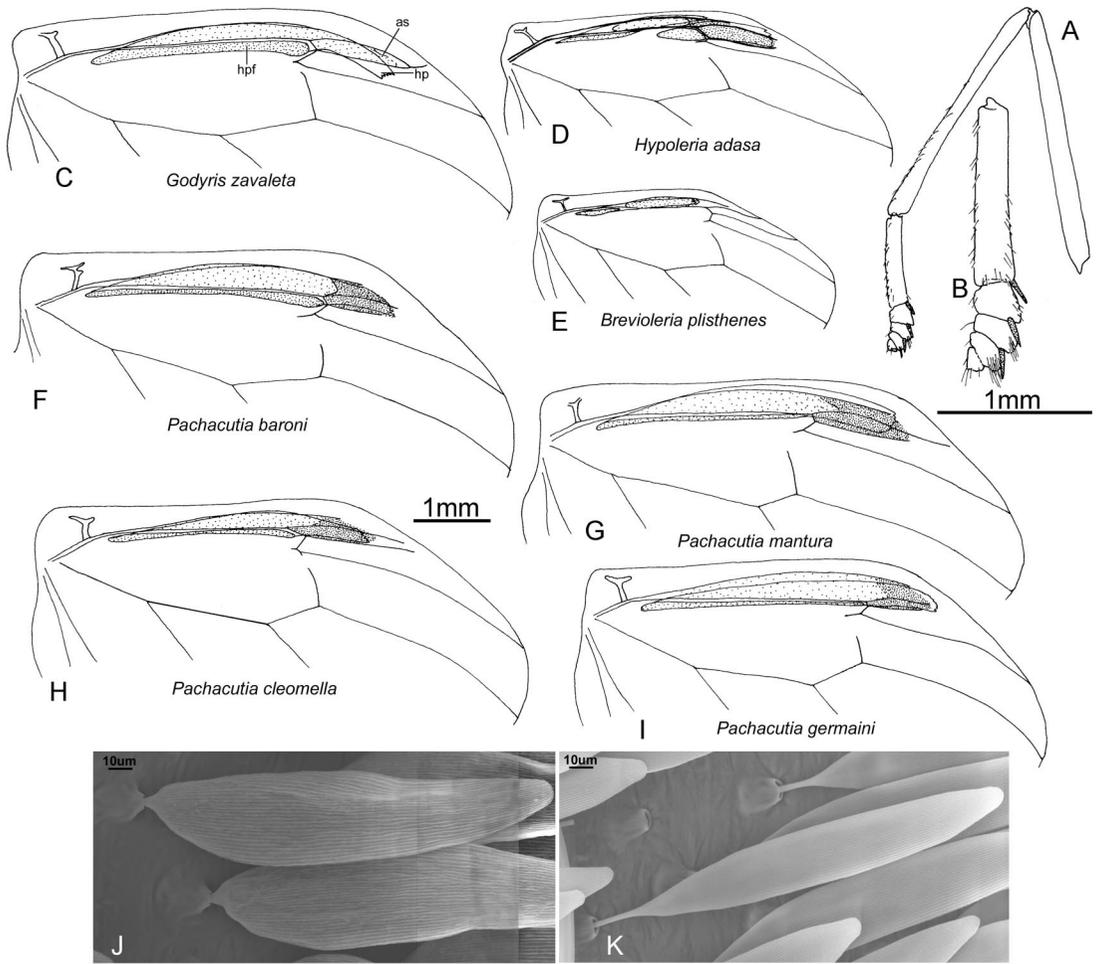


Fig. 2. Female foreleg (A and B) and male androconia (C–K). (A) *Pachacutia mantura honrathi*, female foreleg. (B) *P. mantura honrathi*, female foretarsus. Anterior half of dorsal hindwing showing distribution of androconial hair pencil (hp), hair pencil “footprint” (hpf) and androconial scales (as). (C) *Godyris zavaleta sosunga*, Costa Rica, BMNH. (D) *Hypoleria adasa*, Brazil, BMNH. (E) *Brevioleria aelia plisthenes*, Brazil, UFP. (F) *Pachacutia baroni*, holotype, Ecuador, BMNH. (G) *P. mantura honrathi*, Peru, BMNH. (H) *P. cleomella*, Brazil, MNRJ. (I) *P. germaini*, paratype, Bolivia, BMNH. *Pachacutia mantura honrathi*, Peru, BMNH, androconial scales in cell Rs-Sc+R₁. (J) Basal patch. (K) Distal patch.

like scales (“hair pencil”) extending from just distal of humeral vein to base vein Rs, patch “footprint” tapering distally; androconial scale patch beneath hair pencil throughout cells Rs-Sc+R₁ and M₁-Rs where bounded by veins, making up two distinct but contiguous scale types, basal type extending in cell Rs-Sc+R₁ from near base to distal of 1d, distal type in remainder of Rs-Sc+R₁ and M₁-Rs; basal scales mixed light and darker gray-brown, dense, leaf-shaped, blunt, thin (almost translucent), slightly wrinkled, vanes clearly visible throughout, pedicel short, sockets conical with narrow mouth; distal scales similar except pale gray with brown tips, more elongate, flat, pedicel very narrow and elongate, sockets tubular with wide mouth.

Head: Eyes dark brown and smooth; labial palpi white with black ventro-lateral outer and medial inner stripes of dense black scales and hairs; antennae pale yellow in terminal third, dark brown basal two

thirds; frons black with white tapering stripe ventral of antenna socket, white streak mid-dorsally behind eyes.

Thorax: Patagia white laterally and black on inner edges at middle; tegula black with yellowish to white scales scattered sparsely along posterior projection, anterior ventral lobe white; thorax dorsally black with pale yellowish brown to white dorsal midline; ventrally black with white spots at dorsal edge of meron and episternum.

Legs: Foreleg tarsus and tibia fused into a single, small, rounded joint; legs black with variable sparse white ventral scaling on femur of mid- and hindleg, white scaling on coxa and outer edge of foreleg femur when folded.

Abdomen: Dorsally dark brown with variable lateral whitish scaling on segments of anterior half, restricted to anterior portion of more distal segments, and in soft pleural tissue between tergites and sternites; ventrally

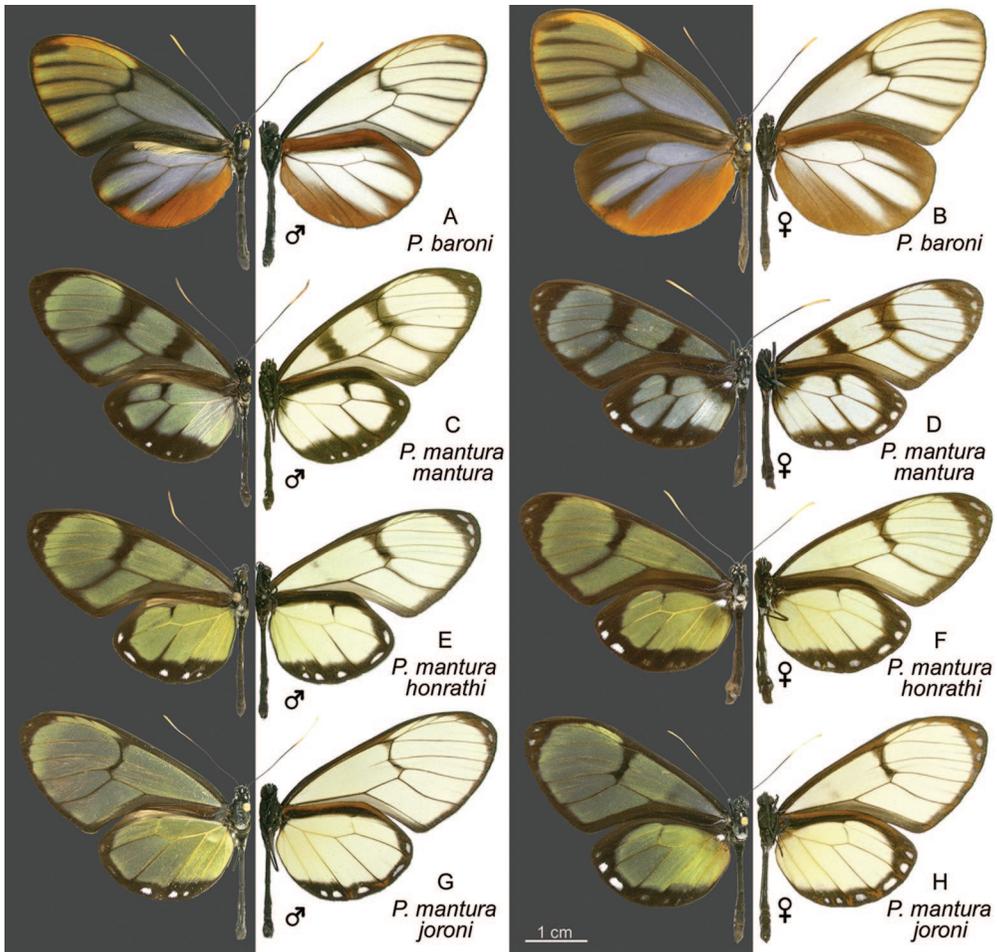


Fig. 3. *Pachacutia baroni* (A and B) n. sp. and *P. mantura* (C–H), left wings dorsal over dark background, right wings ventral. (A) *P. baroni*, ♂, paratype, Ecuador, Morona-Santiago, Yakunk-Cutucú trail, KWJH. (B) *P. baroni*, ♀, paratype, Ecuador, Morona-Santiago, Río Abanico, PB. (C) *P. mantura mantura*, ♂, Peru, “Huánuco, Acomayo”, GTB. (D) *P. mantura mantura*, ♀, Peru, BMNH. (E) *P. mantura honrathi*, ♂, Peru, Junín, Satipo, GTB. (F) *P. mantura honrathi*, ♀, Peru, Junín, La Merced, BMNH. (G) *P. mantura joroni*, ♂, paratype, Peru, San Martín, Juanjui, GTB. (H) *P. mantura joroni*, ♀, paratype, Peru, San Martín, Juanjui, GTB.

black except for variable white lateral scaling along dorsal half of sternites.

Genitalia and terminal sclerites (Figs. 6–9): Terminal tergite and sternite simple, tergite slightly medially cleft; uncus short, stout, tapering only slightly, ventrally slightly curved at tip with sparse setae ventrolaterally, fused at base to tegumen and base of appendices angulares; appendices angulares essentially absent, represented by a slight bump, except in *P. germaini*; tegumen relatively small, simple; gnathos a broad, complete sclerotized band, forming a ventral, posteriorly projecting “scoop” or point that is rugose in all species except *P. mantura* and increasingly less sclerotized posteriorly; gnathos, uncus and tegumen may be rotated slightly clockwise in posterior view; juxta a broad, flat v-shaped plate; vinculum straight, even in width; valva relatively large, triangular, with two broad, short, posterior projections, dorsally a blunt point, ventrally a curved, slightly bifurcate

flange; saccus expanded into a bulb at anterior tip, of similar length to valva up to almost 4× length of valva; aedeagus narrow, elongate (2–5× length valva), smooth, slightly bent laterally just posterior of zone (junction between anterior and posterior parts of aedeagus), base of vesica swollen forming a small, slightly lateral bulge visible when not everted, vesica straight and sharply angled to aedeagus with patch of tiny apparently encircling cornuti near base, ventral anterior tip of aedeagus broadening laterally, ductus ejaculatorius rotated 90° to right to lie flat against base of aedeagus, aedeagus rotated laterally 90° to right.

Female. *Wings* (Figs. 3 and 4). Differs from male as follows: forewing length 33–41 mm; very slightly more rounded. *Dorsal surface* (Figs. 3 and 4): Dark opaque areas typically broader, white DHW submarginal markings more pronounced. *Ventral surface* (Figs. 3 and 4): When white submarginal spots present on VHW, an additional spot in cell M_2 - M_1 present; VHW

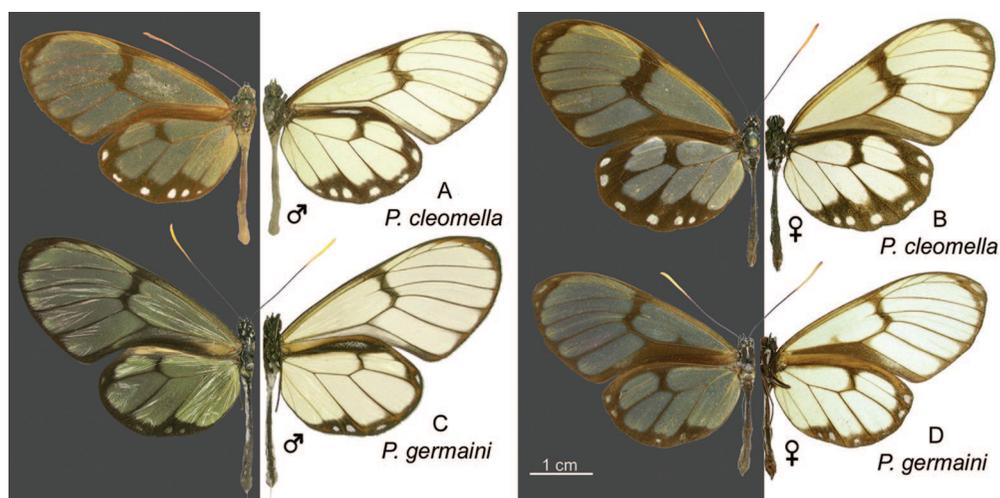


Fig. 4. *Pachacutia cleomella* (A and B) and *P. germaini* n. sp. (C and D), left wings dorsal over dark background, right wings ventral. (A) *P. cleomella*, ♂, Peru, MNRJ. (B) *P. cleomella*, ♀, Peru, Cuzco, Río Pilcopata, GTB. (C) *P. germaini*, ♂, paratype, Bolivia, La Paz, Caranavi area, GTB. (D) *P. germaini*, ♀, paratype, Bolivia, Cochabamba, Yungas del Espíritu Santo, BMNH.

costal white dash absent. *Venation* (Fig. 1): All veins present (except HW 1d) and typical of Godyridini except FW medial recurrent vein (Mr) on 2d in all species, sometimes relatively long; HW with 1d absent, veins M_1 and Rs merging near base; Mr short and on 3d; humeral vein distinctly bifid with distal and basal arms of similar length. *Wing androconia*: Absent.

Legs: Forelegs almost entirely black, five tarsal segments.

Genitalia and terminal sclerites (Figs. 11 and 12): Eighth tergite slightly cleft posteriorly, medially desclerotized in some species either anteriorly or posteriorly; eighth sternite lateral plates fused to form a broad, well-sclerotized lamella postvaginalis (LPV), which is entirely fused with antrum, creating a broad, funnel-like entrance to ductus bursae; LPV indented at mid-dorsal edge; minute spines adorn LPV near ostium bursae; LPV and terminal sclerites asymmetrical, both in lateral and ventral view, with sternite nearer tergite on left side; seventh sternite variable, may be rather elongate or heavily indented at posterior edge to accommodate LPV; antrum opens to left, ductus bursae of similar length to corpus bursae, becoming more sclerotized internally toward junction with corpus bursae; ductus seminalis arising near junction of ductus bursae and corpus bursae, either directly from latter, or from an expanded base of ductus bursae; appendix bursae present.

Etymology. The generic name is derived from that of the emperor Pachacutec Inca Yupanqui (?-1471), who expanded the Inca empire from southern Peru to Ecuador, a similar range to that of this genus. The name is considered to be feminine.

Discussion. Three of the existing species-level names for *Pachacutia* were described in the genus *Ithomia* Hübner, 1816, in common with most other contemporaneous ithomiine taxa. The remaining name was described in *Dircenna* Doubleday, 1847, and

both described taxa of *P. mantura* were treated at one time or other as members of this genus, presumably simply because of their similarity in wing pattern to certain *Dircenna* species. Subsequent authors recognized that *Pachacutia* species bore no relationship at all to *Dircenna*, resulting in the transfer of all species to *Godyris* (D'Almeida 1978, Mielke and Brown 1979, Lamas 2004). Although no reason has ever been given for this placement, obvious features such as the undivided male DHW androconial hair pencil, similar venation (including the bifid humeral vein), and large size are superficially similar to *Godyris*. However, most species are so rare that opportunities for detailed morphological examination have been limited in the past, and female genitalia, which are so informative in *Pachacutia*, have historically often been overlooked (e.g., Fox 1940). A number of convincing characters show that *Pachacutia* is more closely related to species of several other genera outside *Godyris* (discussed above), and all members of *Pachacutia* lack the two universal synapomorphies for *Godyris*: the aedeagus posterior tip with a line of small teeth along the left lateral edge (Fig. 5E; unique to *Godyris*), and the distal coalescence of male hindwing veins M_1 and Rs first mentioned by Lathy (1901) (Fig. 1A; also in *Greta morgane*; Geyer 1837).

Phylogenetic analyses based on morphology place the sister group as the well-supported clade of *Brevioleria* + *Mcclungia* (Willmott and Freitas 2006). This topology has strong bootstrap (87%) support, and despite weak Bremer support, two characters that are relatively convincing: 1. Male DHW basal androconial patch scales beneath hair pencil mixed light and darker gray-brown, a character state also occurring in some Melinaeini but otherwise unique in Godyridini; 2. Male DHW basal androconial patch scales beneath hair pencil curled longitudinally at edges and wrinkled (Fig. 2J), rather than flat or lightly curved, an uncom-

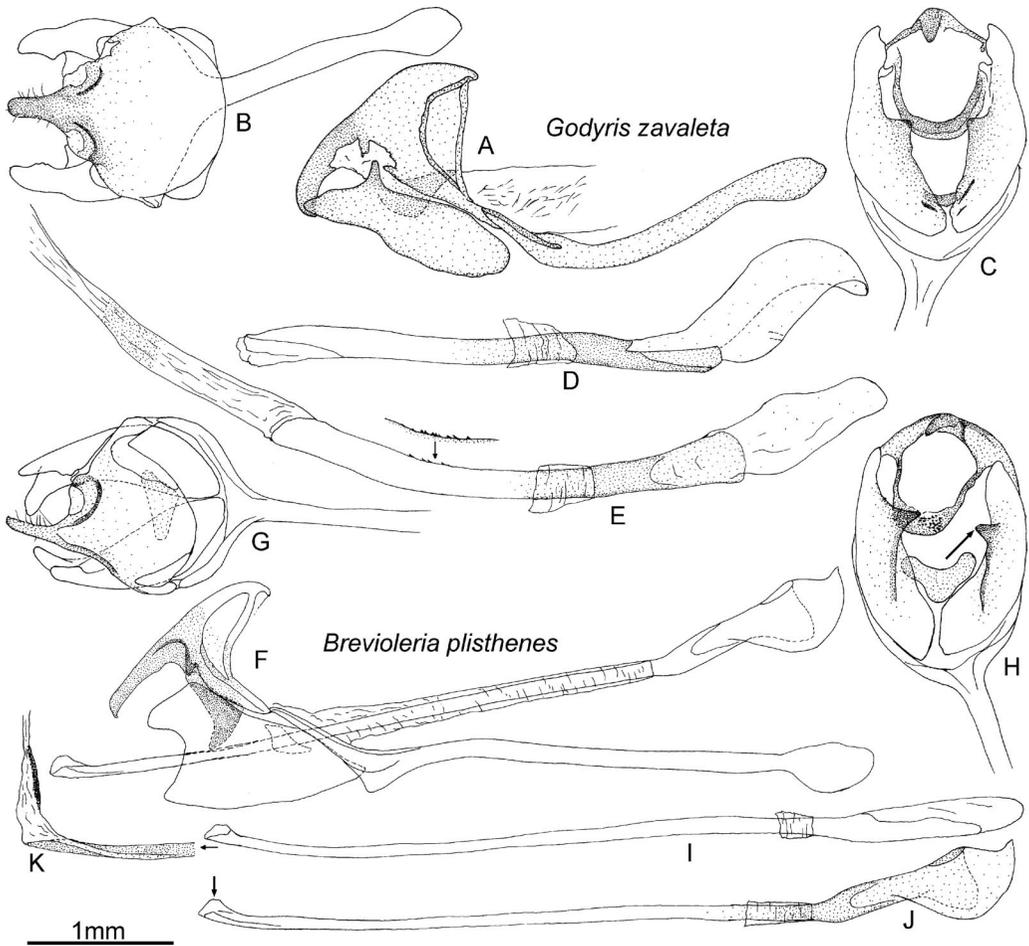


Fig. 5. Male genitalia, outgroup taxa. *Godyris zavaleta rosata* Vitale & Rodríguez, 2004, BMNH (A–E) and *Brevioleria aelia plisthenes*, UFP (F–J). (A and F) Lateral view (aedeagus removed in A). (B and G) Dorsal view. (C and H) Posterior view. (D and I) Aedeagus lateral view. (E and J) Aedeagus dorsal view (vesica everted in E). (K) Everted vesica, lateral view.

mon character state also occurring in *Hypoleria lavinia* (Hewitson, [1855]) (Willmott and Freitas 2006).

Discovery that *Pachacutia* members do not belong in *Godyris* does not by itself justify description of a new genus, because an existing genus might become paraphyletic or inclusion in another genus might be appropriate. However, neither of these two considerations apply. Both *Mcclungia* (monotypic) and *Brevioleria* are clearly monophyletic, with the latter supported by several convincing synapomorphies (Willmott and Freitas 2006). Although these last two genera and *Pachacutia* also are closely related to *H. adasa* and several other *Hypoleria* species, *Hypoleria* as currently recognized is clearly paraphyletic, without any evidence that the type species, *H. lavinia*, is even sister to the *Mcclungia* clade (see below). The *Hypoleria* species within the *Mcclungia* clade therefore already require reclassification. Given that the kinds of characters used to identify ithomiine genera (male DHW hair pencil, androconia, and venation) all differ between *Pachacutia* and other *Mcclungia* clade members (so much so that *Pachacutia* species were treated in *Godyris* until now) and that there are marked

ecological differences between *Pachacutia* and its related genera (see below), we feel description of a new genus is appropriate.

Cladistic analyses found *H. lavinia*, the type of the genus, to be sister to a clade containing *Greta* Hemming, 1934 and *Pseudoscada* Godman & Salvin, 1879, although this relationship is only very weakly supported (Willmott and Freitas 2006). *H. lavinia* shares very similar genitalia with *H. alema* (Hewitson, [1857]), *H. xenophis* Haensch, 1909, and *H. mulviana* D'Almeida, 1958 [the latter regarded as a subspecies of *H. lavinia* by Lamas (2004)], and it seems likely that these four species form a clade. Unfortunately, there is yet no evidence that the remaining *Hypoleria* species in the *Mcclungia* clade (*H. adasa*, *H. ocalea*, *H. sarepta*, and *H. aureliana*) form a monophyletic group, for which *Pigritina* Hedicke, 1923 (type species *Ithomia adasa* Hewitson) would be available as a generic name. The relationships of *H. aureliana* are particularly unclear, because it has genitalia typical of the *Mcclungia* clade but wing androconia similar to *H. lavinia*, and it may prove to be sister to remaining

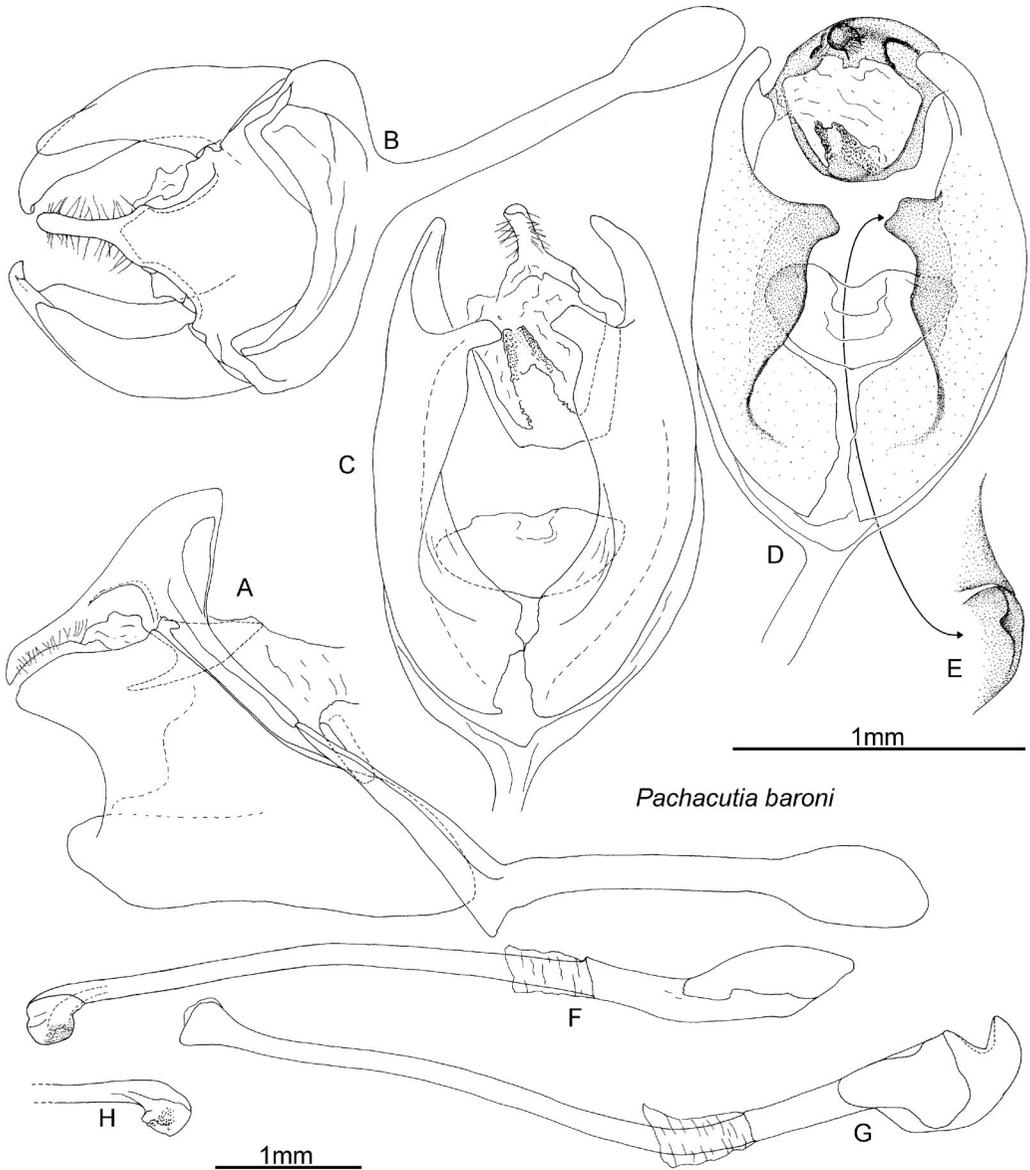


Fig. 6. Male genitalia, *Pachacutia baroni* n. sp. (A) Lateral view. (B) Dorsal view. (C) Ventral view. (D) Posterior view. (E) Valva ventral flange, interior view. (F) Aedeagus lateral view. (G) Aedeagus dorsal view. (H) Posterior tip of aedeagus, lateral view (left side).

members of the *McClungia* clade. There is, then, clearly work to be done in unraveling the relationships among these species and establishing a stable natural classification.

Phylogeny. In total, 23 characters (21 parsimony informative) were coded from the antenna, wing pattern and venation, male androconia, and genitalia of both sexes (Tables 2 and 3). A single, fully resolved most parsimonious tree was recovered, of length 32 steps (CI = 0.79, RI = 0.80), with *Brevioleria aelia plisthenes* + *Hypoleria adasa* sister to *Pachacutia* (Fig. 14). *Pachacutia* species were related as follows: (*P. baroni* + (*P. mantura* + (*P. cleomella* + *P. germaini*))).

Only the relationship (*mantura* + (*cleomella* + *germaini*)) was not strongly supported, although the distinctive hindwing venation (char 8:1, short discocellular vein Cu_1-M_3) is a convincing synapomorphy. Characters supporting other nodes are given on Fig. 14, with reference to Table 2.

Distribution and Natural History. *Pachacutia* occur exclusively in premontane to montane rain forest habitats in the eastern Andes from ≈ 500 to 2,500 m. The genus ranges from southern Ecuador (Morona-Santiago, Zamora-Chinchipe) to Bolivia, with its center of diversity in southern Peru (Cuzco, Puno) and Bolivia (La Paz), where three of the four species occur. All

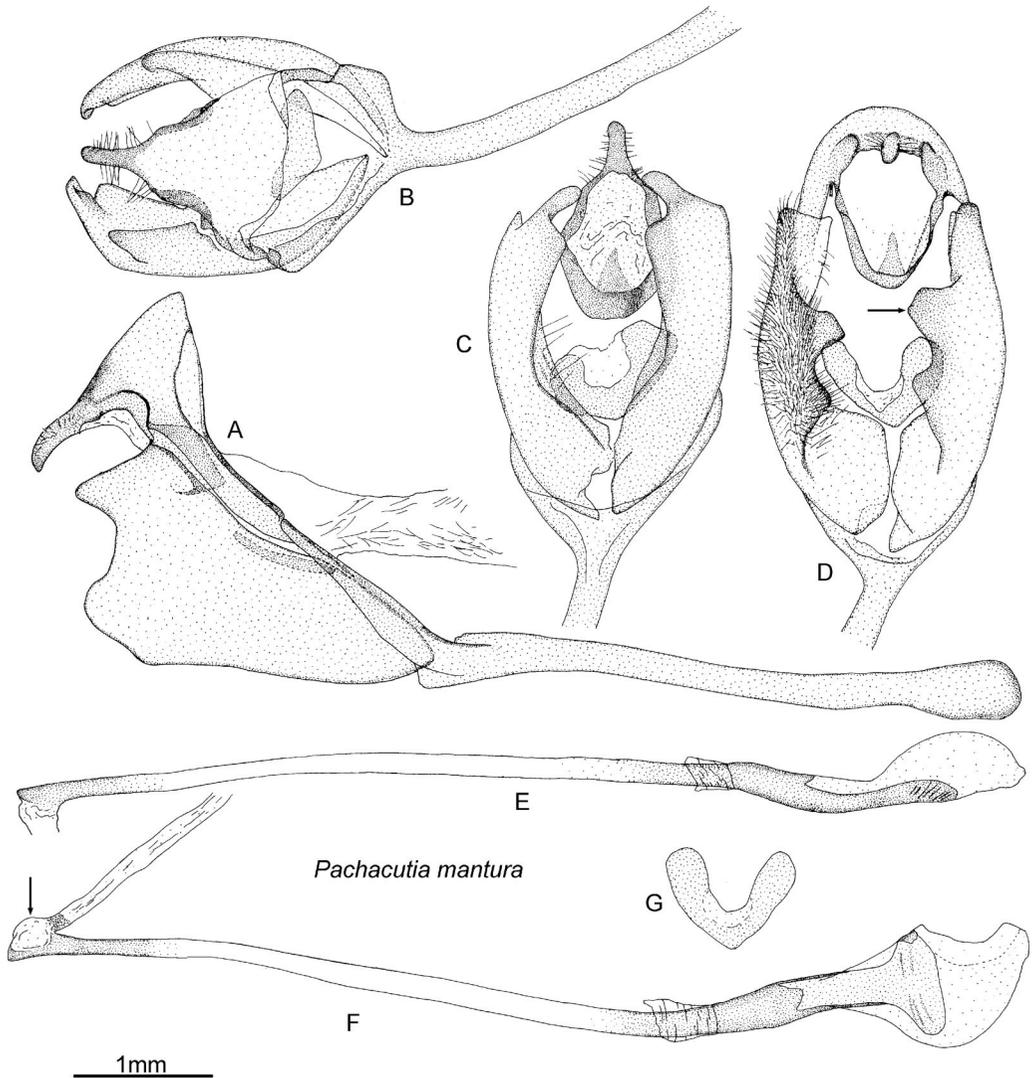


Fig. 7. Male genitalia, *Pachacutia mantura honrathi*. (A) Lateral view. (B) Dorsal view. (C) Ventral view. (D) Posterior view. (E) Aedeagus lateral view. (F) Aedeagus dorsal view, vesica everted. (G) Juxta.

species in the genus are extremely rare in collections (only 75 specimens examined, including 37♂ and 38♀) and in the field, contrasting strongly with their lowland forest relatives, which are often abundant. The only species for which we have any field observations, *P. cleomella* and *P. baroni*, have only been found inside undisturbed forest (see under those species). The larval host plants and immature stages are not known for any species.

All species are strongly mimetic of other ithomiines, especially in the tribes Dircennini and Godyradini and the genus *Methona*. Although the southern Andean species are members of relatively large mimicry rings, *P. baroni* is the third known member of a highly distinctive complex composed of exceptionally accurate mimics. There is some evidence that *Pachacutia* species overlap little in elevation, and they therefore tend to mimic different suites of species, with *P. mantura*

and *P. germaini* occurring at relatively lower elevations, *P. cleomella* the highest flying member, and *P. baroni* confined to a narrow band in the middle of the generic elevational range.

Species Accounts

Pachacutia Willmott & Lamas, n. gen.

Type Species. *Ithomia mantura* Hewitson, 1876.

baroni Willmott & Lamas, n. sp.
mantura (Hewitson, 1876) (*Ithomia*) n. comb.
-honrathi (Srnka, 1885) (*Ithomia*) n. comb.
-barrettii (Dannatt 1900) (*Dircenna*) n. comb.
-joroni Lamas & Willmott, n. ssp.
cleomella (Hewitson, 1874) (*Ithomia*) n. comb.
germaini Lamas & Willmott, n. sp.

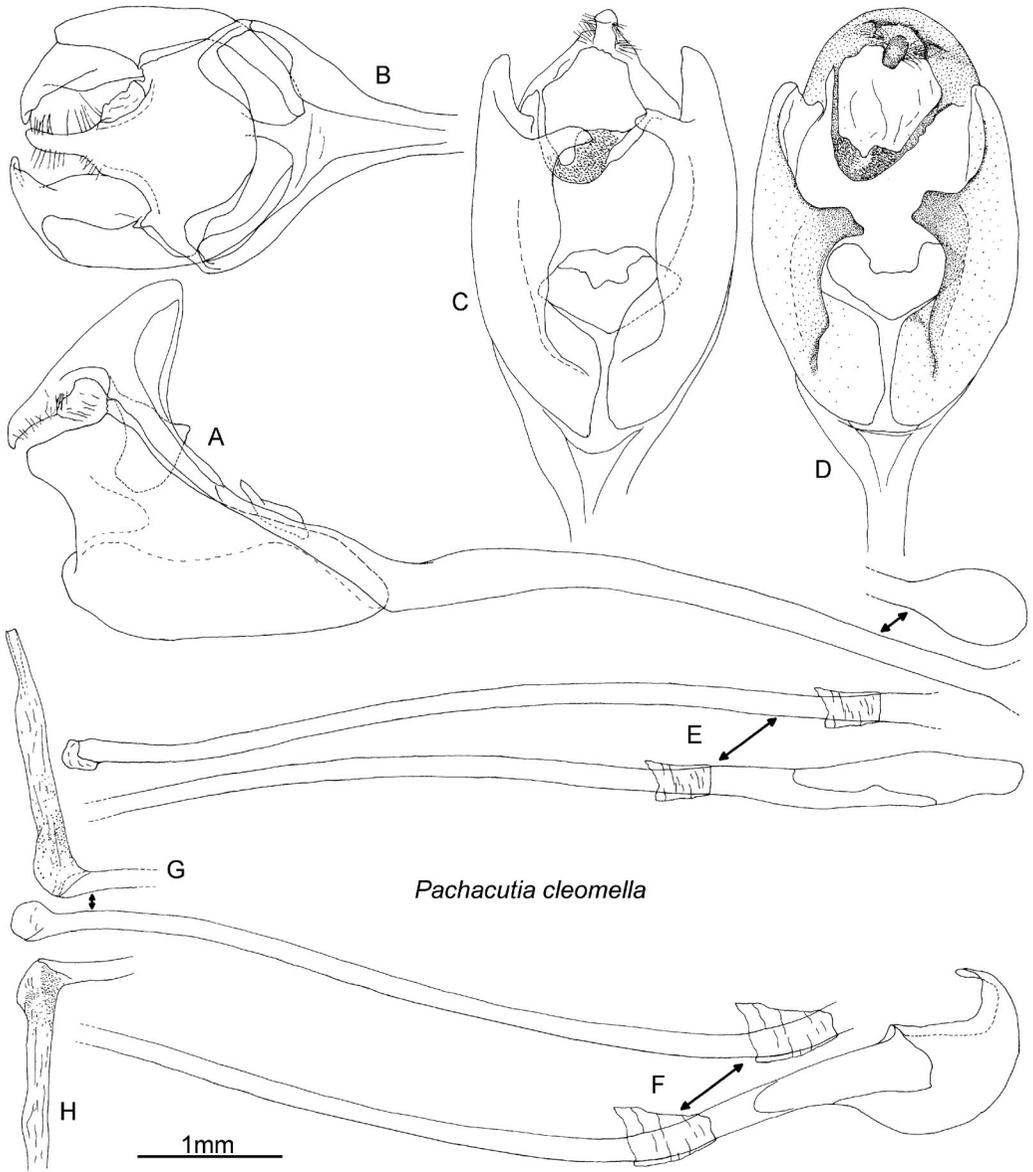


Fig. 8. Male genitalia, *Pachacutia cleomella*. (A) lateral view. (B) Dorsal view. (C) Ventral view. (D) Posterior view. (E) Aedeagus lateral view. (F) Aedeagus dorsal view, vesica not everted. (G) Posterior tip of aedeagus, dorsal view, vesica everted. (H) Posterior tip of aedeagus, ventral view, vesica everted.

Key

1. Hindwing anal margin with basal half translucent yellow or white, with broad black margin at tornus; VHW marginal white spots present 2
- Hindwing anal margin opaque, broad reddish brown from wing base to tornus; VHW marginal white spots absent *baroni*
2. Forewing discal cell without broad (3 mm), opaque black bar across middle (trace of scales or darker shading may be present) . . 3
- Forewing discal cell with broad (3 mm), opaque black bar across middle . . . *mantura mantura*
3. (Male) VHW with white streak at costa in cell Rs-Sc+R₁ near cell end; (Female) DHW with no white spot at base 2A-Cu₂; hindwing with heavy black discocellular bar at discal cell end; DHW marginal white spot in cell Cu₁-M₃ absent or smaller than that in cell Cu₂-Cu₁; forewing with inner edge of distal margin border indented 4
- (Male) VHW without white streak at costa in cell Rs-Sc+R₁ near cell end; (Female) DHW with white spot at base 2A-Cu₂; hindwing without black discocellular bar at discal cell end (slight scaling may be present at anterior

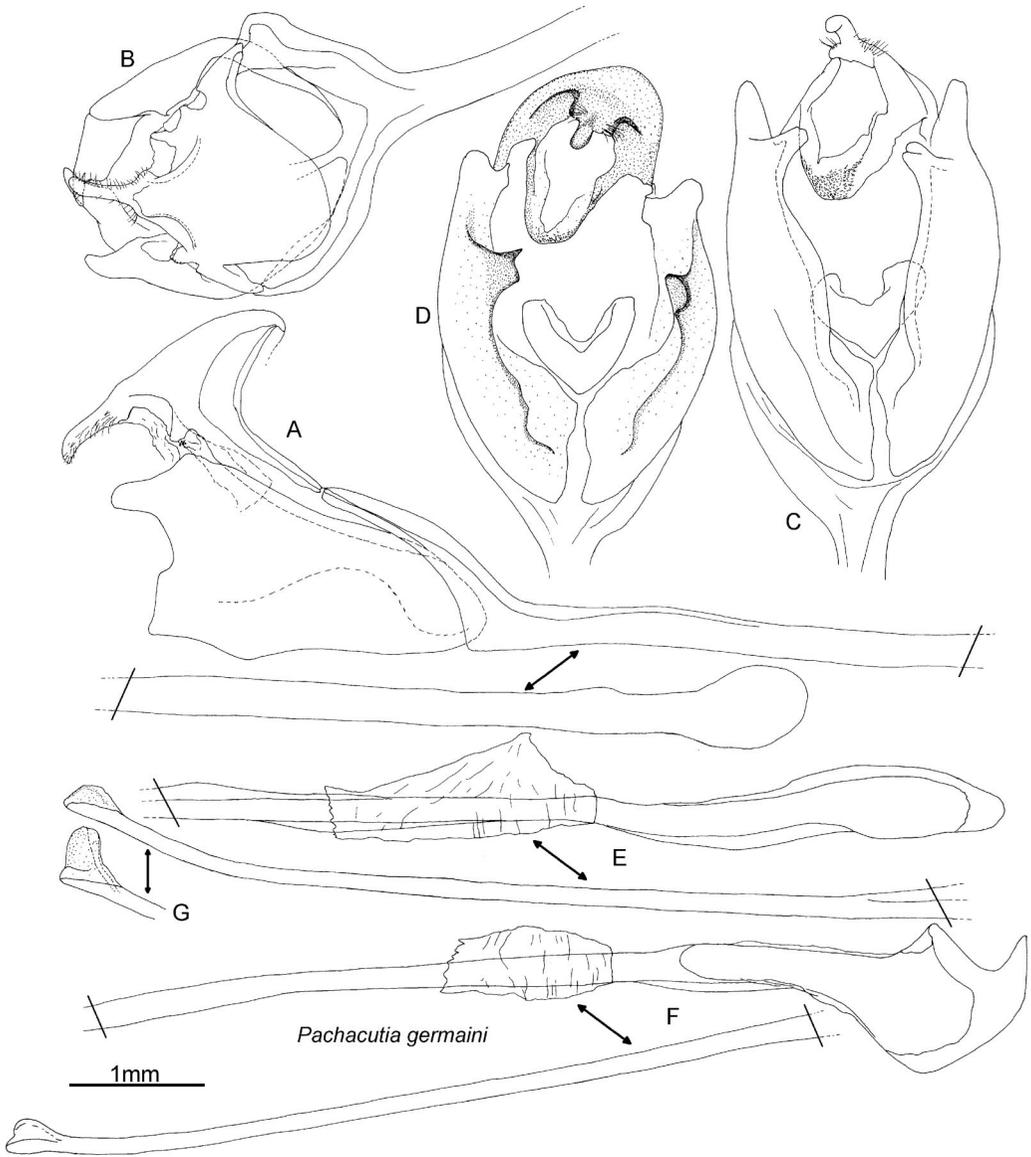


Fig. 9. Male genitalia, *Pachacutia germani* n. sp. (A) Lateral view. (B) Dorsal view. (C) Ventral view. (D) Posterior view. (E) Aedeagus lateral view, vesica not everted. (F) Aedeagus dorsal view, vesica not everted. (G) Posterior tip of aedeagus, lateral view, vesica partially everted.

- tip); DHW marginal white spot in cell Cu_1-M_3 much larger than that in cell Cu_2-Cu_1 , which may be absent; forewing with inner edge of distal margin border even (*mantura*) 5
4. DHW with prominent white marginal spots; hindwing black distal margin broad (4–5 mm) *cleomella*
 DHW with faint or absent white marginal spots; hindwing black distal margin narrow (2–3 mm) *germaini*
5. Forewing with all translucent areas uniform intense yellow; broad black forewing discocellular bar, continuing more narrowly along vein Cu_1 to distal margin . . . *mantura honrathi*

Forewing with all translucent areas yellow, post-discal area of forewing with less intense color than remainder of wing; narrow black forewing discocellular bar, not continuing along vein Cu_1 to distal margin (vein may have slight black scaling) *mantura joroni*

Species Accounts

Pachacutia baroni Willmott & Lamas, n. sp.
 (Figs. 1D and I, 2F, 3A and B, 6, 11A–F, 13A)

Godyris n. sp. Lamas 2004: 189, no. 320.

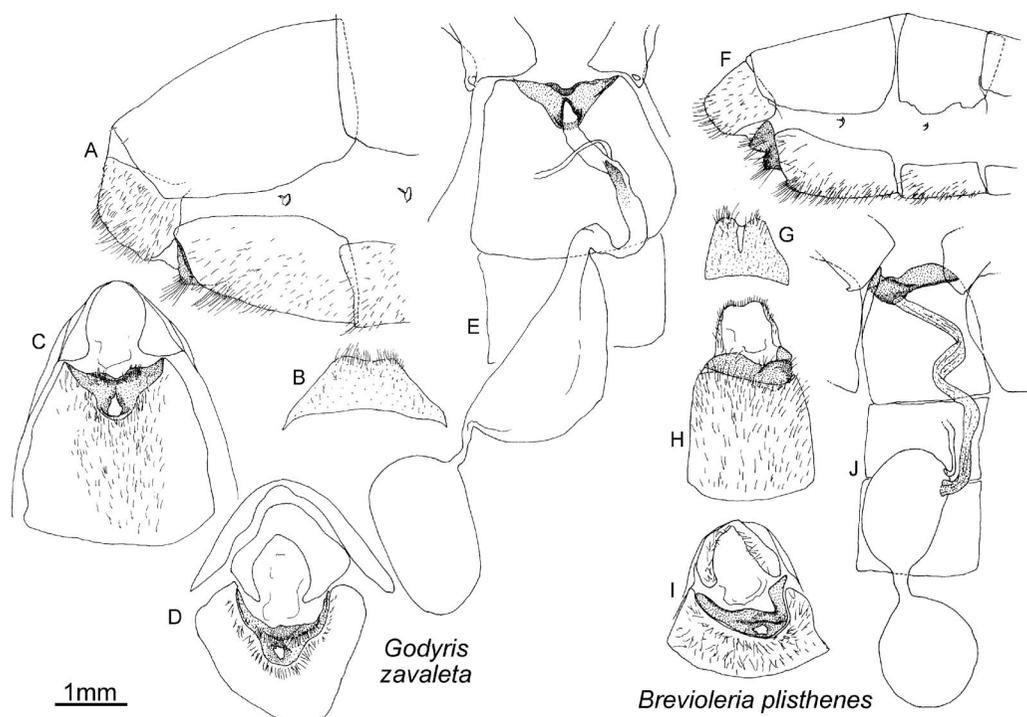


Fig. 10. Female genitalia, outgroup taxa. *Godyris zavaleta telesilla* (Hewitson, 1863), BMNH (A-E), *Brevioleria aelia plisthenes*, UFP (F-J). (A and F) Abdomen terminal sclerites, lateral view. (B and G) Terminal tergite, dorsal view. (C and H) Abdomen terminal sclerites, ventral view. (D and I) Abdomen terminal sclerites, posterior view. (E and J) Genitalia, dorsal view.

Diagnosis and Identification. This species is easily distinguished from all other *Pachacutia* by the distinctive wing pattern (Fig. 3A and B), being much more similar to two other species of Godyridini, *Godyris duillia* and *Greta alphisiboea* (Hewitson, 1869). It is most easily distinguished from both of these by the yellow antennal clubs. The species has the following autapomorphies within *Pachacutia*: FW distal half intense translucent orange, FW veins M_3 - M_1 with heavy dark brown scaling, HW tornus and anal margin broadly red-brown, no ventral white submarginal spots, VHW margins entirely red-brown. Further distinguished from all other species by having saccus relatively short (similar in length to valva), aedeagus relatively short (posterior portion c. two x anterior portion, instead of $>2.3\times$), lamella postvaginalis relatively narrow, male FW vein Mr on 3d, male HW discocellular vein Cu_1 - M_3 relatively long. Some of the latter characters also may prove to be autapomorphies, especially the short saccus and aedeagus.

Description: Male. (Figs. 1D, 2F, 3A, 6). **HOLOTYPE**, FW length 38 mm. **Wings** (Fig. 3A): Elongate triangular, apex rounded, FW anal margin concave. **Dorsal surface** (Fig. 3A): Forewing: Costal and anal margin, and discocellular bar, opaque black; heavy black scaling along veins Cu_1 - M_1 ; thin black distal margin, cell R_5 - R_4 black; distal of discocellulars intense translucent orange, extending into cells R_4 - R_3 , R_3 - R_2 and R_2 - R_1 ; discal cell and basal part of cell

Cu_2 - Cu_1 translucent whitish. Hindwing: Costa and apex opaque black, black extending in from distal margin along veins Cu_1 and M_3 ; anal margin, distal half cell 2A- Cu_2 and distal margin cell Cu_2 - Cu_1 opaque red-brown; remainder of wing translucent whitish except for diffuse yellow submarginal spot in cell Cu_1 - M_3 and streak in cell Cu_2 - Cu_1 . **Ventral surface** (Fig. 3A): Similar to dorsal surface, all opaque markings entirely red-brown except FW basal half costal margin, discocellular bar and veins; no submarginal or marginal white spots. **Androconia** (Fig. 2F): Typical of genus (see generic description). **Venation** (Fig. 1D): Typical of genus (see generic description) except FW medial recurrent vein (Mr) on 3d, not 2d. **Body**: Typical of genus (see generic description) except legs almost entirely black except for white fused tibio-tarsus of foreleg; tegula black with white scaling at anterior lobe and sparsely along posterior projection; thorax dorsal midline white; abdomen mostly black except very sparse lateral white scaling on more anterior tergites and posterior sternites. **Genitalia** (Fig. 6): Typical of genus (see generic description) except valva upper lobe relatively large; uncus near to valva upper edge in lateral view; gnathos ventral portion indistinctly sclerotized, blunt, posteriorly elongate; saccus relatively short (similar to valva); aedeagus correspondingly short (similar to valva + saccus), posterior section slightly curved ventrally (in lateral view) and sharply bent to left just posterior of zone (junction

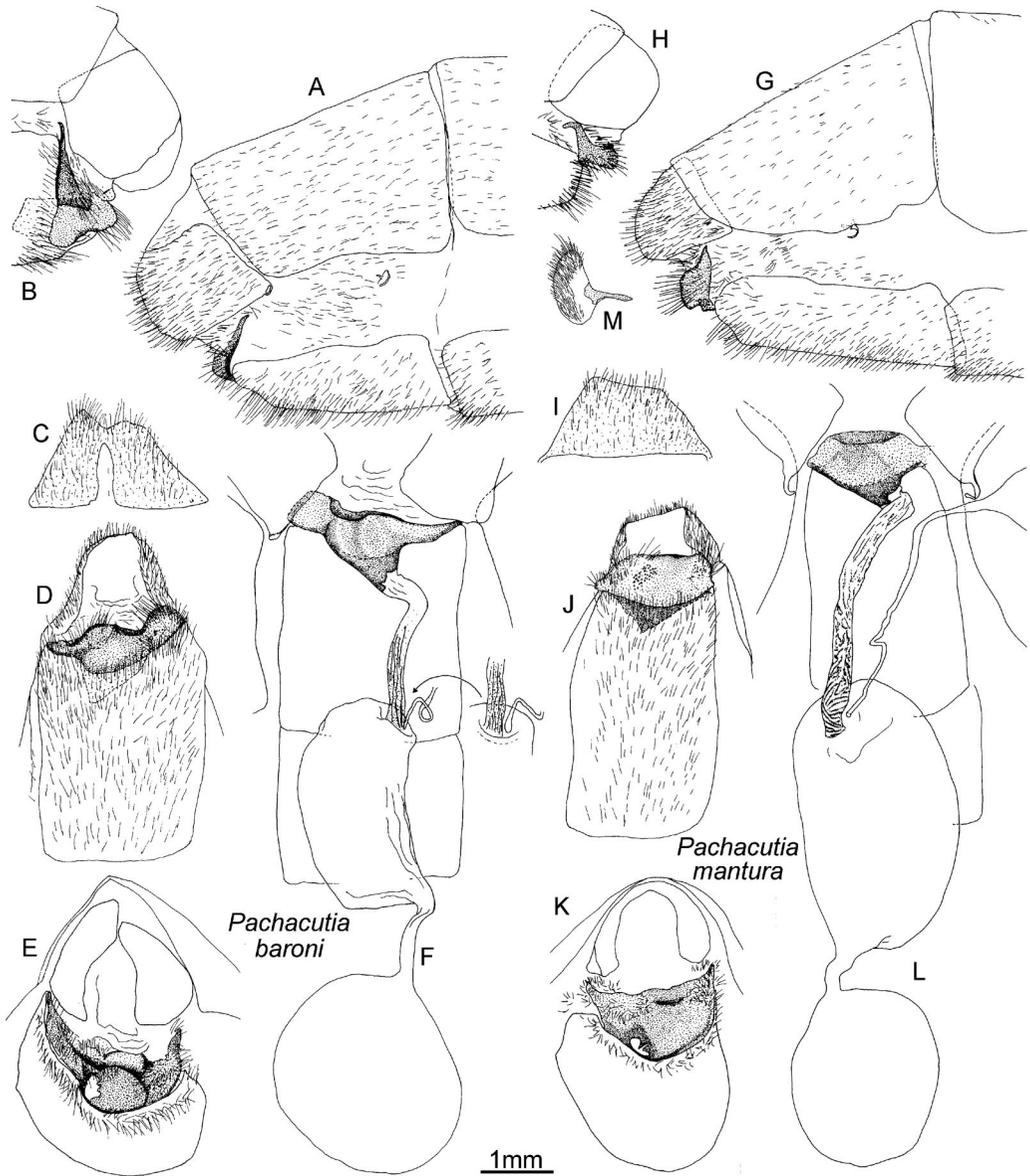


Fig. 11. Female genitalia, *Pachacutia baroni* n. sp. (A-F) and *P. mantura honrathi* (G-M). (A and G) Abdomen terminal sclerites, lateral view (right). (B and H) Abdomen terminal sclerites, lateral view (left). (C and I) Terminal tergite, dorsal view. (D and J) Abdomen terminal sclerites, ventral view. (E and K) Abdomen terminal sclerites, posterior view. (F and L) Genitalia, dorsal view; M, papilla analis, lateral view.

between anterior and posterior parts of aedeagus) (in dorsal view); cornuti tiny, apparently encircling vesica near base.

Female. (Figs. 11, 3B, 11A-F). **PARATYPE**, FW length 38 mm. Differs from male as follows. **Wings** (Fig. 3B): Slightly more rounded. **Androconia**: Absent. **Venation** (Fig. 11): Typical of genus (see generic description), FW medial recurrent vein (Mr) on 2d. **Genitalia** (Fig. 11A-F): Typical of genus (see generic description) except terminal tergite almost entirely medially desclerotized; eighth sternite plates on right narrow and detached from seventh sternite, seventh

sternite asymmetrical in ventral view; antrum still a visible tube, not completely merging with eighth sternite plates; ductus bursae becoming internally sclerotized near junction with corpus bursae; ductus seminalis arising directly from corpus bursae near junction with ductus bursae.

Type Material. **HOLOTYPE**: ♂. ECUADOR, *Zamora-Chinchi*: Zamora [4° 04' S, 78° 58' W], 3,000-4,000 feet (O.T. Baron) (BMNH).

Etymology. This species is named for Oscar Theodor Baron (1847-1926), collector of the holotype and first known specimen, in recognition of the pioneering

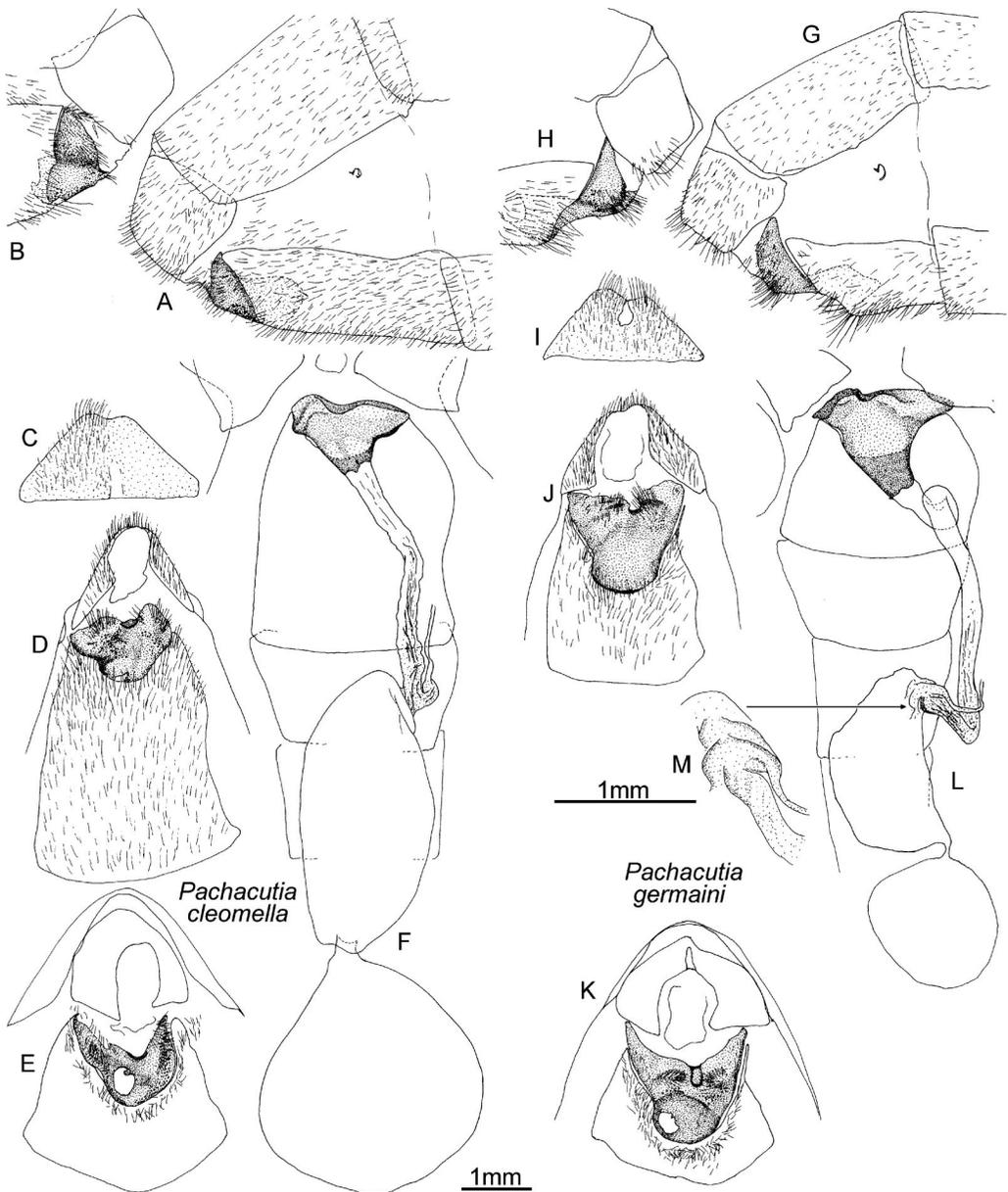


Fig. 12. Female genitalia, *Pachacutia cleomella* (A–F) and *P. germaini* n. sp. (G–L). (A and G) Abdomen terminal sclerites, lateral view (right). (B and H) Abdomen terminal sclerites, lateral view (left). (C and I) Terminal tergite, dorsal view. (D and J) Abdomen terminal sclerites, ventral view. (E and K) Abdomen terminal sclerites, posterior view. (F and L) Genitalia, dorsal view. (M) Junction of ductus bursae and corpus bursae.

and important collections that he made in southern Ecuador.

Discussion. This species is the sister to the remaining three species in the genus, and it is not known to be sympatric with any of them. *Pachacutia baroni* is superficially very different in wing pattern from other members of the genus, although the thoracic markings and yellow antennal clubs, which are common features of the genus and of species mimicked by other *Pachacutia* (e.g., *Dircenna* and *Methona*), but not by this species, suggests that it has diverged

sharply from the ancestral mimicry pattern. This divergence may have been driven by an upward shift in elevational range, removing *P. baroni* from the communities of co-mimics in which other members of the genus occur.

Range, Habitat, and Adult Ecology. This species is known to date only from the southeast Ecuadorian Andes in the provinces of Morona-Santiago and Zamora-Chinchipec, although it certainly should occur in northern Peru in the Cordillera del C6ndor (Amazonas), if not further south. All modern specimens

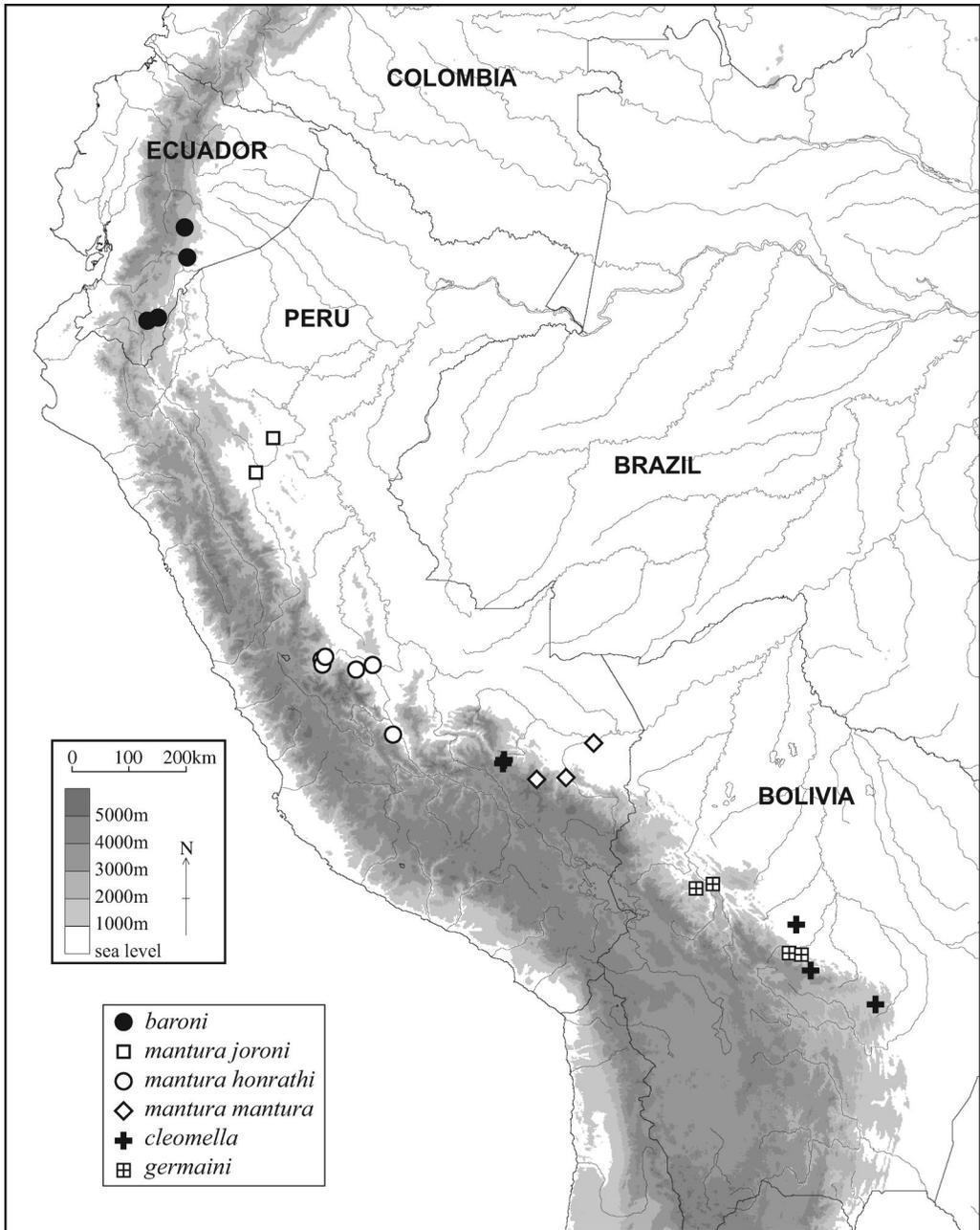


Fig. 13. Locality records for *Pachacutia* species.

have been collected along ridge tops in primary forest in a narrow elevational range, from 1,340 to 1,600 m. Even in such localities, the species is apparently very rare, and single individuals may be encountered flying 1–2 m above the ground in the forest interior. *P. baroni* is a remarkable mimic of *G. duillia* (Colombia to Bolivia) and *Greta alphasiboea* (eastern Ecuador and northern Peru), both of which are much more common in the same habitats and elevational range.

Specimens Examined. (5♂, 2♀). ECUADOR: *Morona-Santiago*: Río Abanico [2° 08' S, 78° 12' W], 1,600 m (P. Boyer), 6-XII-1998, 1♀ [PT *baroni*] (PB); Santa Cruz-Nambija, Cordillera de Nanguipa [4° 00' S, 78° 45.48' W], 1,600–2,000 m (P. Boyer), 30-XI-1998, 1♂, 1♀ [PT *baroni*] (PB), 30-XI-1998, 2♂ [PT *baroni*] (GTB); Yakunk-Cutucú trail, lower ridge [2° 45.66' S, 78° 09.66' W], 1,340–1,400 m (G. Mankash, K. Willmott), 5-XII-2003, 1♂ [PT *baroni*] (KWJH); *Zamora-Chinchipe*: Zamora [4° 04' S, 78°

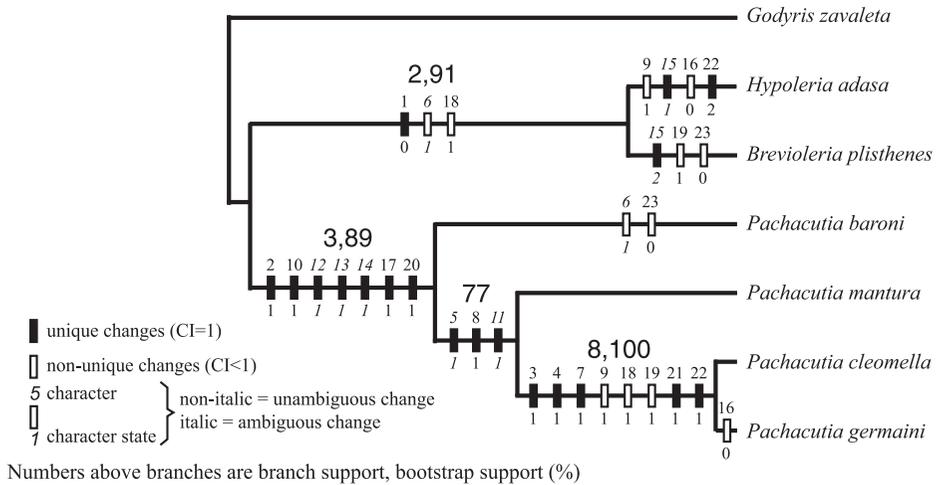


Fig. 14. Single most parsimonious tree illustrating relationships among *Pachacutia* species. See text for details of character optimization.

58' W] (O.T. Baron), 1♂ [“3,000–4,000 feet”; HT *baroni*] (BMNH).

***Pachacutia mantura* (Hewitson, 1876)**
(Figs. 1E and J, 2A and B, G, J, K, 3C–H, 7, 11G–M, 13)

Identification and Taxonomy. Males of *P. mantura* are most easily distinguished from similar congeners by the lack of a white costal streak on the VHw, and females by the first two of the following autapomorphies. The species has the following autapomorphies within *Pachacutia*: female DHW with white spot at base 2A-Cu₂; female DHW with submarginal spot in cell Cu₁-M₃ larger than that in cell Cu₂-Cu₁; posterior portion of tegumen relatively broad; gnathos forming a well-defined, posteriorly pointed ventral projection; ventral edge of valva produced into a second lobe anterior of main posterior lobe; posterior edge of seventh sternite smoothly curving, not indented. A further distinguishing character is the moderately long aedeagus and saccus (longer than *P. baroni*, but shorter than other species). The species is sister to *P. cleomella* + *P. germaini* (Fig. 14).

Range. Northern Peru (Amazonas) to Bolivia, from ≈300–1,500 m.

Specimens Examined. Forty one (16♂, 25♀).

Pachacutia mantura mantura
(Hewitson, 1876), n. comb.
(Figs. 3C and D, 13)

Ithomia mantura. Hewitson 1876: [26], pl. [13], fig. 237. Type locality: Bolivia. Lectotype (designated here) ♀, “Mantura Hew.//Type//Holo-type//SYN-TYPE//SYNTYPE *Ithomia mantura* Hewitson, 1876 det. W. J. Reynolds 1994//B.M. TYPE No. Rh. 7266 *Ithomia mantura*, ♀ Hew.//Bolivia Hewitson Coll. 79. 69. *Ithomia mantura*.1.”, BMNH.

Ithomia mantura. Kirby 1877: 696; Kirby 1879: 41; Riley and Gabriel 1925: 32.

Dircenna mantura. Haensch 1909: 139, pl. 36 g, fig. [2]; Bryk 1937: 547; Fox 1940: 197; Lewis 1973: 228; D’Almeida 1978: 286.

Godyris mantura mantura. Mielke and Brown 1979: 176; D’Abbrera 1984: 272, fig.; Lamas 2004: 189.

Identification and Taxonomy. Distinguished from the other two subspecies by the broad black FW discal cell bar and heavier black HW discocellular scaling. The translucent color varies from pale greenish yellow (e.g., Fig. 3C) to almost white (e.g., Fig. 3D). Hewitson (1876) described this species from an unspecified number of female specimens collected by C. Buckley in his own collection, and the single female Hewitson specimen now in the BMNH, closely matching the original color figure, is designated here as lectotype. Haensch (1909) transferred the species to *Dircenna*, presumably based on the wing pattern similarity to several species in that genus. Mielke and Brown (1979) then transferred it to *Godyris*, presumably based on the large size and single hindwing hair pencil.

Range, Habitat, and Adult Ecology. This subspecies occurs from southern Peru (Cuzco, Puno) to Bolivia, presumably the department of La Paz, from 650 to 1,400 m. The records from “Tingo María” and “Acomayo”, in Huánuco, Peru (see below), are most likely erroneous. It is superficially very similar to and apparently involved in mimicry with a number of sympatric ithomiines, in particular, several species in *Methona* and *Dircenna*.

Specimens Examined. (4♂, 6♀). BOLIVIA: *No specific locality*: “Bolivia” ([C. Buckley]), 1♀ [LT *mantura*] (BMNH). PERU: *Cuzco*: Marcapata [13° 26' S, 70° 55' W], 1,425 m, 1♀ (BMNH), 1♂ (MUSM); San Lorenzo, Marcapata, 400–1,000 m, VI-1995, 1♀ (GTB); *Huánuco*: Acomayo [9° 48' S, 76° 04' W]-(dubious), 15-II-1998, 1♂ [“2,500 m”] (GTB); Tingo María [9° 18' S, 76° 00' W]-(dubious), 650 m (M. Büche), 3-XII-1986, 1♀

(GTB); Tingo María [9° 18' S, 76° 00' W]-(dubious), 800 m 1♀ (MUSM); *Puno*: Río Inambari [12° 43' S, 69° 44' W], 1,000 m (Watkins), 1918, 1♂ (BMNH); Río San Gabán [13° 24' S, 70° 18' W], 4-IV-1997, 1♂ (GTB); *No specific locality*: "Peru", 1♀ (BMNH).

Pachacutia mantura honrathi

(Srška, 1885), n. comb.

(Figs. 1E and J, 2A, B, G, J, K, 3E and F, 7, 11G-M, 13)

Ithomia honrathi Srška, 1885: 125, pl. 1, Fig. 4. Type locality: Peru, [Junín], Río Chanchamayo. Holotype ♀, Peru, [Junín], Chanchamayo (O. Schunke), 1882, BMNH.

= *Dircenna barrettii*. Dannatt 1900: 299, fig. Type locality: Peru, [Junín], Perené. Lectotype (designated here) ♂, Peru (Lloyd), BMNH.

Hymenitis barrettii. Lathy 1901: 10.

Dismenitis barrettii [sic]. Haensch 1903: 207.

Dircenna honrathi. Haensch 1909: 139, pl. 36 g, fig. [1]; Bryk 1937: 545; Fox 1940: 197; D'Almeida 1978: 283.

Dismenitis dircenna barrettii [sic]. Haensch 1910: 162.

Godyrus dircenna barrettii. Bryk 1937: 627.

Godyrus barrettii. D'Almeida 1978: 338.

Godyrus honrathi. Mielke and Brown 1979: 196.

Godyrus mantura honrathi. D'Abbrera 1984: 272, fig.; Lamas 2004: 189.

Identification and Taxonomy. Distinguished from other subspecies in the accounts of those taxa. Srška (1885) described this subspecies based on a single female specimen from Peru, Chanchamayo, and the holotype is in the BMNH. Fifteen years later, and apparently unaware of Srška's description and figure, Dannatt (1900) described the same taxon as *Dircenna barrettii*, based on an unspecified number of male specimens, one of which was clearly figured; this specimen is in the BMNH and is designated as lectotype. Shortly thereafter, Lathy (1901) moved *barrettii* to *Hymenitis* Hübner, 1816 (now recognized as a homonym), stating that the merging of veins M₁ and R_s near the hindwing apex was similar to *G. zavaleta*, then placed in the same genus. It is true that this character is a synapomorphy for *Godyrus*, but it is not present in *P. mantura*, the veins being merely close together. Presumably based on Lathy's note, Haensch (1903) moved *barrettii* into his new genus *Dismenitis* (a synonym of *Godyrus*), so it is rather ironic and somewhat perplexing that he shortly afterwards (Haensch 1909) transferred Srška's earlier name *honrathi* to *Dircenna*. Thus, the two names remained in different genera until Mielke and Brown (1979) also placed *honrathi* in *Godyrus*, but their synonymy seems to have gone unnoticed until D'Abbrera (1984). This history of confusion was presumably due to a lack of specimens for examination, with authors seldom providing any explanation for these changes in classification.

Range, Habitat, and Adult Ecology. This subspecies is the most common *Pachacutia* taxon in collections, and it occurs in central Peru (Ayacucho, Junín) from ≈600 to 1,500 m. Sympatric co-mimetic ithomiines

include *Dircenna adina* (Hewitson, [1855]), *Pteronymia ozia* (Hewitson, 1870), *P. tamina* Haensch 1909, *Pagyrus priscilla* Lamas, 1986 and *Oleria canilla* (Hewitson, 1874).

Specimens Examined. (7♂, 15♀). PERU: *Ayacucho*: La Mar [Hacienda] Candalosa [12° 35' S, 73° 52' W], 1,300 m (F. Woytkowski), 17 and 22-VI-1941, 1♂, 1♀ (CMNH); *Junín*: "Oroya", [= La Oroya]-(error), 1♂ (BMNH); Chanchamayo [11° 04' S, 75° 19' W] (Hoffmanns), VI-VIII-1901, 1♀ (BMNH) (O. Schunke), 1882, 1♀ [HT *honrathi*] (BMNH); Chanchamayo [11° 04' S, 75° 19' W], 750-1,250 m (F. König), 22-IX-1957, 1♂ (ZSBS); La Merced [11° 03' S, 75° 19' W], 790 m, 1♀ (MUSM) (Watkins & Tomlinson), V-VI-1903, 5♀ (BMNH); Montaña, Perené Dist[ri]ct (A.G. Duff), "≈1905", 1♀ (BMNH); Río Colorado [10° 58' S, 75° 18' W], 610-760 m (Watkins & Tomlinson), VIII-1903, 1♂ (BMNH); Río Perené [11° 09' S, 74° 18' W] (Simons), III-1900, 1♀ (BMNH); San Francisco, Chanchamayo [11° 02' S, 75° 22' W], 1,500 m, 1♀ (KSB); San Ramón [11° 08' S, 75° 21' W] (F. König), 23-IX-1957, 1♀ (MUSM); Satipo [11° 15' S, 74° 38' W], 1998, 1♂ (GTB); Satipo [11° 15' S, 74° 38' W], 600-700 m, 1♀ (GTB); Valle de Chanchamayo [11° 03' S, 75° 19' W] (F. König), 10-VIII-1960, 1♂ (MUSM); *No specific locality*: "Peru", 1♀ (MGCL) (Lloyd), 1♂ [LT *barrettii*] (BMNH).

Pachacutia mantura joroni Lamas &

Willmott, n. ssp.

(Fig. 3G and H)

Godyrus mantura n. ssp. Lamas 2004: 189.

Description and Diagnosis. HOLOTYPE: ♂, FW length 34 mm. This new subspecies is most similar to the neighboring *P. mantura honrathi*, but it differs from it in having narrow dark margins and discocellular bars, with the latter being absent on the HW, and less intense yellow coloring in the translucent postdiscal areas of both wings anterior of vein Cu₂.

Type Material. HOLOTYPE: ♂, PERU, [San Martín]: Tarap[oto] [6° 29' S, 76° 22' W, 350 m] (MUSM).

Etymology. This taxon is named for Mathieu Joron, in recognition of his significant contributions to knowledge of the ithomiines of San Martín.

Taxonomy and Variation. There is little variation among the few specimens examined.

Range, Habitat, and Adult Ecology. This subspecies occurs in northern Peru (Amazonas, San Martín) from 300 to 1,500 m. It seems to be involved in mimicry with *Dircenna adina*, *D. dero* (Hübner, 1823), *D. loreta* Haensch, 1903, *Pteronymia ozia*, and *P. teresita* (Hewitson, 1863).

Specimens Examined. (6♂, 4♀): PERU: *Amazonas*: "Rodríguez de Mendoza", [=Mendoza] [6° 24' S, 77° 29' W]-(dubious), 1,500 m, 25-XII-1999, 1♂ [PT *joroni*] (GTB); *San Martín*: environs de Juanjui [7° 11' S, 76° 44' W], 400-800 m, IX-2003, 1♀ [PT *joroni*] (OD); Juanjui [7° 11' S, 76° 44' W], 300 m, 10-VI-1999, 1♀ [PT *joroni*] (GTB), 15-VIII-1999, 1♀ [PT *joroni*] (GTB), 17-X-1999, 1♀ [PT *joroni*] (GTB), 20-VII-

1999, 1♂ [PT *zoroni*] (GTB), 22-V-1999, 1♂ [PT *zoroni*] (GTB); Sacanchillo, Juanjui [$\approx 7^{\circ} 11' S$, $76^{\circ} 44' W$], 1,000 m (A. Calderón), 10-XI-1999, 1♂ [PT *zoroni*] (FV); Tarapoto [$6^{\circ} 29' S$, $76^{\circ} 22' W$], 350 m, 1♂ [HT *zoroni*] (MUSM) (M. Rodríguez), X-2005, 1♂ [PT *zoroni*] (MUSM).

Pachacutia cleomella (Hewitson, 1874), n. comb.

(Figs. 1F and K, 2H, 4A and B, 8, 12A–F, 13)

Ithomia cleomella Hewitson, 1874a: [19], pl. [10], fig. 210. Type locality: Bolivia. Lectotype (designated here) ♀, “Holo-type//Type//SYN-TYPE//SYN-TYPE *Ithomia cleomella* Hewitson, 1874 det. W. J. Reynolds 1994//B.M. TYPE No. Rh. 7504 *Ithomia cleomella*, ♀ Hew./Bolivia Hewitson Coll. 79. 69. *Ithomia cleomella*.2.”, BMNH.

Ithomia cleomella. Hewitson 1874b: 5; Kirby, 1877: 696; Kirby, 1879: 43; Riley and Gabriel 1925: 13.

Dismenitis cleomella. Haensch 1910: 163.

Godryris cleomella. Bryk 1937: 626; Lewis 1973: 228; D’Almeida 1978: 338; Mielke and Brown 1979: 174; D’Abrera 1984: 272–273, fig.; Lamas 1999: 6, 12, pl. 15, fig. 9; Lamas 2004: 189.

Identification and Taxonomy. Males of this species are distinguished from *P. mantura* by the white VHW costal streak, females by the entire series of DHW white submarginal spots, and both sexes by the yellowish VFW costa adjacent to the discal cell. The species is distinguished from *P. germaini* by the much broader black HW marginal markings, white submarginal spots, and discocellular bar. The species has no easily defined autapomorphies, although the relative length of aedeagus and saccus, and shape of the fused eighth sternite plates and antrum, are unique within the genus. Hewitson (1874a) described and figured this species based on an unspecified number of female specimens from Bolivia, collected by C. Buckley in his own collection. The single female in the BMNH matches the description and figure in all respects and is designated here as lectotype. Without any discussion Haensch (1910) moved the species into *Dismenitis* Haensch, 1903, a subjective junior synonym of *Godryris*, in which genus it has remained until now.

Range, Habitat, and Adult Ecology. This very rare species occurs from southern Peru (Cuzco) to Bolivia, from 2,150 to 2,500 m. The female from Quebrada Morro Leguía, Peru, was collected inside primary montane forest along a small mountain stream. It is sexually dimorphic in mimicry pattern, with males apparently mimicking *P. germaini* and other co-mimics listed under that species, and female co-mimics including *Oleria deronda* (Hewitson, 1876), *O. derondina* (Haensch 1909), and *Veladyris pardalis cytharista* (Hewitson, 1874).

Specimens Examined. (8♂, 5♀). BOLIVIA: *Cochabamba*. Chaparé, Yungas del Palmar [$16^{\circ} 30' S$, $65^{\circ} 30' W$], “600–1,000 m”, (Schönfelder), 2-IX-1948, 1♂, 1♀ (ZSBS); Sihuencas, Yungas de Arepucho [$17^{\circ} 27' S$, $65^{\circ} 13' W$], 2,200–2,500 m (W. Forster), 25-IX-1953, 1♀ (ZSBS); *Santa Cruz*: “Ost-Cordillere bei Santa Cruz”

(Herzog), 1♂ (ZSBS); Samaipata [$18^{\circ} 09' S$, $63^{\circ} 52' W$], 1,500–2,500 m (Steinbach), III-1920, 2♂ (CMNH); “Santa Cruz”-(error) (Herzog), 1♂ (ZSBS); *No specific locality*: “Bolivia” ([C. Buckley]), 1♀ [LT *cleomella*] (BMNH). PERU: *Cuzco*: Quebrada Morro Leguía, Cosñipata [$13^{\circ} 08' S$, $71^{\circ} 35' W$], 2,150 m (G. Lamas), 28–30-IX-1989, 1♀ (MUSM); Río Pilcopata [=Río Cosñipata] [$13^{\circ} 10' S$, $71^{\circ} 36' W$], 2,500 m (M. Büche), III-1991, 1♀ (GTB); *No specific locality*: “Peru”, 1♂ (MUSM), 1♂ [“No. 17/275”] (MNRJ). NO LOCALITY DATA: No data, 1♂ [“No. 17/276”] (MNRJ).

Pachacutia germaini Lamas & Willmott, n. sp.

(Figs. 1G and L, 2I, 4C and D, 9, 12G–L, 13)

Godryris n. sp.: Lamas 2004: 189, no. 311.

Diagnosis and Identification. This species is most similar to *P. cleomella* and most easily distinguished by the much narrower black marginal markings and smaller white submarginal spots. It may be distinguished from *P. mantura* in the same way as *P. cleomella*. This species has the following autapomorphies within *Pachacutia*: female seventh sternite reduced in size and strongly indented to accommodate enlarged fused eighth sternite plates and antrum, these being similar in size in ventral view to seventh sternite; saccus and aedeagus highly elongate (saccus $3.2\times$ length valva versus $2\times$ length in *P. cleomella*); aedeagus approximately straight in dorsal view, not bent sharply to left just posterior of zone (junction between anterior and posterior parts of aedeagus); valva relatively elongate.

Description: Male. (Figs. 1G, 2I, 4C, 9). HOLOTYPE, FW length 35 mm. *Wings* (Fig. 4C): Elongate triangular, apex rounded, FW anal margin concave. *Dorsal surface* (Fig. 4C): Forewing: anal, distal and apical margin opaque black, narrow, black slightly extending inwards along veins, narrow black discocellular bar extending to base vein Cu_1 ; costal margin adjacent to discal cell dirty yellowish brown, distal of discal cell translucent yellow in basal half of cell R_4-R_3 and in cells R_3-R_2 and R_2-R_1 ; remainder of wing pale translucent yellowish brown. Hindwing: costal and distal margin opaque black, narrow, broadest in cell $2A-Cu_2$, then Cu_2-Cu_1 and M_3-M_2 , then Cu_1-M_3 , with trace white submarginal spots in cells $2A-Cu_2$ (two spots), and Cu_2-Cu_1 and M_3-M_2 ; narrow black scaling along veins Cu_1 , M_3 and discocellular veins $3d$ and Cu_1-M_3 ; remainder of wing pale translucent yellowish brown. *Ventral surface* (Fig. 4C): Similar to dorsal surface except: white submarginal spots slightly larger on HW, present in FW apex, HW with a white costal streak in cell $Rs-Sc+R_1$ terminating near origin Rs , a yellow, elongate triangle at base of wing on costa and distal margin black with broken reddish brown line along basal edge; FW margins reddish brown (yellowish brown adjacent to discal cell). *Androconia* (Fig. 2I): typical of genus (see generic description). *Venation* (Fig. 1G): Typical of genus (see generic description) except FW medial recurrent vein (Mr) on 2d and relatively long.

Body: Typical of genus (see generic description) except: pale scales on tegula yellowish, not white; thorax with pale yellowish brown dorsal midline; legs black with sparse white ventral scaling on femur of mid- and hindleg, white scaling on coxa and outer edge of foreleg femur when folded; abdomen dorsally dark brown with lateral whitish scaling on segments of anterior half, restricted to anterior portion of more distal segments, and in soft pleural tissue between tergites and sternites; ventrally black except for white lateral scaling along dorsal half of sternites.

Genitalia (Fig. 9): Typical of genus (see generic description) except valva relatively elongate, ventral posterior lobe angular in lateral view; uncus relatively far from valva upper edge in lateral view; gnathos only broadening slightly in ventral portion; gnathos, uncus and tegumen asymmetrical, rotated clockwise in posterior view; saccus very elongate ($\approx 3.2 \times$ length of valva) and aedeagus correspondingly elongate (similar to valva + saccus), posterior section slightly bent dorsally near tip and slightly to right near middle in dorsal view; cornuti tiny or absent (vesica not fully everted).

Female. (Figs. 1L, 4D, 12G-L). **PARATYPES**, FW length 33-34 mm. Differs from male as follows. **Wings** (Fig. 4D): Slightly more rounded, HW costal edge straighter. **Dorsal surface** (Fig. 4D): All dark markings broader. Forewing: discocellular bar extending along Cu_2 - Cu_1 to dark anal margin; trace dark discal cell bar basal of end vein Cu_2 on posterior side of cell. Hindwing: broad black HW discocellular bar extending posteriorly to base vein Cu_1 . **Ventral surface** (Fig. 4D): White submarginal spots more prominent. Forewing: Reddish brown scaling on costal margin adjacent to discocellular bar and in apex. Hindwing: Costa entirely dirty yellowish to reddish brown (no white streak or yellow triangle at base), distal margin with some reddish brown scaling; prominent white apical spot in cell M_2 - M_1 . **Androconia:** Absent. **Venation** (Fig. 1L): typical of the genus (see generic description).

Legs: Forelegs almost entirely black.

Genitalia (Fig. 12G-L): Typical of the genus (see generic description) except terminal tergite only slightly medially desclerotized at posterior edge; eighth sternite plates adjacent to posterior edge seventh sternite on both sides, asymmetrical, entirely fused with antrum to form a broad funnel; seventh sternite short, indented substantially to accommodate antrum; medial dorsal edge of fused eighth sternite plates infolded forming a very narrow semicircular indentation (Fig. 12J); ductus bursae slightly sclerotized anteriorly; ductus seminalis arising from swollen and convoluted base of ductus bursae at junction with corpus bursae.

Type Material. **HOLOTYPE:** ♂. **BOLIVIA:** La Paz: Caranavi [15° 46' S, 67° 36' W], 1,200 m (C. Tello), II-1989 (MUSM).

Etymology. This species is named for Philibert Germain (1827-1913), who collected the earliest known specimens of this taxon.

Discussion. This species is sister to *P. cleomella*, with which it shares a number of synapomorphies (Fig. 14). They seem to be broadly sympatric, as both occur in La Paz and Cochabamba departments, Bolivia, although perhaps at different elevations. Despite their outward similarities there are significant genitalic differences between the two species. There is slight variation among the examined specimens in the intensity of the yellow translucent wing coloration.

Range, Habitat, and Adult Ecology. This species is known only from the Andes of Bolivia (La Paz, Cochabamba), where it seems to fly mainly at $\approx 1,200$ -m elevation, although it is expected to occur in southeastern Peru as well. It seems to be involved in mimicry with male *P. cleomella* and a number of other ithomiine species, in particular *Pteronymia calgria* Schaus, 1902, *P. teresita*, *P. ozia*, *P. t적이다* (Hewitson, 1869), *P. tamina*, *Oleria canilla*, and *Pagyris priscilla*.

Specimens Examined. (7♂, 6♀). **BOLIVIA:** Cochabamba. "5 days north from Cochabamba", 12-IX-1899, 1♂ [PT *germaini*] (MCZ); Yungas del Espíritu Santo [17° 06' S, 65° 40' W] (P. Germain), 1888-1889, 1♀ [PT *germaini*] (BMNH); Yungas del Palmar [17° 08' S, 65° 25' W], 2,000 m (R. Zischka), 8-III-1953, 1♂ [PT *germaini*] (ZSBS); Yungas del Río Bo[o]pi [15° 41' S, 67° 15' W], 700 m (M.A.Z.), 10-IV-1955, 1♂ [PT *germaini*] (MGCL); La Paz: Caranavi area [15° 46' S, 67° 36' W], 1,100-2,100 m (C. Tello), XI-2002, 1♂ [PT *germaini*] (BMNH); Caranavi area [$\approx 15^\circ 46'$ S, $67^\circ 36'$ W], 800-1,800 m (C. Tello), X-2002, 1♂, 1♀ [PTs *germaini*] (GTB); Caranavi [15° 46' S, 67° 36' W], 1,200 m (C. Tello), II-1989, 1♂, 2♀ [HT, PTs *germaini*] (MUSM); Río Bronzini, 700-1,700 m (C. Tello), XII-2001, 1♀ [PT *germaini*] (GTB), I-2002, 1♂ [PT *germaini*] (GTB); No specific locality: "Bolivia" (P. Germain), 1♀ [PT *germaini*] (BMNH).

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