RESEARCH ARTICLE



Aphaereta ceratitivora sp. n. (Hymenoptera, Braconidae), a new parasitoid of Ceratitis capitata (Wiedemann) (Diptera, Tephritidae) from the Azores

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Abstract

A new gregarious larval-pupal endoparasitoid of *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) is described and illustrated: *Aphaereta ceratitivora* **sp. n.** (Braconidae: Alysiinae: Alysiini).

Keywords

Aphaereta ceratitivora, Ceratitis capitata, new species, Azores, gregarious parasitoid

Introduction

In recent years interest in the parasitoid Hymenoptera has grown as a result of the increasing demand for biological methods for pest control and their possible use as natural enemies. The Braconidae are the second largest family of this order, the major-

ity of species are primary parasitoids of immature stages of Lepidoptera, Coleoptera and Diptera (Sharkey 1993).

Ceratitis capitata (Wiedemann, 1824) (Diptera: Tephritidae) or Mediterranean fruit fly (Medfly) is a pest that causes substantial economic losses in the Mediterranean fruit production due to their high dispersal ability and ecological plasticity (Liquido et al. 1991; Gillani et al. 2002). In Azores (Portugal) a survey was done to see if there were possible candidates for the control of *C. capitata*, before considering the introduction of exotic species, that can cause adverse effects on the native parasitoids and non-target species (Oliveira et al. 2008).

From two parasitized pupae of *C. capitata* collected in São Miguel Island (Azores, Portugal) emerged in total 12 adult parasitoids, belonging to a new species of the genus *Aphaereta* Foerster, 1862 (Alysiinae: Alysiini). Six adult parasitoids emerged per pupa; rearing in the lab resulted in four parasitoids per host pupa at 20°C (the optimum temperature for development). The subfamily Alysiinae, with 2321 catalogued species worldwide (Yu et al. 2012) has a prominent position within the Braconidae family (van Achterberg 1993, Dolphin and Quicke 2001) and consists of the tribes Alysiini and Dacnusini. The species of this subfamily are endoparasitoids of dipterous larvae, with oviposition into the egg or the larva of the host and emergence from the host puparium. Wharton (2002) used this character, along with the possession of exodont mandibles, to define the subfamily. Almost all Dacnusini are parasitoids of leaf- and stem-mining dipterans, usually Agromyzidae (Wharton 2002), but Alysiini attacks a wide range of dipterous hosts from at least 20 different families (Wharton 1980).

Description

Aphaereta (A.) *ceratitivora* van Achterberg & Oliveira, sp. n. urn:lsid:zoobank.org:act:6AA4B4C3-1AD2-4453-B9F3-E63425D9302A http://species-id.net/wiki/Aphaereta_ceratitivora

Type material. Holotype, \bigcirc (RMNH), "Portugal: Azores, Ponta Delgada, reared in lab., summer 2010, L. Oliviera, RMNH'11", "ex *Ceratitis capitata* (Wied.)". Paratypes: 19 \bigcirc + 20 \bigcirc (RMNH), with same label data; 10 \bigcirc + 3 \bigcirc (RMNH), "Portugal: Azores, S. Miguel Isl., Vila Franca, 15.x.2008, [reared] in lab. ex pupae of *Ceratitis capitata* (Tephrit.) coll. from *Capsicum annuum*, L. Oliviera, RMNH'09".

Diagnosis. Antenna of \bigcirc with 18–20 segments and 1.1–1.2 times as long as fore wing; pedicellus yellowish-brown, not contrasting with scapus; third antennal segment of \bigcirc dark brown or brown basally and comparatively slender (Fig. 6); outer side of fourth antennal segment of \bigcirc straight or nearly so (Fig. 6); fourth-seventh antennal segments of \bigcirc moderately shiny and dark brown; ventral convex area of side of pronotum moderately narrow and yellowish-brown; medio-posterior depression of mesoscutum absent; wing membrane slightly infuscate; axillar depression narrow to medium-sized and smooth; tegulae brown or dark brown, darker than fore femur;



Figures 1–13. *Aphaereta ceratitivora* sp. n., holotype, ♀. I wings 2 mandible full view of third tooth 3 hind leg 4 apical segments of antenna 5 head anterior 6 basal segments of antenna 7 hind tarsus 8 head dorsal 9 mesosoma dorsal 10 mandible full view of first tooth 11 first metasomal tergite dorsal 12 habitus lateral 13 axillar depression.

ventrally hind basitarsus narrowly acutely protruding postero-ventrally; hind tibia distinctly setose baso-dorsally; hind basitarsus moderately slender and often more or less infuscate; tarsal claws narrow (Fig. 7); median carina of propodeum in lateral view hardly protruding and narrowly lamelliform (Fig. 12); first metasomal tergite strongly widened posteriorly, medially densely and finely rugulose and dark or pale brown (Fig. 11); setose part of ovipositor sheath 0.6 times as long as metasoma and 0.7–0.8 times as long as hind tibia; length of fore wing 1.6–2.4 mm and of body 1.6-2.2 mm.

Description. Holotype, \mathcal{Q} , length of body 1.7 mm, of fore wing 1.8 mm.

Head. Antenna 1.2 times length of fore wing and 1.6 times body (Fig. 12), with 19 segments, setae erect and about 1.3 times as long as width of segment, length of third segment 0.8 times fourth segment (Fig. 6), length of third, fourth and penultimate segments 4.0, 5.0 and 2.6 times their width, respectively; apex of scapus oblique and pedicellus medium-sized (Fig. 6); maxillary and labial palp with 6 and 4 segments, respectively; length of maxillary palp equal to height of head; Ocular Ocellar Line : diameter of posterior ocellus : Posterior Ocellar Line = 8:3:4; frons glabrous and smooth, nearly flat; length of eye in dorsal view 1.7 times the temple (Fig. 8); eyes glabrous except for a few setae; temples parallel-sided behind eyes (Fig. 8); median groove of vertex shallow; face smooth, but medio-ventrally punctulate and somewhat rugulose, with long erect setae; clypeus largely smooth (but somewhat punctate laterally), flattened medially, long, setose, not tuberculate laterally and ventral rim truncate (Fig. 5); epistomal groove rather wide, laterally smooth and distinct (Figs 10, 12); anterior tentorial pits medium-sized (Fig. 5); length of malar space 0.2 times basal width of mandible; mandible largely smooth, hardly widened subapically, its medial length 1.75 times maximum width, second tooth much longer than both other lobe-shaped teeth, without incision between first and second tooth, third tooth with curved carina (Figs 2, 10); head 1.6 times as wide as mesoscutum (Figs 5, 9).

Mesosoma. Length of mesosoma 1.3 times its height; pronope absent, but with a transverse crenulate groove and no antescutal depression; side of pronotum smooth, antero-medially and ventro-posteriorly finely crenulate (Fig. 12), ventral area slightly convex, medium-sized and yellowish-brown; precoxal sulcus only anteriorly and medially moderately crenulate (Fig. 12); mesosternal sulcus wide and coarsely crenulate; metapleuron smooth dorsally and medially, crenulate-rugose ventrally; notauli absent, only anteriorly with horizontal carina (Fig. 9); medio-posterior depression of mesoscutum absent; mesoscutum glabrous (except for a few setae), smooth and with complete lateral carina; scutellar sulcus wide, semi-circular and deep, with one short crenula; axillar depression narrow and rectangular, smooth and rather shallow (Fig. 13); scutellum slightly convex; anteriorly metanotum without median carina and not protruding dorsally (Fig. 12); surface of propodeum mainly smooth dorsally and remainder rather sparsely rugulose (Fig. 9), without lateral protuberance, its median carina moderately protuberant and with narrow triangular medial area (Fig. 9).

Wings. Fore wing: 1-SR normal; 2-SR oblique; r:3-SR:SR1 = 3:16:51; r somewhat widened (about 3 times as long as its own width), 0.7 times width of pterostigma and issued just before middle of pterostigma (Fig. 1); pterostigma narrow, elliptical (Fig.



Figures 14–25. *Aphaereta* spp. 14, 16 head and mesosoma lateral 15, 17 ovipositor sheath 18, 19 hind tarsal claw 20, 21 hind tarsus 22, 23 scutellum, metanotum and propodeum lateral 24 convex ventral part of pronotal side 25 mesothorax dorsal.

1); SR1 straight and ending at apex of wing (Fig. 1); 1-CU1:2-CU1 = 1:6; 2-SR:3-SR: r-m = 19:32:8; first subdiscal cell open ventrally and apically; CU1a just below level of 2-CU1; m-cu converging to 1-M. Hind wing: no trace of cu-a and m-cu (Fig. 1), others veins completely sclerotized.

Legs. Hind coxa smooth; tarsal claws very slender (Fig. 7), no distinct protuberance but widened basally; length of femur, tibia and basitarsus of hind leg 5.0, 11.0, and 4.3 times their width, respectively; hind femur largely smooth and parallel-sided; hind tibia somewhat widened apically and subbasally setose; hind tarsal segments with a short and sparsely setose ventro-apical protuberance (Fig. 7); hind basitarsus comparatively robust and slightly narrowed basally (Fig. 7); length of hind tibial spurs 0.4 and 0.5 times hind basitarsus.

Metasoma. Length of first tergite equal to its apical width, its surface distinctly convex and finely rugose medially, remainder largely smooth (Fig. 11), its dorsal carinae distinct in basal 0.8 and tergite widened behind spiracles (Fig. 11); dorsope rather large; second tergite smooth; ovipositor straight; length of setose part of ovipositor sheath 0.27 times fore wing, 0.6 times metasoma and 0.7 times hind tibia, with long setae, ribbon-shaped (except apically) and with a short apical spine (Fig. 12); hypopyg-ium medium-sized and apically subtruncate (Fig. 12).

Colour. Black or dark brown; scapus and pedicellus of antenna, mandible (but margins darkened), metasoma largely ventrally and legs (but telotarsi, apex of hind tibia and hind basitarsus slightly infuscate) yellowish-brown; palpi pale yellowish; propleuron, pronotal side ventrally, tegulae, first tergite and veins brown; pterostigma (but pale apically), parastigma and remainder of metasoma rather dark brown; wing membrane slightly infuscate.

Variation. Antenna of \bigcirc with 18 (4), 19 (17) or 20 (7) segments (but one female with 20 segments in left antenna has 21 segments in right antenna) and 1.1–1.2 times as long as fore wing, of \bigcirc with 19 (1), 20 (3), 21 (8), 22 (5) or 23 (3) segments and 1.2–1.5 times as long as fore wing; length of fore wing 1.6–2.4 mm, and of body 1.6–2.2 mm; first metasomal tergite 1.0–1.2 times longer than its apical width; length of setose part of ovipositor sheath 0.27–0.32 times fore wing and 0.7–0.8 times hind tibia; axillar depression narrow to medium-sized, rectangular to narrow triangular; tegulae brown or dark brown, darker than fore femur; third antennal segment dark brown or largely brown and rest dark brown; hind tarsus often entirely dark brown or infuscate; second submarginal cell of fore wing parallel-sided or widened basally.

Biology. Gregarious parasitoid of the Mediterranean fruit fly, *C. capitata* (Wiedemann, 1824) (Tephritidae).

Distribution. Portugal (Azores); most likely also France, but no material available for study (see below).

Etymology. From the generic name of its host (*Ceratites*) and "voro" (Latin for "devour"), because it is devouring this host.

Notes. Similar to the gregarious Nearctic *A. pallipes* (Say, 1829), but this species is a parasitoid of other families and has the setose part of the ovipositor sheath about as long as the metasoma and longer than the hind tibia. The Mediterranean fruit fly

has been reported as host of *A. minuta* (Nees, 1911) from South France (Ghesquière 1950, Martin 1952, Narayanan and Chawla 1962), but this is most likely a misidentification. *A. minuta* is very similar, but differs in having the hind basitarsus slenderer (Fig. 21) (less so in *A. ceratitivora*; Fig. 7), the antennal segments of \mathcal{Q} up to 22 (up to 20 segments), the axillar depression wide and finely crenulate (comparatively narrow and smooth), clypeus low basally (steeply elevated), the first tergite less widened posteriorly (more widened posteriorly; Fig. 11)), the tegulae and fore femur similarly coloured (tegulae darker than fore femur) and gregarious parasitoid of dipterous larvae in dung and rotting organic matter; e.g., *Scatophaga* species in rotting seaweed, and *Sarcophaga* species in human excrements and rotting *Sepia* species (gregarious parasitoid of *C. capitata* in fruits).

Key to main groups of the genus Aphaereta Foerster in Europe

1	Lateral carina of mesoscutum absent in front of tegulae (Fig. 14a); ovipositor
	sheath very aberrantly shaped, widened submedially and up curved apically
	(Fig. 15); labial palp with 2 segments (Fig. 14b) and maxillary palp with 4–5
	segmentsAphaereta falciger Graham, 1960
_	Lateral carina of mesoscutum present in front of tegulae (Fig. 16a); shape of
	ovipositor sheaths normal, parallel-sided and straight (Fig. 17); labial palp
	with 3-4 segments (fig. 16b) and maxillary palp with 5-6 segments2
2	Tarsal claws comparatively robust, gradually widened submedially (Figs 18,
	19) and third antennal segment of female about 3 times as long as wide
	Aphaereta stigmaticalis group
_	Tarsal claws very slender, hardly widened submedially (Figs 20, 21); third
	antennal segment of female usually 4-7 times as long as wide
3	Medio-posterior depression of mesoscutum absent (Fig. 9); setose part of oviposi-
	tor sheath 0.8–1.1 times as long as hind tibia; Aphaereta minuta group
_	Medio-posterior depression of mesoscutum present (Fig. 25), but sometimes
	minute; setose part of ovipositor sheath 0.3–1.5 times as long as hind tibia
	Aphaereta tenuicornis group
4	Scutellum distinctly convex medially (Fig. 22; hind femur erect bristly setose
	and comparatively widened apically in lateral view
	Aphaereta difficilis Nixon, 1939
_	Scutellum slightly convex medially (Fig. 23): hind femur less bristly setose
	and more slender in lateral view (Fig. 3)
5	Tegulae brown or dark brown, darker than fore femur; hind basitarsus less
-	slender (Fig. 7: about 4.5 times as long as its maximal width): axillar depres-
	sion narrow to medium-sized and smooth (Fig. 13); ventral convex area of
	side of pronotum comparatively narrow (Fig. 12): antenna of $^{\circ}$ with 18–20
	segments: gregarious parasitoid of Tephritidae: Azores, and probably south-
	ern France Aphaereta ceratitivora sn. n.

Note. Similar to the Nearctic *A. pallipes* (Say, 1829), but this species is a gregarious parasitoid of other Diptera families and has setose part of ovipositor sheath about as long as metasoma and longer than hind tibia.

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RESEARCH ARTICLE



Review of the species level taxonomy of the neotropical butterfly genus Oenomaus (Lycaenidae, Theclinae, Eumaeini)

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Abstract

Seven new species of the Neotropical hairstreak genus *Oenomaus* are described: *O. mancha* Busby & Faynel, **sp. n.** (type locality Ecuador); *O. gwenish* Robbins & Faynel, **sp. n.** (type locality Panama); *O. lea* Faynel & Robbins, **sp. n.** (type locality Ecuador); *O. myrteana* Busby, Robbins & Faynel, **sp. n.** (type locality Ecuador); *O. mentirosa* Faynel & Robbins, **sp. n.** (type locality Peru); *O. andi* Busby & Faynel, **sp. n.** (type locality Ecuador) and *O. moseri* Robbins & Faynel, **sp. n.** (type locality Brazil, Santa Catarina). For each new *Oenomaus* species, we present diagnostic characters and notes on its habitat and biology. We illustrate adults, genitalia, and distribution. New distributional and biological data are presented for 21 previously described *Oenomaus* species. *Oenomaus melleus guyanensis* Faynel, 2008 is treated as a new synonym of *O. m. melleus* (Druce, 1907). Females are described and associated with males for ten species using a variety of factors, including mitochondrial COI DNA "barcode" sequences. We summarize the reasons why the number of recognized *Oenomaus* species has grown in the past decade from one species to 28 species. Finally, we overview the habitats that *Oenomaus* species occupy and note that the agricultural pest on Annonaceae, *O. ortygnus*, is the only *Oenomaus* species that regularly occurs in greatly disturbed habitats.

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Résumé

Sept nouvelles espèces appartenant au genre néotropical *Oenomaus* Hübner sont décrites : *O. mancha* Busby & Faynel, **sp. n.** (localité type : Equateur); *O. gwenish* Robbins & Faynel, **sp. n.** (localité type : Panama); *O. lea* Faynel & Robbins, **sp. n.** (localité type : Equateur); *O. mentirosa* Faynel & Robbins, **sp. n.** (localité type : Pérou); *O. andi* Busby et Faynel, **sp. n.** (localité type : Equateur); *O. mentirosa* Faynel & Robbins & Faynel, **sp. n.** (localité type : Pérou); *O. andi* Busby et Faynel, **sp. n.** (localité type : Equateur) et *O. moseri* Robbins & Faynel, **sp. n.** (localité type : Brésil, Santa Catarina). Pour chaque nouvelle espèce, les caractères diagnostiques sont présentés et sont accompagnés de remarques sur l'habitat et la biologie. Les faces dorsales et ventrales des adultes et les organes génitaux sont illustrés et des cartes de répartition sont données. Dans une deuxième partie, de nouvelles données sont présentées pour 21 espèces d'*Oenomaus* précédemment décrites. *Oenomaus melleus guyanensis* Faynel, 2008 est mis en synonymie avec *O. m. melleus* (Druce, 1907). Les femelles sont décrites et associées avec des mâles en utilisant plusieurs moyens, y compris les séquences d'ADN mitochondrial COI. Les raisons pour lesquelles le nombre d'espèces d'*Oenomaus* décrites a fortement augmenté ces dernières années sont évoquées. Finalement, une vue d'ensemble des habitats occupés par les différentes espèces d'*Oenomaus* est présentée. *O. ortygnus*, qui est un parasite agricole connu sur Annonaceae, est la seule espèce d'*Oenomaus* qui se trouve régulièrement dans des habitats perturbés.

Keywords

Annonaceae, Neotropics, Porthecla

Introduction

The widespread Neotropical hairstreak *Oenomaus ortygnus* (Cramer) is a pest of cultivated soursop (*Annona muricata* L.) and relatives (Annonaceae), and aspects of its biology have been documented for nearly a century (e.g., Dampf 1929; Fennah 1937; Ballou 1945; Guagliumi 1965, 1967; Araque 1967; d'Araújo e Silva et al. 1967–1968; Leal 1970; Kendall 1975; Domínguez 1978; Peña et al. 2002; Castañeda-Vildózola et al. 2011). In contrast, the taxonomy of the genus *Oenomaus* Hübner (Lycaenidae: Theclinae) was not addressed until recently. *Oenomaus* was considered to be a monotypic genus of uncertain affinity (Clench 1964) until Robbins (2004) listed 22 Neotropical species (18 undescribed). Shortly thereafter, Faynel (2006, 2008) and Faynel and Moser (2008) documented the substantive variation of male genitalic structures in *Oenomaus* and described 12 new species from male holotypes. However, associating females with the males was problematic for many of these species.

A close phylogenetic relationship between *Oenomaus* and *Porthecla* Robbins was suggested when Robbins and Duarte (2004) described the latter genus. However, the distinction between these two genera has been disputed because of different interpretations of male genitalic morphology, which has resulted in the uncertain generic placement for a few species (Faynel 2007; Faynel et al. 2011). The species level taxonomy of *Porthecla* has been treated (Faynel et al. 2011), but a similar overview for *Oenomaus* is lacking.

We present new species level taxonomic information for *Oenomaus* in this paper. We describe seven new *Oenomaus* species. Next, we update information on the distribution, habitat, variation, and biology of the 21 species that were previously described in or transferred to *Oenomaus* (Robbins 2004; Faynel 2007; Faynel et al. 2011). We also associate females with males for many species based on male-female pairs collected *in copula* or on similarity of ventral wing patterns, geographic distribution, and DNA 'barcode' sequences (the mitochondrial COI gene). The morphology of newly associated females is detailed. With the species level taxonomy of *Porthecla* recently reviewed (Faynel et al. 2011), the goal of this paper is do the same kind of review for *Oenomaus*. This information will serve as the foundation for a phylogenetic analysis of *Oenomaus* and *Porthecla*.

Materials and methods

Genitalic terms follow those in Klots (1970), as modified for the Eumaeini in Robbins (1991). Wing veins are named following Comstock (1918), and wing cells are named by the veins that border them. Otherwise, morphological terms follow Snodgrass (1935). Abbreviations used repeatedly in the text are FW: forewing, HW: hindwing, D: dorsal, V: ventral and SD: standard deviation. Brazilian states are noted by their standard two letter abbreviations.

Illustrated adults of *Oenomaus* are noted in the material examined sections, and each genitalia drawing is of the adult illustrated. The structure of the male genitalia valvae in *Oenomaus* is complex, for which reason we present them in ventral, lateral, and dorsal views.

Biogeographical zones follow Brown (1982), who partitioned the forested continental Neotropics into the Transandean Region, Andean Region, Amazon Region, and Atlantic Region. Larval food plant nomenclature follows the Tropicos database of the Missouri Botanical Garden (http://www.Tropicos.org, accessed April 2012). Following Holdridge (1967), we classify lowland forests as humid/wet (> 200 cm annual precipitation) or dry/deciduous (100–200 cm annual precipitation). Many eumaeines display male territorial behavior on hilltops (Nicolay 1971; Alcock and O'Neill 1986; 1987; Prieto and Dahners 2006, 2009; Robbins et al. 2012). Males wait on hilltops for receptive females to fly through the territory and "defend" these areas by flying at other males that enter the territory. Recorded times from our fieldwork for hilltopping behavior are the standard time at that locality. Finally, traps baited with decaying fish attract some lycaenid species and not others. We note the gender for each species which has been collected using fish-baited traps.

The ventral wing pattern in *Oenomaus* is sexually monomorphic, so associating the sexes of species with distinct ventral wing patterns, such as *O. ortygnus*, is straightforward. However, a majority of *Oenomaus* species have a ventral wing pattern that is similar to that of *O. atena* (Hewitson). Among these, some can be associated because they have distinct ventral wing pattern elements, such as those of *O. isabellae* (Faynel 2008), or because a mating pair was collected *in copula*. In other cases, we associate females with males if at least three of the following four criteria are met: (1) females have a ventral wing pattern that is indistinguishable from that of males, (2) females have a geo-

graphic distribution that is similar to that of males, (3) both sexes are found in a locality where other species with the same wing pattern are unrecorded, and (4) divergence of DNA "barcode" sequences between the sexes is less than 2% (see next paragraph).

The mitochondrial COI gene sequence (commonly called a DNA "barcode") has been useful, when combined with other characters, in distinguishing lepidopteran species in a single area (e.g., Hebert et al. 2004; Hajibabaei et al. 2006; Janzen et al. 2009). Because genitalic and wing pattern characters generally provide clear species boundaries in *Oenomaus*, our purpose in determining COI gene sequences was to aid in associating females with males, as noted.

We use the following acronyms for collections, following those for public institutions listed on the website hbs.bishopmuseum.org/codens/codens-inst.html (accessed April 2012):

AMNH	American Museum of Natural History, New York, New York, USA.						
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.						
CF	Private collection of Christophe Faynel, France.						
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.						
DZUP	Universidade Federal do Paraná, Curitiba, Paraná, Brazil.						
FSMC	Florida Museum of Natural History, Allyn Museum, University of Florida,						
	Gainesville, Florida, USA.						
JFLC	Private collection of Jean François Le Crom, Bogotá, Colombia.						
LYD	Private collection of Louis and Yvan Diringer, France.						
MC	Private collection of Alfred Moser, São Leopoldo, Rio Grande do Sul, Brazil.						
MNHN	Muséum national d'Histoire naturelle, Paris, France.						
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos,						
	Lima, Perú.						
OSAC	Oregon State University Corvallis, Oregon, USA.						
PB	Private collection of Pierre Boyer, Le Puy Sainte Réparade, France.						
RCB	Private collection of Robert C. Busby, Andover, Massachusetts, USA.						
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt-am-Main,						
	Germany.						
USNM	Smithsonian Institution, Washington, DC USA.						

New species

A distinguishing trait of *Oenomaus* and *Porthecla* among members of the *Panthiades* Section of the Eumaeini is the lack of an orange cubital spot (Robbins and Duarte 2004, Faynel et al. 2011). Of the seven new species described in this paper, six lack the spot while some specimens of the seventh species may have a vestigial remnant composed of a few orange scales (Figs 1–11). *Oenomaus* and *Porthecla* are distinguished from each other by shape of the valvae in lateral aspect, but interpretation of this morphology has varied for some species (Robbins and Duarte 2004, Faynel 2007, Faynel

et al. 2011). However, six of the newly described species have non-triangular, bifurcate valvae in lateral aspect (Figs 20–25), which is characteristic of *Oenomaus*. The seventh species is known only from a female, but the similarities in its wing pattern (Figs 2–3) and genitalia (Figs 28–29) to two other *Oenomaus* species support its generic placement. For these reasons, the following new species are described in *Oenomaus*.

Oenomaus mancha Busby & Faynel, sp. n.

urn:lsid:zoobank.org:act:4DF6102F-0A25-46B8-8F56-6E33D791A5F2 http://species-id.net/wiki/Oenomaus_mancha Figs 1, 2, 20, 26, 38, 46

Type-locality. Ecuador: Sucumbíos, 5 km Puerto Libre-La Bonita Road, 0°13.0'N, 77°29.3'W, 700 m. The road going west from Puerto Libre increases in elevation as the terrain becomes hillier. The collecting spot was in wet forest and was easily accessed by a muddy logging trail. Since 2005, logging has continued, leaving very few tall trees in the once beautiful forest.

Type-specimen. Holotype ♂ (Fig. 1) labeled as "ECUADOR: Sucumbios / 5 km Puerto Libre-La Bonita Road / 0°13.0'N, 77°29.3'W, 700 m / 23 February 2005 / Robert C. Busby, leg." [rectangular, white, printed], "11:00 hrs / 5 m" [rectangular, white, handwritten, blue ink], "GENITALIA No. / 2011: 419♂ / C. FAYNEL" [rectangular, green, printed] "Holotype ♂ / *Oenomaus mancha* / Busby & Faynel, 2012" [rectangular, red, printed]. Deposited in USNM.

Paratypes: Ecuador. 2 \mathcal{J} : Napo, 14 km Tena-Puyo Road, 1°06.7'S, 77°46.9' W, 600 m, 24.IX.2011, (Apuya) Robert C. Busby leg. (RCB); Napo, Pimpilala, [GPS data : 1°04.6 S, 77°56.2'W], 600-700 m, Euclides Aldaz leg., XII.2003, gen. prep. CF n°290 (PB); **10**⊊: Napo, 28 km Tena-Puyo Road, 1°11.3'S, 77°49.9'W, 800 m, VIII.2006 (El Capricho) I. Aldas & R. C. Busby leg. (RCB); Napo, 12 km Tena-Puyo Road, 1°05.3'S, 77°47.4' W, 600 m, 28.VIII.2009, (Finca San Carlo) D. H. Ahrenholz, R. C. Busby, leg. (RCB); Napo, 14 km Tena-Puyo Road, 1°06.7'S, 77°46.9'W 600 m, VIII.2005, (Apuya) I. Aldas & R. C. Busby leg. (RCB) ; Napo, 14 km Tena-Puyo Road, 1°06.7'S, 77°46.9'W, 600 m, 17.X.2010, (Apuya) I. Aldas & R. C. Busby leg. (RCB); Napo, 14 km Tena-Puyo Road, 1°06.7'S, 77°46.9'W, 600 m, 22.X.2010, (Apuya) I. Aldas & R. C. Busby leg. (RCB); Pastaza Province, 32 km S. of Puyo, 1000 m, 21–23.X.1995 Robert C. Busby leg. (RCB); Pastaza Province, 45 km Puyo-Arajuno Rd, 1000 m, 15.IX.1999, Robert C. Busby leg., gen. prep. CF n°420 (RCB); Pastaza Province, 45 km Puyo-Arajuno Rd, 1000 m, 26.IX.1999, Robert C. Busby leg., gen. prep. CF n°421 (RCB); Pastaza Province, 45 km Puyo-Arajuno Rd, 1000 m, 26.IX.1999, Robert C. Busby leg. (RCB); Pastaza, Puyo, 1000 m, 14.X.1989, D.H. Ahrenholz leg., gen. prep. CF n°407 (USNM ENT 00180037) (Fig. 2).

Description, diagnosis and recognition as a distinct species. Male FW length: 20.8 mm (SD = 1.9, N = 2). Female FW length: 19.4 mm (SD = 0.5, N = 3). Wing pattern (Figs 1, 2) and genitalia (Figs 20, 26) illustrated. *Oenomaus mancha*, *O. ortyg*-



Figures 1–11. Oenomaus, new species: adults (dorsal surface at left, ventral surface at right). I ♂ O. mancha (holotype, Ecuador) 2 ♀ O. mancha (paratype, Ecuador) 3 ♀ O. gwenish (holotype, Panama) 4 ♂ O. lea (holotype, Peru) 5 ♂ O. myrteana (holotype, Ecuador) 6 ♀ O. myrteana (paratype, Ecuador) 7 ♂ O. mentirosa (holotype, Peru) 8 ♂ O. andi (holotype, Ecuador) 9 ♀ O. andi (paratype, Ecuador) 10 ♂ O. moseri (holotype, Brazil) 11 ♀ O. moseri (paratype, Brazil).

nus, and *O. gwenish* (named below) share a unique ventral wing pattern in which the VFW postmedian line (displaced basally, but by tradition still called the postmedian line) is composed of "disjointed" large black spots on a gray ground color (Fig. 3 for *O. gwenish* and Figs 2, 4 for *O. ortygnus* in Faynel 2006). *Oenomaus mancha* differs from *O. ortygnus* by (1) a black patch in the distal part of the VHW cell Sc+R1-Rs, elongated basally, (2) no black mark in VFW cell Costa-Sc, and (3) a black band crossing the VFW discal cell. In addition, females of *O. mancha* are a brighter blue dorsally, while the blue on the DFW of males is somewhat less expansive with the scent pad not completely encircled by blue scales as in *O. ortygnus*. Male and female genitalia of *O. mancha* and *O. ortygnus* also differ (Figs 25, 28 for *O. ortygnus* in Faynel 2006). In particular, the dorsal part of the valvae of the male genitalia in lateral aspect is shorter and has a more sharply tapered posterior end in ventral view. In the female, the bifd

posterior end of the lamella postvaginalis is less marked and the anterior end of the ductus bursae is curved more sharply. One paratype from Ecuador has been barcoded (CF-LYC-190), and its sequence is 3.5% divergent from the sequences of two males of *O. ortygnus* (CF-LYC-147 from Peru and CF-LYC-146 from Mexico, see Table 1) while the two *O. ortygnus* sequences differ by only 1.5%. *Oenomaus ortygnus* and *O. mancha* are sympatric in eastern Ecuador in Napo Province at approximately 450 m.

Etymology. The name of this species is derived from the Spanish word "mancha", which means spot, referring to the very distinctive, elongated black spot in VHW cell Sc+R1-Rs. The name is a feminine noun in apposition.

Habitat and distribution. *Oenomaus mancha* occurs widely in wet forest in eastern Ecuador at elevations ranging from 400 to 1100 m (Fig. 46). Although it is sympatric with *O. ortygnus* in wet forest, it does not occur in the highly disturbed habitats in which *O. ortygnus* sometimes occurs. It is yet an open question whether *O. mancha* is a lowland or lower montane species.

Behavior. The holotype male was landed on a leaf about 5 m above the ground at 11:00 hours. Males and females are attracted to traps baited with rotting fish (vouchers in RCB).

	. ambiguu). aten). ates). brule). cortic). curios). cyanovenat). gai). isabella	. jauffret). le	. magnu). manch	. morroensi	. moser). nigr	. ortygnu	. poirier). tau
	sO	aC	aC	i0	aC	aC	aC	aC	вC	i0	aC	s0	aC	ŝ	i0	аС	sO	i0	aC
O. ambiguus (3)	0.2																		
<i>O. atena</i> (1)	6.9																		-
<i>O. atesa</i> (1)	7.2	7.0																	
O. brulei (2)	6.2	6.2	7.4	0.3															
O. cortica (3)	2.8	5.5	7.5	5.9	0.5														
O. curiosa (4)	7.9	6.5	5.3	6.9	7.4	0.6													
O. cyanovenata (4)	7.1	5.4	7.2	7.3	5.8	6.4	0												
<i>O. gaia</i> (3)	2.4	5.3	7.0	5.6	1.0	7.2	5.9	0.7											
O. isabellae (1)	6.2	6.7	7.6	7.3	5.8	7.9	6.1	5.6											
O. jauffreti (4)	7.0	6.5	7.0	6.2	6.4	7.6	6.9	6.1	4.9	1.6									
<i>O. lea</i> (1)	6.9	4.7	6.7	6.3	6.1	6.2	5.9	5.9	7.3	5.8									
O. magnus (1)	7.9	6.9	7.6	7.6	7.0	7.5	6.9	6.8	4.5	5.9	7.7								
O. mancha (1)	5.2	5.2	5.7	5.7	4.9	5.9	5.6	4.3	4.9	5.4	5.6	6.4							
O. morroensis (1)	2.3	4.8	7.1	4.8	0.9	7.1	5.4	0.9	5.7	6.3	5.7	6.8	5						
O. moseri (2)	5.7	5.9	6.7	6.9	5.7	6.9	4.0	5.2	5.6	5.8	5.8	6.6	4.9	5.1	0				
<i>O. nigra</i> (1)	7.7	6.7	5.7	8.4	7.8	5.9	7.6	7.2	7.8	6.9	5.9	7.2	6.4	7.7	7				
O. ortygnus (2)	6.7	5.7	6.6	7.1	6.3	6.4	6.3	6.1	6.3	6.3	6.3	6.2	3.5	6.2	5.4	6.6	1.5		
O. poirieri (1)	7.7	6.9	7.5	7.2	7.5	8.0	6.6	7.0	5.2	4.6	7.5	6.2	6.1	6.9	5.3	7.6	6.2		
<i>O. taua</i> (2)	5.9	5.2	5.4	6.1	5.3	6.0	5.1	4.9	5.2	4.7	4.3	5.9	4.1	5.4	4.8	6.1	4.9	5.6	0

Table 1. Comparison of inter- and intraspecific divergences (in % rounded to the nearest tenth) for the DNA "barcodes" of 19 *Oenomaus* male species obtained with BOLD (noted as -- when not available). Number of males examined in brackets.

Species	Sample ID	Locality	GenBank Accession Numbers				
O. ambiguus Faynel, 2008	CF-LYC-025	Peru	HQ966548				
O. ambiguus Faynel, 2008	CF-LYC-183	Peru	JX458731				
O. ambiguus Faynel, 2008	CF-LYC-189	Peru	JX458734				
O. atena (Hewitson, 1867)	CF-LYC-084	Peru	HQ966592				
O. atesa (Hewitson, 1867)	CF-LYC-003	French Guiana	HQ966543				
<i>O. brulei</i> Faynel, 2008	CF-LYC-033	French Guiana	HQ966552				
<i>O. brulei</i> Faynel, 2008	CF-LYC-035	French Guiana	HQ966554				
O. cortica (D'Abrera, 1995)	CF-LYC-051	Brazil	HQ966565				
O. cortica (D'Abrera, 1995)	CF-LYC-052	Brazil	HQ966566				
O. cortica (D'Abrera, 1995)	CF-LYC-188	Peru	JX458722				
O. curiosa Faynel & Moser, 2008	CF-LYC-036	French Guiana	HQ966555				
O. curiosa Faynel & Moser, 2008	CF-LYC-037	French Guiana	HQ966556				
O. curiosa Faynel & Moser, 2008	CF-LYC-016	Peru	JX458726				
O. curiosa Faynel & Moser, 2008	CF-LYC-184	Peru	JX458730				
O. cyanovenata (D'Abrera, 1995)	CF-LYC-049	Brazil	HQ966564				
O. cyanovenata (D'Abrera, 1995)	CF-LYC-048	Brazil	HQ966563				
O. cyanovenata (D'Abrera, 1995)	CF-LYC-047	French Guiana	JX458737				
O. cyanovenata (D'Abrera, 1995)	CF-LYC-182	Peru	JX458728				
O. gaia Faynel, 2008	CF-LYC-024	Peru	JX458720				
O. gaia Faynel, 2008	CF-LYC-023	French Guiana	JX458719				
O. gaia Faynel, 2008	CF-LYC-187	Peru	JX458721				
O. isabellae Faynel, 2006	CF-LYC-006	Brazil	HQ966545				
O. jauffreti Faynel & Moser, 2008	CF-LYC-030	Brazil	JX458724				
<i>O. jauffreti</i> Faynel & Moser, 2008	CF-LYC-029	French Guiana	HQ966549				
O. jauffreti Faynel & Moser, 2008	CF-LYC-028	Brazil	JX458727				
O. jauffreti Faynel & Moser, 2008	CF-LYC-186	Peru	JX458732				
O. lea Faynel & Robbins, 2012	CF-LYC-005	Peru	HQ966544				
O. magnus Faynel & Moser, 2008	CF-LYC-020	Peru	HQ966547				
O. mancha Busby & Faynel, 2012	CF-LYC-190	Ecuador	JX458723				
O. morroensis Faynel & Moser, 2008	CF-LYC-015	Brazil	JX458736				
O. moseri Robbins & Faynel, 2012	CF-LYC-012	Brazil	JX458735				
O. moseri Robbins & Faynel, 2012	CF-LYC-063	Brazil	HQ966576				
O. nigra Faynel & Moser, 2008	CF-LYC-148	Peru	JX458729				
O. ortygnus (Cramer, 1779)	CF-LYC-146	Mexico	JX458738				
O. ortygnus (Cramer, 1779)	CF-LYC-147	Peru	JX458733				
O. poirieri Faynel, 2008	CF-LYC-011	French Guiana	JX458725				
O. taua Faynel & Moser, 2008	CF-LYC-085	Peru	HQ966593				
O. taua Faynel & Moser, 2008	CF-LYC-185	Peru	JX458739				

Table 2. Species of *Oenomaus* sampled with BOLD (project NLYCA), with sample identifications, localities and GenBank accession numbers.

Oenomaus gwenish Robbins & Faynel, sp. n.

urn:lsid:zoobank.org:act:D35807B0-C3C3-4384-BB59-E294B3E06F97 http://species-id.net/wiki/Oenomaus_gwenish Figs 3, 27, 46

Type-locality. Panama: Darién, Serranía de Pirre, Cana, 7°55'57"N, 77°42'58"W, 1000 m. Serranía de Pirre at 1000 m was uncut wet lower montane forest in 1984. The only disturbance was a defunct gold mine camp and associated dirt runway at Cana.

Type-specimen. Holotype \bigcirc (Fig. 3) labeled as "PANAMA: Darien: / Serrania de Pirre: / Cana: 1,000 m / 5 January 1984 / Leg. G.B. Small" [rectangular, white, printed and handwritten], "GENITALIA NO. / 2011: 406 \bigcirc / C. FAYNEL" [rectangular, green, printed] "Holotype \bigcirc / *Oenomaus gwenish* / Robbins & Faynel, 2012" [rectangular, red, printed]. Deposited in USNM.

Description, diagnosis and recognition as a distinct species. Female FW length: 20 mm (N = 1). Wing pattern (Fig. 3) and genitalia (Fig. 27) illustrated. The wing patterns of *O. gwenish* and *O. mancha* are distinguished from that of *O. ortygnus* by the black patch in the distal part of the VHW cell Sc+R1-Rs and by the absence of a black mark in VFW cell Costa-Sc. However, the ventral wing pattern of *O. gwenish* differs from that of *O. mancha* by (1) the lack of a black band crossing the VFW discal cell, (2) the absence of a black spot in VFW cell M3-Cu1, and (3) the presence of two black spots of equal size along VHW veins mdc and ldc instead of a single large black spot at vein mdc with no mark or a faint vestigial mark at vein ldc. The female genitalia of *O. gwenish* (Fig. 27) are similar to those of *O. mancha*.

We hesitated to describe this species because we cannot assess its intraspecific variation. However, the series of 10 females of *O. mancha* show little variation in the traits that distinguish them from the holotype of *O. gwenish*. For this reason, a hypothesis of specific distinctness is better supported than a hypothesis of geographical variation.

Etymology. The holotype of *O. gwenish* is a unique and distinctive female, for which reason it gives us great pleasure to name this species for entomologist Dr. Jennifer (Gwen) Shlichta. The name is a feminine noun in apposition.

Habitat and distribution. *Oenomaus gwenish* is probably a lower montane species, so far known only from wet forest at 1000 m elevation in Darién, Panama (Fig. 46). While *O. gwenish* and *O. ortygnus* are both known from Panama, we do not know if they are sympatric.

Oenomaus lea Faynel & Robbins, sp. n. urn:lsid:zoobank.org:act:A8315354-6FFF-4C71-AEE5-92925AE8833B http://species-id.net/wiki/Oenomaus_lea Figs 4, 21, 39, 47

Type-locality. Ecuador: Napo, Misahuallí Rd, Latas Grande, 7.7 km E Puerto Napo, 1°02.0'S, 77°44.1'W, 470 m. The holotype was collected along the road from Tena to Misahuallí, which in 1991 was a patchwork of "fincas" and remnant second growth forest.

Type-specimen. Holotype (Fig. 4) labeled as "ECUADOR Napo / Misahualli Rd. 470m / Latas Grande / 9 Nov.' 91 / S. S. Nicolay" [rectangular, white, printed and handwritten], "USNM ENT 00180040" [rectangular, white, printed], "GENITALIA NO. / 2011: 408 / C. FAYNEL" [rectangular, green, printed] "Holotype / *Oenomaus lea* / Faynel & Robbins, 2012" [rectangular, red, printed]. Deposited in USNM.

Paratypes: Ecuador. 1 ♂: La Merced on Río Pastaza below Baños, Alt. 4000 ft. [= 1220 m], W. J. Coxey, III.1930, A.N.S. Lot 217, genitalia NO. 1992: 12 ♂ R.K. Robbins (ANSP). **Peru. 3** ♂: UC, Pucallpa, 200 m, X.2007, Michael Büche leg. (CF); LO, Contamana, Río Ucayali, 300 m, 7°19'S, 74°48'W, IX.2010, leg J. Ramírez (LYD); SM, Juanjui, upper Huallaga River, IX. 1934, collector G. Klug, collection E.I. Huntington NO. 1055 (AMNH).

Description, diagnosis and recognition as a distinct species. Male FW length: 18.2 mm (SD = 0.8, N = 4). Wing pattern (Fig. 4) and genitalia (Fig. 21) illustrated. Oenomaus lea and O. atesa (Hewitson, 1867) are the only two Eumaeini sharing the striking underside wing pattern with two transverse brown bands on the VHW. However, males of Oenomaus lea differ from males of O. atesa (Figs 5, 6 in Faynel 2006) by (1) a greater expanse of the DFW blue, especially in the area from vein R3 to vein Cu1, (2) two brown patches on the VFW instead of a single median brown band; one patch is located along the costa, and the other is triangular and situated in the basal part of cell Cu1-Cu2, and (3) a lighter dorsal blue color with a different hue of blue along the HW veins M2, M3, Cu1 and Cu2. Moreover, the black spot in VHW cell Cu1-Cu2 is usually more apparent in O. atesa than in O. lea. Males of O. lea also differ genitalically from those of O. atesa (Fig. 26 in Faynel 2006) by (1) a longer and wider saccus, (2) the dorsal part of the valvae in lateral aspect shorter than the ventral part, and not pointed at the posterior end, (3) a straight penis in lateral view, and (4) no tooth at the end of the penis. The eighth tergum shows no difference from that of *O. atesa*. Lastly, the divergence of "barcode" DNA sequence data between O. lea (CF-LYC-005) and O. atesa (CF-LYC-003) is more than 6% (Table 1). The female of O. lea is unknown.

Etymology. This species is named for Léa Faynel, daughter of Christophe Faynel. The name is a feminine noun in apposition.

Habitat and distribution. *Oenomaus lea* occurs in wet lowland forest up to 1200 m elevation in eastern Ecuador and eastern Peru (Fig. 47).

Oenomaus myrteana Busby, Robbins & Faynel, sp. n. urn:lsid:zoobank.org:act:B8EBB664-61DA-4178-91C8-52D2D9BFF0AC http://species-id.net/wiki/Oenomaus_myrteana Figs 5, 6, 22, 28, 41, 46

Type-locality. Ecuador: Morona Santiago, Santiago (Hill North of Town), 3°02.3'S, 78°00.3'W, 350 m. The holotype was collected in wet secondary forest in the low hills on the north edge of Santiago.

Type-specimen. Holotype ♂ (Fig. 5) labeled as "ECUADOR: Morona Santiago / Santiago (Hill North of Town) / 3°02.3'S, 78°00.3'W 350 m / 20 September 2004 /

Robert C. Busby, leg." [rectangular, white, printed], "GENITALIA NO. / 2003: 35⁽³⁾ / R.K. ROBBINS" [rectangular, green, printed] "Holotype ⁽³⁾ / *Oenomaus myrteana* / Busby, Robbins & Faynel, 2012" [rectangular, red, printed]. Deposited in USNM.

Paratypes: Ecuador. 1 \Diamond : Morona Santiago, Santiago (Hill North of Town), 3°2.3'S, 78°0.3'W, 350 m, 20.IX.2006, Robert C. Busby leg. (RCB) ; 1 \heartsuit : Morona-Santiago Province, 1.8 km Santiago-Puerto Morona Rd., 3°2.4'S, 77°59.7'W, 300–350 m, 20.IX.2006, D.H. Ahrenholz & Robert C. Busby leg., gen. prep. CF n°415 (RCB) (Fig. 6). **Brazil. 2** \Diamond : RO, Cacaulândia, 1–5.IX.1997, E. Furtado & A. Moser leg., gen. prep. CF n°442 (MC 250); RO, Candeias do Jamari, Rio Preto, 27–31. VIII.1997, E. Furtado & A. Moser leg., gen. prep. CF n°443 (MC 251).

Description, diagnosis and recognition as a distinct species. Male FW length: 12.8 mm (SD = 0.1, N = 3). Female FW length: 12.1 mm (N = 1). Wing pattern (Figs 5, 6) and genitalia (Figs 22, 28) illustrated. *Oenomaus myrteana* has a conspicuous round white spot in VHW cell Sc+R1-Rs, which is similar to those species of *Oenomaus* with a ventral wing patterns similar to that of *O. atena*. However, *O. myrteana* lacks the inclined white median line of the VFW, which is characteristic of species with the *O. atena* wing pattern. Instead, *O. myrteana* has a vertical, distally displaced postmedian line of white dashes, inwardly bordered by black. This character appears to be unique among *Oenomaus* species. In addition, *O. myrteana* may have a few redorange scales in VHW cell Cu1-Cu2. This red-orange cubital spot is uniformly lacking in other *Oenomaus* and *Porthecla*. The male genitalia of *O. myrteana* are very similar to those of *O. nigra*, which has an "*atena*-like" ventral wing pattern. The female genitalia of *O. myrteana* are similar to those *Oenomaus* that have a bifid posterior end of the ductus bursae and a signa with a two pointed spine in the middle of the corpus bursae.

The ventral wing pattern of *O. myrteana* is superficially similar to those of *Enos myrtea* (Hewitson) and *Allosmaitia myrtusa* (Hewitson), but in these genera, males lack a scent pad on the DFW. The genitalia of *O. myrteana*, as noted, are typical of *Oenomaus*.

Etymology. The name *O. myrteana* is intended to highlight the striking resemblance between the ventral hindwing of this species and that of *Enos myrtea* (Hewitson). The name is a feminine noun in apposition.

Habitat and distribution. *Oenomaus myrteana* occurs in lowland wet forest from eastern Ecuador to western Brazil (Rondônia) (Fig. 46). Busby observed males in Ecuador low in the understory at 11:00 hours. This species and *E. myrtea* have been found at the same site.

Oenomaus mentirosa Faynel & Robbins, sp. n. urn:lsid:zoobank.org:act:FDD83214-61B2-4B8A-B468-984D9DA0560D http://species-id.net/wiki/Oenomaus_mentirosa Figs 7, 23, 40, 47

Type-locality. Peru: Madre De Dios, Río La Torre, Tambopata Res., 12°50'13"S, 69°17'35"W, 300 m. Tambopata is at the mouth of the Río La Torre. In 1986 there was a lodge and a network of trails through uncut wet lowland forest. The holotype

was collected during the transition between the dry and wet seasons when butterfly abundance and diversity generally peak.

Type-specimen. Holotype ♂ (Fig. 7) labeled as "PERU Madre De Dios / Rio La Torre 300m / Tambopata Res. / 3 Oct.' 86 / S. S. Nicolay" [rectangular, white, printed and handwritten], "GENITALIA NO. / 2011: 409♂ / C. FAYNEL" [rectangular, green, printed] "Holotype ♂ / *Oenomaus mentirosa* / Faynel & Robbins, 2012" [rectangular, red, printed]. Deposited in USNM.

Paratypes: Peru. 4 ♂: LO, km 28, Iquitos-Nauta, 180 m, 0359/7326, 30.X.2003, J.J. Ramírez leg. (MUSM) ; MD, Boca Río La Torre, 300 m, 17.IX.1984, I. Bohórquez leg., Genitalia NO. 1992: 47♂ R.K. Robbins (MUSM); MD, Boca Río La Torre, 300 m, 27.X.1981, G. Lamas et al., Genitalia NO. 1992: 48♂ R.K. Robbins (MUSM) ; MD, Tambopata Reserve, 12°50'S, 69°17'W, 300 m, 27.X.1990, Leg. R. Robbins, Genitalia NO. 1992: 39♂ R.K. Robbins (USNM ENT 00180049).

Description, diagnosis and recognition as a distinct species. Male FW length: 14.9 mm (SD = 0.3, N = 2). Wing pattern (Fig. 7) and genitalia (Fig. 23) illustrated. The ventral wing pattern of *O. mentirosa* is very similar to some species of the *Porthecla gemma* group (Faynel et al. 2011), but the male genitalia have the non-triangular bifurcate valvae in lateral aspect that are characteristic of *Oenomaus*. Its genitalia, especially the valvae, are very similar to those of *O. cortica* (D'Abrera) and *O. druceus* Faynel & Moser. *Oenomaus mentirosa* is the only known *Oenomaus* species with red scales at the base on the VHW. In addition, it has a distinctive white spot along the VFW costa in cell Sc-R1. This feature occurs in no other Eumaeini except *Porthecla minyia* (Hewitson) where there are two white markings placed side by side in the cell between the costa and Sc. In male *Oenomaus* species, the eighth tergum is generally rectangular, but the anterior and posterior edges may be modified. In *O. mentirosa*, the male eighth tergum has a slightly modified anterior edge which looks like a shallow "W". The female of *O. mentirosa* is unknown.

Etymology. The name of this species comes from the Spanish word 'mentirosa', which means a feminine liar. We picked this name because the underside wing pattern resembles that of *Porthecla gemma* (Druce) and *P. minyia* (Druce), but this resemblance appears to be a false indicator of relationship. We treat the name as a feminine noun in apposition.

Habitat and distribution. *Oenomaus mentirosa* is known from lowland wet forest in Amazonian Peru (Fig. 47).

Remarks. Resemblance of the ventral wing patterns of *O. mentirosa* and *P. gemmal P. minyia* was noted in the etymology. Adults of all three species fly in the same habitats at the same time of year in the vicinity of Puerto Maldonado, Peru.

Oenomaus andi Busby & Faynel, sp. n. urn:lsid:zoobank.org:act:C6C09BC9-F0B9-4E7A-8951-0D9923BE9E73 http://species-id.net/wiki/Oenomaus_andi Figs 8, 9, 24, 29, 42, 43, 47

Type-locality. Ecuador: Zamora Chinchipe Prov., Zamora (ridge W. of town), 4°04.5'S, 78°58.1'W, 1450 m. The ridge west of Zamora rises rather sharply from

the city and is accessed by a dirt road which goes up to about 1300 m. The top of the ridge is still forested but a significant part of the surrounding land has been turned into pasture.

Type-specimen. Holotype ♂ (Fig. 8) labeled as "ECUADOR / Zamora Chinchipe Prov. / Zamora (ridge W. of town) / 18. ix. 2000 (1450m) / leg. Robert C. Busby" [rectangular, white, printed], "GENITALIA NO. / 2009: 344♂ / C. FAYNEL" [rectangular, green, printed] "Holotype ♂ / *Oenomaus andi* / Busby & Faynel, 2012" [rectangular, red, printed]. Deposited in USNM.

Paratypes: Ecuador. 3: Morona-Santiago, 1 km E Río Abanico, 1600 m, 2°15.4'S; 78°11.7'W, 15.IX.2003, Robert C. Busby leg., gen. prep. CF n°416 (RCB) (Fig. 9) ; Morona-Santiago, 14 km W. of Macas, 1600m, 28.IX.1998, Río Abanico, leg. Robert C. Busby (RCB); Zamora Chinchipe, Zamora (ridge W. of town), 4°04.5'S, 78°58.1'W, 1450 m, 06.X.2007, D. H. Ahrenholz, R. C. Busby leg. (RCB).

Other specimen examined. Bolivia. 1^Q: La Paz, Nor Yungas, Caranavi, 1500 m, XII. 2004, gen. prep. CF n°445 (MC 253).

Description, diagnosis and recognition as a distinct species. Male FW length: 16.3 mm (N = 1). Female FW length: 16.7 mm (SD = 0.8, N = 2). Wing pattern (Figs 8, 9) and genitalia (Figs 24, 29) illustrated. The ventral wing pattern of *O. andi* is similar to that of many other *Oenomaus*, but this species is distinguished by (1) a white spot on the basal side of VHW cell Rs-M1, (2) an elongated double valvae of equal size, (3) a large posterior part of the saccus in lateral view, (4) a swollen terminal end of the penis, and (5) modified anterior and posterior edges of the male 8th tergum (detailed under remarks).

Etymology. This species is named for Andrea (Andi) Busby, wife of Robert Busby, in appreciation for her long standing support of his research. The name is a feminine noun in apposition.

Remarks. Valvae structure in *O. andi* is very similar to that found in *O. gaia* Faynel, suggesting that this new species belongs to the *O. cortica* subgroup (as characterized by Faynel and Moser, 2008). Species in this subgroup have a modified 8th tergum (except for *O. druceus* Faynel & Moser 2008). In the male of *O. andi* (Fig. 42), the posterior edge of the 8th tergum has a deep depression in the middle, while the anterior edge is shaped like a wide "W". In the female, the posterior edge is nearly straight but is split in the middle. The anterior edge is similar to that of the male, but is laterally sclerotized (Fig. 43). The white spot on the basal side of VHW cell Rs-M1 occurs in only a few other *Oenomaus* species including *O. geba* (Hewitson), *O. melleus* (Druce), *O. morroensis* Faynel & Moser, and *O. jauffreti* Faynel & Moser. Regardless of whether the presence of this spot is evidence of relationship, it is very useful for separating *O. andi* from the other species of the *O. cortica* subgroup.

Habitat and distribution. *Oenomaus andi* is a species of montane forest (> 1300 m) that is recorded from Ecuador to Bolivia (Fig. 47).

Behavior. A male and two females were attracted to traps baited with rotting fish (vouchers in RCB).

Oenomaus moseri Robbins & Faynel, sp. n.

urn:lsid:zoobank.org:act:DC5D1BF6-2149-4BB9-802D-58C27D11AB38 http://species-id.net/wiki/Oenomaus_moseri Figs 10, 11, 25, 30, 44, 45, 46

Type-locality. Brazil: SC, Joinville, 26°19'39"S, 48°57'38"W, 10–200 m. Miers collected butterflies for decades in the wet lowland forests around Joinville, where he lived. His favorite collecting spot was a hill that he called "Serrinha" (little hill in Portuguese) in Vila Nova, approximately 10 km west, south-west of the center of Joinville. According to DZUP butterfly curator Olaf Mielke, specimens collected on Serrinha, including the holotype, have an elevation label 10–200 m, which distinguishes them from those specimens collected in other parts of the Joinville area.

Type-specimen. Holotype \Diamond (Fig. 10): **Brazil**, SC, Joinville, 10–200 m, 2.IV.1978, Miers leg., gen. prep. CF n°218, DZ 10.065, CF-LYC-012 (DZUP).

Paratypes: Brazil. 12 d: SC, Joinville, 200 m, 26°19'S, 48°58'W, 20.V.1971, H.Miers leg., gen. prep. CF n°444 (MC 252) ; SC, São Bento do Sul, 600 m, 25.IV.2002, Moser & Rank leg., gen. A. Moser, n°234 (MC 034) ; SC, Joinville, 200 m, 5.II.1993, A. Moser leg., gen. A. Moser, n°226 (MC 032); SC, Joinville, 200 m, 5.II.1993, A. Moser leg., gen. A. Moser n°233 (MC 033) ; SC, Joinville, 10-200 m, 8.XII.1983, Leg. H. Miers, R.K. Robbins collection (USNM) ; SC, Joinville, 10-200 m, 6.I.1984, Leg. H. Miers, R.K. Robbins collection (USNM); PR, Ponta Grossa, Buraco do Padre, 900 m, 20.II.2009, Carlos Mielke leg., CF-LYC-063 (CF); SP, Serra do Japi, 110[0m], 23°15'S, 46°54'W, 12.IV.1991, Robbins & K. Brown, territorial behavior at 14:23, Genitalia NO. 1992: 27♂ R.K. Robbins (USNM) ; SP, Serra do Japi, 110[0]m, 23°15'S, 46°54'W, 12.IV.1991, Robbins & K. Brown, territorial behavior at 14:48 (USNM) ; SP, Serra do Japi, 800-1250 m, 23°12'-17'S, 46°53'-47°02'W, 25.III.1990, Leg. K. Brown (x2, USNM); SP, Serra do Japi, 800-1250 m, 23°12'-17'S, 46°53'-47°02'W, 28.III.1990, Leg. K. Brown (USNM) ; RJ, Petrópolis, 6.I.1980, Leg. C. Callaghan, R.K. Robbins collection, Genitalia NO. 1992: 798 R.K. Robbins (USNM ENT 00180045). 12: SC, Joinville, 10–200 m, 9.III.1973, Leg. H. Miers, R.K. Robbins collection, gen. prep. CF n°410 (USNM) (Fig. 11).

Description, diagnosis and recognition as a distinct species. Male FW length: 16.1 mm (SD = 0.9, N = 8). Female FW length: 15.7 mm (N = 1). Wing pattern (Figs 10, 11) and genitalia (Figs 25, 30) illustrated. The adult wing pattern of *O. moseri* is similar to that of the sympatric *O. morroensis* Faynel & Moser and to that of *O. cyanovenata* (D'Abrera); the species with which it was previously confused (Faynel 2008). *Oenomaus moseri* (Figs 25, 45) differs from *O. morroensis* (plate 11 in Faynel and Moser, 2008) by its male genitalia having (1) a smaller dorsal part of the valvae attached to the top of the ventral part, not to the bottom, (2) a swollen posterior part of the male penis, and (3) a larger posterior part of the saccus in lateral view. *Oenomaus moseri* differs from O. *cyanovenata* by (1) a wider DFW black margin at the tornus, (2) a central depression on the posterior edge of the eighth tergum, and (3) a swollen posterior part of the male penis. *Oenomaus moseri* differs from the sympatric *O. geba*

by lacking a white spot on the basal side of VHW cell Rs-M1 (Figs 10–12). The lack of geographical variation in the characters distinguishing *O. moseri* and *O. cyanovenata* argues against the hypothesis that the former is a geographical variant of the latter.

Preliminary data on divergence of "barcode" DNA sequence data is consistent with morphology. The divergence among three individuals of *O. moseri* (CF-LYC-012 & CF-LYC-063) is 0%, among four individuals of *O. cyanovenata* (CF-LYC-047, CF-LYC-048, & CF-LYC-049) is 0%. In contrast, the divergence between *O. moseri* and *O. cyanovenata* is more than 4% and between two *O. moseri* and a paratype of *O. morroensis* (CF-LYC-015) is more than 5%.

Etymology. It is with great pleasure that we name this distinctive species for our good friend and collaborator Alfred Moser. Alfred lives in Rio Grande do Sul and has made prodigious contributions to the knowledge of Lepidoptera from southern Brazil, including co-authoring papers on the taxonomy of *Oenomaus* and *Porthecla* (Faynel and Moser 2008, Faynel et al. 2011).

Biology. Robbins observed two males of *O. moseri* exhibiting territorial behavior on a hill top from 14:23 hours to 14:48 hours at Serra do Japi (SP, Brazil) on 12 April 1991 (vouchers in USNM). A male of *Oenomaus moseri* was reared by Hipólito Ferreira Paulino Neto in Itirapina, SP, Brazil on *Duguetia furfuracea* (A. St. Hil) Benth. and Hook. f. (Annonaceae), a plant of frequent occurrence in the cerrado. We identified the male from a digital image and from the locality where it was reared. However, it is possible that it is a male of *O. morroensis*, even though this species is not known to occur as far north as São Paulo.

Habitat and distribution. *Oenomaus moseri* occurs in lowland and lower montane forest in southern Brazil (Fig. 46).

New data for previously described species of Oenomaus

For each of the 21 previously described *Oenomaus* species, we give distribution, habitat, and remarks. We then note, where relevant, new information on taxonomy, intraspecific variation, behavior/biology, associated females, and COI DNA sequences. The species are treated in alphabetical order. *Oenomaus curiosa* and *O. melleus* are included in this section, even though their generic placement is yet unresolved (Faynel et al. 2011).

Oenomaus ambiguus Faynel http://species-id.net/wiki/Oenomaus_ambiguus

Distribution, habitat, and remarks. *Oenomaus ambiguus* is a poorly known, lowland species whose ventral wing pattern is virtually indistinguishable from those of *O. cortica* and *O. gaia*. It has been recorded from French Guiana and Amazonian Peru. The previous record from Amazonas, Brazil (Faynel 2008) was incorrect.

New material examined. French Guiana. 1♂: Bas Maroni, Guyane Française, gen. prep. CF n°319 (MNHN H-452). Peru.– 1♂: MD, Río La Torre, 300 m, Tambopata Res., 27.IX.1987, S.S. Nicolay, gen. prep. CF n°404 (USNM).

Female. Unknown.

COI DNA sequence. The paratype from Peru has been barcoded (CF-LYC-025), and the sequence is 2–3% divergent from those of *O. cortica*, *O. gaia* and *O. morroensis* (Table 1).

Oenomaus atena (Hewitson)

http://species-id.net/wiki/Oenomaus_atena

Distribution, habitat, and remarks. *Oenomaus atena* is a widely distributed lowland species that is reliably recorded from Costa Rica, Panama, western Ecuador, French Guiana, Venezuela, Peru, and Brazil (AM, MT). Most species with an "*atena*-like" ventral wing pattern have historically been identified as *O. atena*, which means that virtually all literature records for *O. atena* from before 2005 are unreliable.

New material examined. Costa Rica.– 13° : Guápiles, 850 ft. alt., June, Schaus and Barnes coll., genitalia on slide X-10-1946, W.D.F. 2333 (USNM). Panama.– 13° : Cerro Campana, 2000', XII-22-1963, G.B. Small, Genitalia 1992: 153 R.K. Robbins (USNM). Ecuador.– 13° : Esmeraldas, 25 km San Lorenzo-Lita Road, 1°10.0'N, 78°40.0'W, 100 m, VI.2003, San Francisco, R. Aldas & Robert C. Busby leg., gen. prep. CF n°343 (RCB). Peru.– 23° : MD, 30 km S.W. Pto. Maldonado, 300 m, 20.X.1983, S.S. Nicolay, Genitalia 1992: 163 R.K. Robbins (USNM); MD, 10 km north Puerto Maldonado, 200 m, $12^{\circ}36'S$, $69^{\circ}11'W$, 26–30.XI.1993, leg. C. Tello (USNM).

Female. The female of this species was determined by a pair collected *in copula* and was illustrated by Faynel (2008, fig. 2).

COI DNA sequence. Three specimens of *O. atena* have been barcoded, including a male from Peru (LO) (CF-LYC-084) and two females from French Guiana (CF-LYC-054 and CF-LYC-057). The latter two have the same brown dorsal wing pattern, ventral wing pattern, and genitalia as the female of *O. atena* found *in copula*. The three barcodes show 0.4% divergence.

Oenomaus atesa (Hewitson)

http://species-id.net/wiki/Oenomaus_atesa

Distribution, habitat, and remarks. *Oenomaus atesa* is a widespread species that has been recorded from Mexico, Panama, western Ecuador, French Guiana, Venezuela, Colombia, eastern Ecuador, Peru, and Brazil (AM, DF, MG, RJ, SP, SC). The vast majority of museum specimens were collected in the lowlands, but males have also been found at 1375–1700 m in western Ecuador and at 2200 m in western Colombia (Prieto and Dahners 2006).

New material examined. Venezuela.– 1 : Venezuela, Aragua, Rancho Grande, 1100 m, 29.V.1985, S.S. Nicolay leg., gen. prep. CF n°404 (USNM). Ecuador.– 23: Pichincha 5 km Nanegal-García Moreno Rd, 0°09.2'N, 78°39.4'W, 4.VI.2008, 1375–1700 m, Robert C. Busby leg., gen. prep. CF n°340 (RCB); Napo Province, 14 km S of Tena, 17–18.X.1996, 600 m, Robert C. Busby leg., gen. prep. CF n°347 (RCB). 1: Río Chuchuví, Lita vers San Lorenzo km12, 700 m (provincia de Esmeraldas), VIII.2001, Euclides Aldaz leg. (PB). **Peru**.– 1: LO, 180 m, San Salvador, 5 km NNW Contamana, 08°19'S, 75°01'W, 27.XI.2002, D.H. Ahrenholz leg., gen. prep. CF n°403 (USNM). **Brazil.**– 1: DF, Parque do Gama, 950 m, 14.V.1969, S.S. Nicolay leg., gen. prep. CF n°405 (USNM ENT 00180586).

Intraspecific variation. Despite substantive geographical variation in *O. atesa*, we lack sufficient material to determine if this variation might represent more than one species. Females from Venezuela and western Ecuador have more extensive dorsal blue and a somewhat lighter color than females from Panama, French Guiana, eastern Ecuador, and Peru. In addition, males from western Ecuador have more blue on the dorsal forewings than males from eastern Ecuador. However, this variation is small compared to that between males of *O. atesa* and *O. lea.* For example, the forewing dorsal blue area never reaches the cells from vein R3 to Cu1 as it does in *O. lea.* Structure of the female genitalia also varies geographically. Females from Venezuela and Peru have two processes at the posterior end of the lamella postvaginalis while a female from French Guiana had none (see Faynel 2006, p. 29).

Behavior/biology. Males exhibited territorial behavior on a hilltop in Panama (Canal Area, Gamboa, Cerro Pelado) from 13:15 to 15:30 hours (19 males, 10 different days during the months of January, February, March, April, August, September, October, and December, 15 vouchers in USNM). Similarly, territorial males on a hilltop in Brazil (Santa Catarina, Villa Nova, Serrinha) were observed from 14:40 to 14:55 hours (3 males, March, 3 vouchers in USNM).

Female. Females are associated with males by their ventral wing pattern, which is unique among the Eumaeini. Characters were noted for distinguishing the ventral wing pattern of *O. atesa* from that of *O. lea*.

COI DNA sequence. One male of *O. atesa* from French Guiana has been barcoded (CF-LYC-003).

Oenomaus brulei Faynel

http://species-id.net/wiki/Oenomaus_brulei

Distribution, habitat, and remarks. Faynel (2008) described *O. brulei* from one male collected in the lowlands of French Guiana. Since then, another male and female from French Guiana have been examined.

New material examined. French Guiana.– 1 $\stackrel{?}{\circ}$: Guyane, no date, S. Fernandez leg., CF-LYC-033 (CF). 1 $\stackrel{?}{\circ}$: Montagne des Singes, 5°07'N, 52°69'W, 5.XII.2007, T. Rosant leg., gen. prep. CF n°440, CF-LYC-034 (CF) (Fig. 14).



Figures 12–19. Oenomaus, newly associated females: adults (dorsal surface at left, ventral surface at right). 12 O. geba (Brazil) 13 O. magnus (French Guiana) 14 O. brulei (French Guiana) 15 O. gaia (Panama) 16 O. cyanovenata (Costa Rica) 17 O. cyanovenata (French Guiana) 18 O. taua (Panama) 19 O. taua (Ecuador).

Female. We associate a female (Figs 14, 31) which has the same ventral wing pattern as the male, which occurs in French Guiana (as do the known males), and which has a very similar COI DNA sequence to that of the males.

COI DNA sequence. Divergence among the three known specimens is 0.2%.

Oenomaus cortica (D'Abrera)

http://species-id.net/wiki/Oenomaus_cortica

Distribution, habitat, and remarks. This species occurs in wet lowland forest and is recorded from Panama, Guyana, Peru, and Brazil (PA, AM). *Oenomaus cortica, O. gaia,* and *O. ambiguus* have very similar wing patterns, but their genitalic structures are distinct.

New material examined. Panama.– 1∂: Gatún, C. Z., 2.V.1970, G.B. Small leg., Genitalia 1992: 13∂ R.K. Robbins (USNM). **Guyana.–** 1∂: Potaro Riv., VIII-IX.1902, C.B. Roberts, Genitalia 1992: 74∂ R.K. Robbins (FSMC). **Peru.–** 1∂: MD, Parque Manu, Pakitza 340 m, 11°55'48"S, 71°15'18"W, 14.X.1991, Leg. R. Robbins, Genitalia No. 1996: 3∂ R.K. Robbins (USNM ENT 00180044). **Intraspecific variation.** The male from Panama has the posterior edge of its 8th tergum more deeply incised than in others.

Female. Unknown. A female paratype of *O. cortica* from Espírito Santo, Brazil was illustrated in D'Abrera (1995), but no definitive evidence was presented to support this identification.

COI DNA sequence. Two males from Brazil, Pará have been sequenced (CF-LYC-051 and CF-LYC-052) and show 0.6% divergence.

Oenomaus curiosa Faynel & Moser

http://species-id.net/wiki/Oenomaus_curiosa

Distribution, habitat, and remarks. *Oenomaus curiosa* is a species of wet lowland forest that is recorded from French Guiana, Peru (LO, MD), and Brazil (RO).

New material examined. Peru. – 23: MD, 300 m, 30 km S. W. Pto Maldonado, 26.X.1983, S.S. Nicolay, Genitalia No. 1992: 253 R.K. Robbins (USNM); LO, 120 m, Pebas, river Amazonas, 03°19'S, 71°51'W, II. 2011, Ramírez leg. (CF). Brazil. – 13: RO, 62 km SW Ariquemes, Línea 20, lot 21, 23, 25 (Fazenda Rancho Grande), 11.X.1993, AVZ Brower, gen. prep. CF n°433 (OSAC).

Female. Unknown

COI DNA sequence. Two males from French Guiana, including one of the paratypes, have been sequenced (CF-LYC-036 and CF-LYC-037) and show 0.8% divergence.

Oenomaus cyanovenata (D'Abrera)

http://species-id.net/wiki/Oenomaus_cyanovenata

Distribution, habitat, and remarks. A species of very wet lowland forest, it has been recorded from Costa Rica, Panama, French Guiana, Venezuela, Bolivia, and Brazil (PA, AM). The previous record for Brazil (SC) was incorrect; this specimen is now treated as *O. moseri*.

New material examined. Costa Rica.– 1*(*: Guápiles, 850 ft. alt., Schaus and Barnes coll., Genitalia 1992: 76*(*) R.K. Robbins (USNM); **2** \square : Area de Conservación Guanacaste, voucher: D.H. Janzen & W. Hallwachs 97-SRNP-62841.1, Genitalia 2009: 30 \square R.K. Robbins (USNM) (Fig. 16); 97-SRNP-6283. **Panama.**– 1*(*: Colón, Piña, 100 m, 9.IV.1971, H.L. King, genitalia slide/vial #4710, prep. S.S. Nicolay (USNM). **French Guiana.**– **3** \square : Roura, Route de Kaw - PK 16, 18.VII.2004, C. Faynel leg., CF-LYC-053 (CF); Roura, Route de Kaw, 26.I.2005, J.Y. Gallard leg., gen. prep. CF n°441, CF-LYC-055 (CF) (Fig. 17); Roura, Route de Kaw - PK 8, 20.XII.2001, J.Y. Gallard leg., CF-LYC-056 (CF). **Brazil.**– **3** \square : PA, Santo Antônio do Tauá, Reserva Sonho Azul, 1°15'S, 48°03'W, 12.VI.2009, P. & J. Jauffret leg., CF-LYC-059 (CF); PA, Santo Antônio do Tauá, Reserva Sonho Azul, 1°15'S, 48°03'W, 8.V.2009, P. & J. Jauffret leg., CF-LYC-061 (CF).



Figures 20-25. Oenomaus male genitalia: ventral view at left (setae drawn only on the right side and penis removed), left lateral view in the middle (with the penis and valvae displaced ~45° to make them more visible), and dorsal view at right (with setae drawn only on the right side and penis removed).
20 O. mancha (holotype, Ecuador) 21 O. lea (holotype, Peru) 22 O. myrteana (holotype, Ecuador) 23 O. mentirosa (holotype, Peru) 24 O. andi (holotype, Ecuador) 25 O. moseri (holotype, Brazil).

Intraspecific variation. Females from French Guiana and Brazil, Pará (Fig. 17) are uniformly brown on the dorsal wing surface while the female from Costa Rica (Fig. 16) has the basal parts of both wings blue. Their genitalia, however, are uniform. Additionally, their COI DNA sequences are similar. This geographic variability is similar to that in *O. taua*.

Behavior/biology. Two females were reared in Costa Rica (97-SRNP-62841.1 and 97-SRNP-6283) from *Guatteria verrucosa* R.E. Fr. (Annonaceae) (adult vouchers in USNM). Details of the rearing records along with images of the immatures can be found in Janzen and Hallwachs (2012).

Female. Females of this species (Figs 16, 17, 32, 33) have the same ventral wing pattern as males, occur at the same localities, and have similar COI DNA sequences.



Figures 26–37. Oenomaus female genitalia: ventral view at left, lateral view on right. 26 O. mancha (paratype, Ecuador) 27 O. gwenish (holotype, Panama) 28 O. myrteana (paratype, Ecuador) 29 O. andi (paratype, Ecuador) 30 O. moseri (paratype, Brazil) 31 O. brulei (French Guiana) 32 O. cyanovenata (French Guiana) 33 O. cyanovenata (Costa Rica) 34 O. gaia (Panama) 35 O. geba (Brazil) 36 O. magnus (French Guiana) 37 O. taua (Panama).



Figures 38–45. *Oenomaus*, eighth abdominal tergum: ventral view, anterior edge at bottom. **38** $\stackrel{\circ}{\circ}$ *O. mancha* (holotype, Ecuador) **39** $\stackrel{\circ}{\circ}$ *O. lea* (holotype, Peru) **40** $\stackrel{\circ}{\circ}$ *O. mentirosa* (holotype, Peru) **41** $\stackrel{\circ}{\circ}$ *O. myrteana* (holotype, Ecuador) **42** $\stackrel{\circ}{\circ}$ *O. andi* (holotype, Ecuador) **43** $\stackrel{\circ}{\circ}$ *O. andi* (paratype, Ecuador) **44** $\stackrel{\circ}{\circ}$ *O. moseri* (holotype, Brazil) **45** Male genitalia in lateral view: *O. moseri* (left) and *O. morroensis* holotypes. Diagnostic characters (1), (2) and (3) are explained in the text.



Figures 46–47. Distributions. 46 O. mancha, O. gwenish, O. myrteana, O. moseri 47 O. andi, O. lea, O. mentirosa.

A female paratype of *O. cyanovenata* from Pará, Brazil was designated and illustrated in D'Abrera (1995) without definitive supporting evidence. This female has a different dorsal wing pattern than the female from Pará that we have associated with the male. We are skeptical of the biological validity of this paratype designation.

COI DNA sequence. Four males and seven females from French Guiana and Brazil, Pará were barcoded. One male (CF-LYC-046) is 6.7% divergent from the other three males, but its sequence is identical with that from a male of *O. magnus* (CF-LYC-020). Potential explanations for this result range from contamination to biologically significant, but until we have additional information, we omit this male from the following results. Divergence among the 10 other specimens of *O. cyanovenata* was 0.1%. The reared females from Costa Rica, which were barcoded in another project, are 0.4% divergent from the South American specimens.

Oenomaus druceus Faynel & Moser

http://species-id.net/wiki/Oenomaus_druceus

Distribution, habitat, and remarks. This species was described from one Brazilian (AM) male, which is the only known specimen. As noted, its genitalia are similar to those of *O. mentirosa*, but it has a distinctly different ventral wing pattern.

Female. Unknown.

Oenomaus floreus (Druce)

http://species-id.net/wiki/Oenomaus_floreus

Distribution, habitat, and remarks. This species occurs in lowland and lower montane habitats with wet or deciduous forest. It is recorded from eastern Ecuador and Brazil (AM, MT, DF, GO, PR).

New material examined. Ecuador.– 1 ?: Pastaza Province, 45 km Puyo-Arajuno Rd., 1000 m, 26.IX.1999, Robert C. Busby leg., gen. prep. CF n°342 (RCB). **Brazil**.– 2 ?: GO, 163 km W. Jataí S. Rita Araguaia, 850 m, 29.V.1969, S.S. Nicolay, genitalia slide/vial #4367, prep. S.S. Nicolay (USNM); PR, Highlands, 24.XI.1934, coll. Karl Schmitt, E.I. Huntington, Genitalia 1992: 19 ? R.K. Robbins (AMNH).

Female. Described by Faynel and Moser (2008).

Oenomaus gaia Faynel

http://species-id.net/wiki/Oenomaus_gaia

Distribution, habitat, and remarks. This species occurs in wet and dry lowland forest. It has been recorded from Panama, French Guiana, Venezuela, eastern Ecuador, Peru (LO, SM, UC, MD) and Brazil (PA, AM, RO, MT, GO). This species, *O. floreus*, and maybe *O. griseus* occur in drier forest than other species with an "*atena-*like" ventral wing pattern.

New material examined. Panama. – 1♂: Los Ríos, C. Z., 15.XII.1964, S.S. Nicolay leg., Genitalia 1992: 73♂ R.K. Robbins (USNM ENT 00180046). 2♀: Los Ríos, C. Z., 27.I.1965, S.S. Nicolay, gen. prep. CF n°430 (USNM) (Fig. 15); Los Ríos, C. Z., 19.XII.1964, G.B. Small, gen. prep. CF n°431 (USNM). **Ecuador.**– 1♂: Morona-Santiago 15 km S Gualaquiza, 850 m, 3°27.6'S, 78°33.1'W, 27.IX.2000, Robert C. Busby leg. (RCB). **Peru**.– 1♂: MD, Parque Manu, Pakitza 340 m, 11°55'48"S, 71°15'18"W, 15.X.1991, Leg. M. Casagrande, Genitalia No. 1992: 38♂ R.K. Robbins (USNM). **Brazil**.– 2♂: PA, Obidos, IX.1930, Ex coll. Le Moult, Genitalia No. 1992: 75♂ R.K. Robbins; PA, Santo Antônio do Tauá, Reserva Sonho Azul, 1°15'S, 48°03'W, 16.VII.2003, P. & J. Jauffret leg., CF-LYC-072 (CF); RO, 62 km SW Ariquemes, Línea 20, lot 21, 23, 25 (Fazenda Rancho Grande), 11.X.1993, AVZ Brower, gen. prep. CF n°411 (OSAC); GO, Pirenópolis, 820 m, 15°49'S, 48°59'W, E. Emery leg. (MC 255).

Female. Four males in the USNM were collected on hills on Los Ríos hill (approximately 9°00'32"N, 79°35'34"W) and in Cocolí (approximately 8°58'46"N, 79°35'59"W), Canal Area, Panama. These areas are drier (<2 m annual precipitation, Rand and Rand 1982) than the forest in which other *Oenomaus* with an "*atena*-like" wing pattern have been found in Panama. Four females from these two localities have the same ventral wing pattern as the males. Since no other males are known from these localities, we associate the sexes and illustrate the adult wing pattern and genitalia of one of these females (Figs 15, 34).

We also associate a female from Brazil, Pará (CF-LYC-072) with a male of *O. gaia* from French Guiana because they have the same ventral wing pattern and have similar barcode sequences (0.2%).

COI DNA sequence. As noted previously, interspecific variation in the barcode sequences of *O. ambiguus*, *O. cortica*, *O. gaia*, *O. morroensis* is less than 2%, in contrast to interspecific divergences among other species in *Oenomaus*. For example males of *O. gaia* (CF-LYC-023) and *O. cortica* (CF-LYC-052) are 0.8% divergent. Another male of *O. gaia* (CF-LYC-024) and *O. morroensis* (CF-LYC-015) are 1.1% divergent.

Oenomaus geba (Hewitson)

http://species-id.net/wiki/Oenomaus_geba

Distribution, habitat, and remarks. This species is a relatively uncommon inhabitant of lower montane forest in southern Brazil, so far known only from the state of Santa Catarina. Previously, it was known only from the male holotype, which lacks locality data.

New material examined. Brazil.– 5♂: SC, Highlands near Massaranduba-Blumenau, Collection E.I. Huntington No. 1009 (AMNH, x4); SC, Highlands near Massaranduba-Blumenau, Collection E.I. Huntington No. 1009, genitalia slide/vial #4705, prep. S.S. Nicolay, Allyn Museum Photo No. 022078-7, 8 VI (AMNH) . 2♀: SC, Rio Vermelho, São Bento do Sul, 10.III.1973, leg. Rank, gen. prep. CF n°414 (USNM ENT 00180041); SC, Highlands near Massaranduba-Blumenau, Collection E.I. Huntington No. 1009, genitalia slide/vial #4707, prep. S.S. Nicolay, Allyn Museum Photo No. 022078-9, 10 VI (AMNH).

Female. The female (Figs 12, 35) occurs in the same habitat as the male and has the same ventral wing pattern.

Oenomaus griseus Faynel & Moser

http://species-id.net/wiki/Oenomaus_griseus

Distribution, habitat, and remarks. This species appears to be endemic to Brazil's central plateau (DF).

Female. Unknown.

Oenomaus isabellae Faynel

http://species-id.net/wiki/Oenomaus_isabellae

Distribution, habitat, and remarks. This widespread South American species occurs in wet and dry lowland forests. It is recorded from French Guiana, Colombia, eastern Ecuador, Peru, Bolivia, and Brazil (AM, MG).

New material examined. Colombia.– 1: Muzo, 400b. 800 m, coll. Fassl (SMF). Ecuador.– 2: Morona-Santiago, Santiago (Hill North of Town), 3°02.3'S, 78°00.3'W, 350 m, 20.IX.2010, Robert C. Busby leg. (RCB); 27 km Santiago-Puerto Moreno Rd., 2°56.4'S, 77°49.5'W, 500–550 m, 17 IX 2005, Robert C. Busby, leg.

(RCB). **Peru.** -1 : JU, Aldea, 600–700 m, 1054/7455, 23.VIII.2003, J.J. Ramírez (MUSM). **Brazil**. -2: MG, km 500 Belo Horizonte-Brasília, Hwy, 11.IV.1973, C. Callaghan, genitalia slide/vial #4737, prep. S.S. Nicolay (USNM); AM, Rio Amazonas, Vila Nova (ca. Tonantins, 0252S/6748), 100 m, IX.1993, M. Büche leg. (MUSM). **Bolivia**. -1: Las Juntas, XII. 1913, Steinbach Acc. 5045, genitalia slide/vial #4743, prep. S.S. Nicolay (CMNH).

Female. The distinctive ventral wing pattern of this species allows identification of the female.

COI DNA sequence. Sequences from a Brazilian male (CF-LYC-006) and French Guiana female paratype (CF-LYC-007) diverge 3.0%.

Oenomaus jauffreti Faynel & Moser

http://species-id.net/wiki/Oenomaus_jauffreti

Distribution, habitat, and remarks. This species inhabits wet lowland forest. It is recorded from French Guiana, eastern Ecuador, Peru, Bolivia, and Brazil (PA, MT).

New material examined. Ecuador.– 13: Pastaza Province, 32 km S. of Puyo, 20–21.X.1996, 1000 m, Robert C. Busby leg., gen. prep. CF n°346 (RCB). Peru.– 13: LO, Agua Blanca, 0356/7328, 130 m, 10.XI.2005, J.J. Ramírez (MUSM). 22: JU, vic. Satipo, c. 800 m, Villa Esperanza, c. 11°16'S, 74°15'W, V.1983, leg. M. Callegari (USNM) ; LO, Cerros de Contamana, El Indio, 200 m, 10.IX.1986, P. Hocking (MUSM). Bo-livia.– 13: Río Songo, 750 m, coll. Fassl, Genitalia No. 2002: 53 R.K. Robbins (SMF).

Intraspecific variation. As noted by Faynel and Moser (2008), *O. jauffreti* is a variable species, especially ventrally. For example, the VHW basal spot in cell Sc+R1 is large and mostly white in French Guiana; is small, black with a white centered pupil in Brazil (MT), and is large, with black and white scales in Ecuador. The only element which seems to be stable is the presence of a white spot on the basal side of VHW cell Rs-M1.

Female. Females were associated with males by their characteristic ventral wing pattern (Faynel and Moser, 2008). Six specimens of *O. jauffreti* have been barcoded (four males and two females), including three male paratypes (CF-LYC-028, CF-LYC-029, CF-LYC-030) and one female paratype (CF-LYC-032). The six barcodes show 1.2% divergence.

Oenomaus magnus Faynel & Moser

http://species-id.net/wiki/Oenomaus_magnus

Distribution, habitat, and remarks. This is a poorly understood species that occurs in South American lowland forest. It has been recorded from French Guiana, Peru, Bolivia, and Brazil (AM, MT).

New material examined. French Guiana.– 1: Approuague - Mapaou, 4°31'N, 52°13'W, 29. XII. 2008, S. Fernandez leg. (CF) (Fig. 13). Peru.– 1: SM, Upper
Huallaga Valley, V-VI 2000, Purch. Thorne 7/01, gen. prep. CF n°428 (USNM). **Brazil**.– 1 \mathcal{J} : MT, Diamantino, Alto Rio Arinos, 5.X.1998, E. Furtado leg., gen. prep. CF n°446 (MC 254). **Bolivia**.– 1 \mathcal{Q} : "Thecla melleus Drc. \mathcal{Q} , Buenavista 750 m, Bolivia Steinbach., Modt. 22/2 1927 af, qui Steinbach Bolivia, Coll. C.S. Larsen, Faaborg, gen. prep. CF n° 449 (MNHN).

Female. We associate females from French Guiana (Figs 13, 36), Peru, and Bolivia with this species. They have the same ventral wing pattern, a similar geographic range, and limited COI DNA sequences are the same.

COI DNA sequence. The sequence of a female from French Guiana (CF-LYC-039) is the same as (0% divergence) that of the male paratype from Peru (CF-LYC-020). This female is the first record of *O. magnus* from French Guiana.

Oenomaus melleus (Druce)

http://species-id.net/wiki/Oenomaus_melleus

Distribution, habitat, and remarks. This species occurs in wet lowland forest. It is recorded from Nicaragua, Costa Rica, French Guiana, Guyana, Venezuela, Colombia, Peru, Bolivia, and Brazil (PA, PE, ES).

New material examined. Costa Rica.– 23° : Heredia, prov. Finca La Selva, 3 km S. Puerto Viejo, 10°26'N, 84°01'W, 26.VII.1992, leg. H.A. Hespenheide (USNM) ; prov. Heredia, F. La Selva, 3 km S. Pto. Viejo, 10°26'N, 84°01'W, 5.IV.1985, H.A. Hespenheide (USNM). 1° : Area de Conservación Guanacaste, voucher Janzen & Hallwachs #97-SRNP-62841, legs away for DNA, Genitalia 2009: 30° R.K. Robbins (USNM) (Fig. 20). **Guyana.–** 1° : Region 7 Lower Cuyuni River nr. Arimu R. 100', 6°34'N, 58°58'W, 2.IX.1991, leg. S. Fratello (USNM ENT 00180024). **Brazil.–** 1° : ES, Itaguassú, IX.1971, Paulo César Elias, A.C. Allyn Acc. 1971-38, genitalia slide/vial #4700, prep. S.S. Nicolay (USNM). 1° : PE, Recife, 5.I.1962, leg. Ebert (USNM).

Taxonomy. Faynel (2007, 2008) partitioned this species into a Transandean Region (terminology from Brown 1982) nominate subspecies and an Amazonian Region subspecies *O. melleus guyanensis* based on size and color of scales at the base of the VFW. The male genitalia of each taxon were the same. As noted in the next paragraph, the new material examined does not confirm this recognition of two taxa. For example, the Costa Rican specimens resemble the Amazonian ones. For this reason, we synonymize *O. melleus guyanensis* Faynel with *O. m. melleus* (Druce), **new synonym**.

Intraspecific variation. The wing pattern of *O. melleus* is highly variable. The type from Colombia and two specimens from Nicaragua and Venezuela are relatively large (male FW length = 16.8 mm, SD = 1.3, N = 3). They have a white spot on the basal part of VHW cell Rs-M1, no reddish scales on the basal part of ventral wing, and a black spot in VHW cell Cu1-Cu2. The specimens from French Guiana, Guyana, Brazil (PA), Venezuela and Peru (UC) are smaller (male FW length = 14.1 mm, SD = 0.4, N = 5). They have a white spot on the basal part of VHW cell Rs-M1, reddish scales on the basal part of VHW cell Rs-M1, reddish scales on the basal part of VHW cell Rs-M1, reddish scales on the basal part of VHW cell Cu1-Cu2. The males

from Costa Rica are also relatively small (male FW length = 14.7 mm, SD = 1.6, N = 3). They have no white spot on the basal part of VHW cell Rs-M1, no reddish scales on the basal part of ventral wing and a black spot in VHW cell Cu1-Cu2.

Female. Described by Faynel (2008).

Oenomaus morroensis Faynel & Moser

http://species-id.net/wiki/Oenomaus_morroensis

Distribution, habitat, and remarks. Described by Faynel and Moser (2008) from five males from Brazil (SC, RS), but no other specimens are known. It appears to be a species of lower montane and subtropical forest.

Intraspecific variation. A small white spot on VHW cell Sc+R1-Rs that is displaced basally (Faynel and Moser 2008) is present in the holotype, but not in the paratypes.

Behavior/biology. Although *O. morroensis* is unrecorded north of Santa Catarina, a reared male from São Paulo (see under *O. moseri*) could possibly be this species.

Female. Unknown.

COI DNA sequence. One paratype has been barcoded (CF-LYC-015). As already noted, this sequence is 5.0% divergent from the sympatric and superficially similar *O. moseri*.

Oenomaus nigra Faynel & Moser

http://species-id.net/wiki/Oenomaus_nigra

Distribution, habitat, and remarks. This species occurs in wet lowland forest. It has been recorded from Peru and Brazil (AM). As noted, the genitalia of this species are similar to those of the newly described *O. myrteana*.

New material examined. Peru.– 33° : LO, Agua Blanca, 0356/7328, 130 m, 17.V.2004, J.J. Ramírez leg. (MUSM, x3). **Brazil**.– 13° : AM, S. Paulo de Olivença, X.1983, Via Kesselring, Genitalia No. 1983: 133 $^{\circ}$ R.K. Robbins (USNM ENT 00180054).

Female. Unknown.

COI DNA sequence. One male of *O. nigra* from Peru has been barcoded (CF-LYC-148).

Oenomaus ortygnus (Cramer)

http://species-id.net/wiki/Oenomaus_ortygnus

Distribution, habitat, and remarks. This species occurs in many different habitats from sea level up to 1000 m. It is unique in the genus in that it is often found in highly disturbed habitats. It is the most common *Oenomaus* species in collections and

has been recorded from the United States, Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, French Guiana, Surinam, Guyana, Trinidad, Venezuela, Colombia, Ecuador, Peru, and many states throughout Brazil. As noted in the introduction, this species is a well-known pest of commercial Annonaceae.

Intraspecific variation. The blacks spots on ventral wings vary in size and the blue on the dorsal wings vary from light cyan to dark purple. The "*Thecla lauta* Draudt" phenotype from western Mexico is smaller and duller than individuals from the remainder of its range.

Behavior/biology. Males were territorial on hilltops between 14:00–15:15 hours in Panama (Canal Area, hilltops in Paraíso, 7 males during June and August, 6 vouchers in USNM) and between 14:29 and 15:15 on Serrinha in Brazil (hilltop in Santa Catarina, Villa Nova, 200 m, 3 males in March, vouchers in USNM).

Female. Both sexes are recognized by their ventral wing pattern, which is unique in the genus.

COI DNA sequence. Sequences from a Peruvian male (CF-LYC-147) and a Mexican male (CF-LYC-146) diverge 1.5%.

Oenomaus poirieri Faynel

http://species-id.net/wiki/Oenomaus_poirieri

Distribution, habitat, and remarks. This species occurs in wet lowland forest. It has been recorded from French Guiana and Brazil (PA, AM).

New material examined. Brazil.–1♂. Santarém, Amazons, A.H. Fassl, 3.IV.1920, gen. prep. CF n°317 (MNHN H-447).

Female. Described by Faynel (2008).

Oenomaus taua Faynel & Moser

http://species-id.net/wiki/Oenomaus_taua

Distribution, habitat, and remarks. This species is widespread in wet lowland forest. It is recorded from Guatemala, Panama, French Guiana, eastern Ecuador, Peru, and Brazil (PA, AM, RO). It is one of the more common species in the genus and mating pairs have been collected in Panama, Ecuador, and Brazil.

New material examined. Guatemala.– 13° : Cayuga, Sept., Schaus & Barnes coll., Genitalia No. 1992: 283 R.K. Robbins (USNM). **Panama.–** 23° : Canal Zone, Gamboa, 5.I.1979, Leg. R. Robbins, *in copula* 15:00, Genitalia No. 1982: 1253 R.K. Robbins (USNM ENT 00180050); Canal Zone, Summit, 17.III.1979, Leg. R. Robbins, *in copula* 15:00, gen. prep. CF n°423 (USNM). 29° : Canal Zone, Gamboa, 5.I.1979, Leg. R. Robbins, *in copula* 15:00, Genitalia No. 1982: 1269 R.K. Robbins (USNM ENT 00180051) (Fig. 18); Canal Zone, Summit, 17.III.1979, Leg. R. Robbins, *in copula* 15:00, gen. prep. CF n°424 (USNM). **Ecuador.–** 23° : Napo, 14 km Tena-Puyo Road, 1°06.7'S, 77°46.9'W, 600 m, X.2010 (Apuya), I. Aldas & Robert C. Busby leg., gen. prep. CF n°418 (RCB); Napo Province, 14 km S. of Tena, 600 m, 17–18.X.1996 (Apuya), mating pair, Robert C. Busby leg., gen. prep. CF n°345 (RCB). 1 \uparrow : Napo Province, 14 km S. of Tena, 600 m, 17–18.X.1996 (Apuya), mating pair, Robert C. Busby leg., gen. prep. CF n°417 (RCB) (Fig. 19). **Brazil**.– 1 $\stackrel{\frown}{\sim}$: RO, 160–350 m, vic. Cacaulândia, 10°32'S, 62°48'W, 19.X.1991, *in copula*, Leg. J. MacDonald, gen. prep. CF n°412 (USNM). 1 $\stackrel{\frown}{\sim}$: RO, 160–350 m, vic. Cacaulândia, 10°32'S, 62°48'W, 19.X.1991, *in copula*, Leg. J. MacDonald, gen. prep. CF n°413 (USNM); PA, Santo Antônio do Tauá, Reserva Sonho Azul, 1°15'S, 48°03'W, 2.III.2010, P. & J. Jauffret leg. (CF).

Intraspecific variation. Females from Brazil and Ecuador (Fig. 19) are uniformly brown on the dorsal wing surface while the female from Panama (Fig. 18) has the basal parts of both wings blue. Their genitalia, however, are uniform. This geographic variability is similar to that in *O. cyanovenata*.

Behavior/ biology. Territorial behavior on a hilltop in Panama (Canal Area, Gamboa, Cerro Pelado) was observed in January and August at 15:00 hours (vouchers in USNM). Two mating pairs were also collected on the same hilltop in January and March at 15:00 hours (vouchers in USNM).

Female. We illustrate adult females that were collected *in copula* (Figs 18–19) and the genitalia of one (Fig. 37).

COI DNA sequence. A female from Brazil, Pará (CF-LYC-064), which has a wing pattern similar to the females collected *in copula*, is 3.1% divergent from a male from Peru (CF-LYC-085).

Discussion

Taxonomy. A decade ago *Oenomaus* was a monotypic genus, but it now consists of 28 described species (albeit, it is still unclear if *O. melleus* and *O. curiosa* belong to *Oenomaus* or *Porthecla*). Further, if a phylogenetic analysis shows that *Porthecla* is paraphyletic in terms of *Oenomaus*, which is possible because *Porthecla* was distinguished by character states that may be plesiomorphic, then Oenomaus will be one of the most species-rich eumaeine genera with 40 species (Robbins 2004).

There are three biological reasons why the diversity of *Oenomaus* was not recognized until recently. First, about ³/₄ of the species have an indistinguishable, or barely distinguishable, ventral wing pattern that is similar to that of *O. atena* (e.g., Figs 12–19). Among species with this wing pattern, there is a great diversity of male genitalic forms that were first documented by Faynel (2006, 2008) and Faynel and Moser (2008). Second, the ventral wing pattern of a few species is different from that of *O. atena* (e.g., Figs 1–7), but similar to that of sympatric species that are now considered to be distantly related. For example, Draudt (1919–1920) in Seitz grouped *O. ortygnus* (the type species of *Oenomaus*), now placed in the *Panthiades* Section, with *Atlides rustan* (Stoll), now placed in the *Atlides* Section (Robbins 2004). Similarly, he placed *O. atesa* in a group with *Enos mazurka* (Hewitson) in the *Brangas* Section. *Oenomaus myrteana*, which is described in this paper, closely resembles *Enos myrtea* while *O. mentirosa*, also newly described, has a ventral wing pattern that resembles species in *Porthecla*, *Olynthus* Hübner, *Janthecla* Robbins & Venables, and *Atlides* Hübner (documented in Faynel et al. 2011). Third, many *Oenomaus* species are exceedingly rare in collections. Indeed, three species are still known from only one individual each.

DNA barcoding. Thirty-eight *Oenomaus* males belonging to 19 species have been successfully "barcoded" (>200 bp) (extraction and sequencing methods given in Hajibabaei et al. 2006). For those nine species for which there is more than one barcode (Table 1), intraspecific divergence calculated on the Bold web site (http:// www.boldsystems.org/views/login.php) using the Kimura 2 parameter with sequences aligned by BOLD varied from 0% to 1.6%. Interspecific divergence (Table 1) varied from 0.8% to 9.7% (672 comparisons, mean distance: 6.1%). It was usually greater than 4% except in the *O. cortica* species group (*O. gaia, O. cortica, O. morroensis*), where it was about 1%. Similarity in COI sequences among closely related species is well-established (e.g., Burns et al. 2007).

Male-female associations. Associating males and females in *Oenomaus* is sometimes very difficult. Only eight of the 28 recognized species previously had the sexes associated. In this paper we associate the sexes of another ten species based on mating pairs collected *in copula* and on similarity of ventral wing patterns, habitats, geographic distributions, and mitochondrial COI DNA sequences. The DNA "barcodes" have great potential (e.g., Janzen et al 2009), especially if there are large samples from geographically diverse sites.

Biology. *Oenomaus ortygnus* is a well-known pest of cultivated soursop (also called guanábana, *Annona muricata* L., Annonaceae) and relatives (e.g., Dampf 1929, Fennah 1937, Ballou 1945, Guagliumi 1965, 1967, Araque 1967, d'Araújo e Silva et al. 1967–1968, Leal 1970, Kendall 1975, Domínguez 1978, Peña et al. 2002, Castañeda-Vildózola et al. 2011). As noted in the results of this paper, two other *Oenomaus* species have now been reared, and Annonaceae (*Duguetia, Guatteria*) is a food plant for each. Although data are yet too scanty to ask why *O. ortygnus* is the only *Oenomaus* species that has been recorded as a pest on cultivated Annonaceae, we note that it is also the only *Oenomaus* species that is regularly found in disturbed habitats.

Most *Oenomaus* species inhabit relatively undisturbed lowland wet forest, but some species seem to be restricted to other habitats. *Oenomaus andi* is montane, being found so far only above 1450 m, while *O. geba* is known only from lower montane forest. *Oenomaus morroensis* occurs so far only in subtropical and lower montane forest. *Oenomaus druceus* has been found only in scrubby deciduous forest. A number of other *Oenomaus* species have broader habitat requirements. Some wet lowland species also occur in montane habitats, for which *O. atesa* and *O. moseri* are representative examples. Others, such as *O. floreus, O. gaia*, and *O. isabellae*, may inhabit dry deciduous forest. As previously noted, *O. ortygnus* is the only *Oenomaus* species that is regularly found in both undisturbed and disturbed habitats.

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RESEARCH ARTICLE



Three new cryptic species of *Euglossa* from Brazil (Hymenoptera, Apidae)

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Abstract

Three new species of orchid bees are described and figured from the Amazon and Atlantic forests of Brazil. *Euglossa clausi* **sp. n.**, *E. moratoi* **sp. n.**, and *E. pepei* **sp. n.** are distinguished from their close congeners *E. crassipunctata* Moure, *E. parvula* Dressler, and *E. sapphirina* Moure, previously placed in the subgenus *Euglossa* (*Glossurella*) Dressler, 1982, a demonstrably paraphyletic assemblage requiring serious reconsideration. Their affinities with related species are discussed and pertinent characters are figured.

Keywords

Amazon Basin, Atlantic Forest, Apoidea, Anthophila, Euglossini, orchid bees, new species, taxonomy

Introduction

The taxonomy of the Neotropical orchid bees (Apinae: Euglossini *sensu* Michener (1944, 2007) [it should be noted that the Brazilian melittological community considers this a subtribe of Apini in a less hierarchical classification of Apoidea whereby bees are relegated to a single family; the differences, however, are semantic and the concepts

of included taxa are equivalent]) received a tremendous boost after the 1960s, when it was realized that males could be attracted easily to synthetic fragrances that mimic the odor of some flowers, especially orchids (Vogel 1966; Dodson et al. 1969). Many unknown species were thus captured, recognized, and subsequently described (e.g., Moure 1968, 1969, 1970; Dressler 1978, 1982a, 1982b, 1982c). Although some orchid bee species continued to be described after this flurry of activity, a period of relative taxonomic stasis developed during late 1980s and through the 1990s, until the end of the 90s when new species again began to be described (e.g., Engel 1999). In addition to a critical reappraisal of historical type material, otherwise 'hidden' sibling and cryptic species were recognized and this led to a new wave of descriptive work over the last decade (e.g., Oliveira and Nemésio 2003; Roubik 2004; Ramírez 2005, 2006; Parra et al. 2006; Rasmussen and Skov 2006; Nemésio 2006, 2007a, 2007b, 2008, 2009, 2010a, 2011b, 2011c, 2011d, 2012; Oliveira 2006, 2011; Bembé 2007, 2008; Hinojosa-Díaz and Engel 2007, 2011a, 2011b; Nemésio and Bembé 2008; Hinojosa-Díaz et al. 2011; Eltz et al. 2011; Faria and Melo 2011, 2012; Nemésio and Ferrari 2012).

Herein we continue this tradition with the recognition and description of three new species of *Euglossa* Latreille. All three species are closely related to species until recently placed in the paraphyletic subgenus *Glossurella* Dressler (Ramírez et al. 2010; Hinojosa-Díaz 2010, in prep.) and here left as *incertae sedis* (as suggested by Hinojosa-Díaz and Engel 2011b; Hinojosa-Díaz et al. 2012). Two of the new species, *Euglossa clausi* sp. n. and *E. moratoi* sp. n., are closely related to the Central American *E. crassipunctata* Moure and *E. sapphirina* Moure and have been identified as *E. crassipunctata* both in the Amazon and Atlantic forests. However, the species can be differentiated not only on the basis of coloration and size, but also in the male terminalia. The third species, *E. pepei* sp. n., is described from the Atlantic forest of southern Bahia, and is one of the most distinctive, apparently sharing some characters with the Amazonian *E. parvula* Dressler, but differing in terms of its genitalia.

Material and methods

Material considered herein is deposited in the collections of the Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (**UFMG**); Florida Museum of Natural History, Gainesville, Florida, USA (**FMNH**); and the Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA (**SEMC**). General morphological terminology for bees follows Engel (2001) and Michener (2007), while specific terms for orchid bees follows Engel (1999), Nemésio (2009: 10, 12), and Hinojosa-Díaz (2008). Metasomal terga and sterna are referred to as T1, T2, ... T*n*, and S1, S2, ... S*n*, respectively. Integumental and setal coloration are those observed by eye under a Leica MZ12 or Olympus SZX-12 stereomicroscope with reflected fiber optic illumination. Measurements provided are those of the name-bearing holotypes. The taxonomic arrangement of genera, subgenera, and species adopted herein follows that of Nemésio and Rasmussen (2011). Material of representative other euglossine species

was examined from UFMG, SEMC, and FMNH. Label data are given with each label separated by "". When data of a label of the subsequent specimen are identical to those of the previously cited specimen, only "idem" is provided. We have provided genitalic characters to distinguish the species. There is variation in the genitalia, particularly in the form of the gonostylus, within some species of *Euglossa* but the presence of such variation within an individual species is not consistent throughout the genus (e.g., Hinojosa-Díaz and Engel 2011a). For the moment there does not appear to be significant genitalic variation within the species considered herein but this should be clarified should the new species herein be discovered at more distant geographic locales. Regardless of this variation, important characters for the recognition of species, species groups, and even larger clades are present within Euglossini (Hinojosa-Díaz 2008).

Systematics

Genus Euglossa Latreille

All three species described herein are left as *incertae sedis* in regard to subgenus (following the suggestion of Hinojosa-Díaz and Engel 2011b; Hinojosa-Díaz et al. 2012), but they share a number of characters which suggest they are closely related such as: small bees with dark blue clypeus, very coarsely punctate mesepisternum and coarsely punctate mesoscutum, anterior mesotibial tuft entire, sternal tufts in semi-circular depressions. Specific characters of each species are given below, as well as between the new species and *E. crassipunctata* and *E. sapphirina* in the diagnoses and discussion (*vide infra*).

Euglossa clausi sp. n.

urn:lsid:zoobank.org:act: http://species-id.net/wiki/Euglossa_clausi Figures 1–11

Holotype. \eth , with the following data: "Euglossini do PERD, Pq. E. Rio Doce, 3859-11105" and "Marliéria, MG, Brasil, 04/07/1999, A. Nemésio" (UFMG). Details of the type locality are: Parque Estadual do Rio Doce (19°43'S, 42°34'W; 200 m a.s.l.), in the municipality of Marliéria, state of Minas Gerais, southeastern Brazil.

Paratypes. 3♂♂, with the following label data: "Euglossini do PERD, Pq. E. Rio Doce, 3859-11106" and "Marliéria, MG, Brasil, 04/07/1999, A. Nemésio"; "idem, 3872-11131" and "idem" (UFMG); "idem, 3876-11137" and "idem" (UFMG). 1♂, "Brazil, E. Santo, No. Linhares, 12.xi.1968, R.L. Dressler" (FMNH). 1♂, "Brazil, Bahia, Res. Mte. Pascoal, 8.xi.1968, R.L. Dressler" (FMNH). 1♂, "Brazil, E. Santo, Conceicao da Barra, 10.xi.1968, R.L. Dressler" (FMNH). 1♂, "Brazil, E. Santo, 19.vi.1971, H. Kennedy, cineole" (SEMC). 1♂, "Brazil, Bahia, Itabuna, 6.xi.1968, R.L. Dressler" (SEMC).



Figures 1–3. Photomicrographs of paratype male of *Euglossa clausi* Nemésio and Engel, sp. n. 1 Lateral habitus 2 Dorsal habitus (arrow points to rounded pronotal angle) 3 Facial aspect.

Diagnosis. *Euglossa clausi* can be distinguished readily from both *E. crassipunctata* and *E. sapphirina* owing to its larger size (ca. 15% larger than both species), and a combination of integumental coloration that exactly matches neither of the aforementioned species (and for this reason has been confused with both: *vide* Nemésio 2009: 85–87). The paraocular ivory markings in *E. clausi* are wider below (Fig. 3) than in both *E. crassipunctata* and *E. sapphirina*. The metatibia and sterna (Figs 1, 6) are blue, contrasting



Figures 4–6. Tibial characters of *Euglossa clausi* Nemésio and Engel, sp. n. 4 Outer surface of mesotibia5 Detail of mesotibial tufts 6 Outer surface of metatibia.

the otherwise green metasoma, a color combination not found in *E. crassipunctata* (green metasoma, including the sterna, and metatibia) and *E. sapphirina* (blue throughout). The apical setae of S7 of *E. clausi* are distributed throughout the invaginated section and the posterolateral projections of the anterior section of S8 angled but not prominent, instead being more strongly developed in *E. moratoi* (Figs 7, 8), as is the development of the basolateral projections of the posterior section. The gonostylus of *E. clausi* is more straight or even slightly downcurved (Figs 9–11), relative to that of *E. moratoi* (Figs 23–25), and both differ from the terminalia of *E. crassipunctata* (Figs 12–15).

Description. \mathcal{J} : Body length ca. 10.0 mm; forewing length ca. 7.7 mm; head width 4.4 mm; interorbital distance at level of antennal sockets 2.5 mm; maximum interorbital distance 2.7 mm; labiomaxillary complex in repose reaching tip of body; scape length 0.8 mm; compound eye length 2.7 mm; mesoscutellum width 2.5 mm, length 1.2 mm; abdominal width 4.2 mm.

Coloration and vestiture: Clypeus and upper frons dark blue, remainder of head greenish-blue (Fig. 3); ivory paraocular markings well developed, reaching malar area, wider below; anterior surface of antennal scape black with very minute ivory marking in some specimens (including holotype); mesoscutum, mesoscutellum, and metasoma bluish-green (Figs 1, 2). Wing membranes lightly infumate. Pubescence very sparse, predominantly fulvous setae on metasoma and around antennal sockets, black and fulvous setae on mesosoma, black setae especially on mesoscutum (compared to predominantly fulvous setae; velvet area occupying all ventral surface of mesotibia, posterior mesotibial tuft approximately one-third size of anterior tuft, almost an isosceles triangle in shape, merging with anterior tuft; anterior mesotibial tuft oval, about three times larger than posterior tuft (Figs 4, 5); metatibia oblong-rhomboid, inflated (Fig. 6).

Punctation: Mesoscutum with punctation separated by a puncture width or less, with large circular punctures; punctures on mesoscutellum sparser than on mesos-



Figures 7–11. Male terminalia of *Euglossa clausi* Nemésio and Engel, sp. n. **7** Seventh metasomal sternum **8** Eighth sternum (note that relative proportions of the anterior section to the posterior section may be distorted owing to position of sclerite when photographed) **9** Genital capsule, dorsal view **10** Genital capsule, lateral view **11** Genital capsule, ventral view.

cutum medioposteriorly, separated there by a puncture width or greater, with larger circular punctures. Punctation on discal base of T1 with large circular punctures of roughly same size more clearly defined medially than in other species and separated by less than a puncture width; punctures of T1–T6 dense, comprised of minute circular punctures; punctures on T7 sparser than on preceding terga, with large circular punctures; S2 with small, widely-separated tufts.

Terminalia: Male terminalia as in figures 7–11. S7 slightly invaginated mesally, forming a shallow incision with converging sides forming angle of ~110°, lateral sections faintly curved; apical setae throughout invaginated section, comprising seven alveoli (with one seta each) on each side; notospiculum weak, slightly divided apically, posterolateral projections of anterior section weak, not prominent; posterior section triangular, sharply pointed, with basolateral points not as sharply developed as in *E. moratoi*, slightly more rounded; anterior-most section of gonobase projected ventrally, forming angle of ~100° with remainder of ventral edge; gonostylus simple ('type V' of Ospina-Torres et al. 2006), lateral lobe pointed and slightly curved downwards; gonostylar setae long throughout; dorsal process of gonocoxa well developed, apical process evenly rounded laterally.



Figures 12–15. Male terminalia of *Euglossa crassipunctata* Moure. **12** Eighth metasomal sternum (note that relative proportions of the anterior section to the posterior section may be distorted owing to position of sclerite when photographed) **13** Genital capsule, dorsal view **14** Genital capsule, lateral view **15** Genital capsule, ventral view.

♀: Unknown.

Etymology. The specific epithet is a patronym honoring Dr. Claus Rasmussen, noted corbiculate bee biologist and systematist, in recognition of his years of kind collegiality.

Baits. Specimens of this species have been collected mostly from baits of cineole and vanillin, while a few specimens were collected from skatole.

Geographic distribution. *Euglossa clausi* sp. n. is a widespread bee in the Atlantic forest. Males have been collected from the state of Pernambuco in the north, to the northern portion of the state of São Paulo in the south (*vide* Nemésio 2009: 115 for specific locations where this species has been recorded).

Comments. Specimens of this species had been labeled in collections under the nomen nudum "*cyanifrons*". It may be that additional material is located in other institutions under this name. In addition, individuals of this species were treated in the literature as *E. sapphirina* (Tonhasca et al. 2002a, 2002b, 2003; Neves and Viana 2003; Nemésio and Silveira 2006, 2007) or *E. crassipunctata* (Milet-Pinheiro and Schlindwein 2005; Moura and Schlindwein 2009; Nemésio 2009, 2010b, 2011a, 2011b). *Euglossa moratoi* sp. n. urn:lsid:zoobank.org:act: http://species-id.net/wiki/Euglossa_moratoi Figures 16–25

Holotype. *(*), with the following data: "EIA Porto Trombetas, Cipó I, Zona Leste, 12200-36025" and "Oriximiná, PA, Brasil 25/02/2007, R. B. Martines" (UFMG). The type locality is: Porto Trombetas, in the municipality of Oriximiná, state of Pará, northern Brazil.

Paratypes. 10 ♂♂, with the following label data: "EIA Porto Trombetas, Monte Branco 2, Zona Leste, 11567-34328" and "Oriximiná, PA, Brasil 11/12/2006, R. B. Martines" (UFMG); "idem, 11575-34366" and "idem" (UFMG); "idem, 11578-34374" and "idem" (UFMG); "idem, Cipó 2, Zona Leste, 11634-34512" (SEMC) and "idem, 13/12/2006" and "idem" (UFMG); "idem, Teófilo 2, Zona Leste, 11545-34254" and "idem, 10/12/2006" (UFMG); "ParNa S. do Divisor, 12512-36708" and "Mâncio Lima, AC, Brasil, 21/11/1996, E. F. Morato" (UFMG); "idem, 12541-36759" and "idem" (UFMG); "14507-42692" and "Santarém, PA, Brasil, 11/12/1978, A. Raw", (UFMG); "14917-43369" and "Manaus, AM, Brasil, 08/10/1988, E. F. Morato" (UFMG); "Santa Maria, 04°13'S, 55°58'W, 14396-42535" and "Itaituba, PA, Brasil, 18/01/1979, J. M. F. Camargo" (UFMG).

Diagnosis. Euglossa moratoi sp. n. can be distinguished most easily from E. crassipunctata, E. sapphirina, and E. clausi due to its small size (ca. 20% smaller than the other species), the projecting pronotal dorsolateral angle which is more acute (slightly pointing) at its apex (differing from the rather bluntly rounded and non-projecting angle in all other species in the crassipunctata group) (Fig. 17; cf. figure 2), and the longer posterior mesotibial tuft relative to those in E. crassipunctata, E. sapphirina, and E. clausi (Figs 19, 20); photographs of the holotypes of E. crassipunctata and E. sapphirina are in Nemésio 2009: 87). The paraocular ivory markings in *E. moratoi* are not as wide below as in the other three species (Fig. 18). Moreover, E. moratoi is the least bluish of all four species in this complex, with bluish coloration only on the clypeus and upper frons, mesoscutum, and S2 (Figs 16-18), although there is some variation whereby the blue is slightly more extensive but still always less so than the other species. Euglossa crassipunctata and E. clausi, on the other hand, have strong bluish hues on the metasoma, particularly the sterna and also on the metatibia in the latter species. *Euglossa sapphirina* is an entirely bluish-violet bee. The apical setae of S7 of *E. moratoi* are restricted to the very outer sides of the invaginated section, whereas such setae are distributed throughout the invaginated section in E. clausi, although these sterna are otherwise virtually identical between the two species. The posterolateral projections of the anterior section of S8 in *E. moratoi* are strongly prominent and angled (Fig. 22), while they are distinctly weaker in E. clausi, as is the development of the basolateral projections of the posterior section. The gonostylus of E. moratoi is comparatively shorter than in E. clausi and slightly upcurved (in E. clausi it is more straight or even slightly downcurved) (Figs 23-25). Euglossa moratoi is among the smallest of all Eu-



Figures 16–18. Photomicrographs of paratype male of *Euglossa moratoi* Nemésio and Engel, sp. n. 16 Lateral habitus 17 Dorsal habitus (arrow points to projected pronotal angle) 18 Facial aspect.

glossa. While the holotype is approximately 8.0 mm in length, some specimens barely exceed 7.0 mm.

Description. \mathcal{J} : Body length ca. 8.0 mm; forewing length ca. 6.7 mm; head width 3.7 mm; interorbital distance at level of antennal sockets 2.1 mm; maximum interorbital distance 2.2 mm; labiomaxillary complex in repose reaching tip of body; scape length 0.56 mm; compound eye length 2.4 mm; mesoscutellum width 2.0 mm, length 0.93 mm; abdominal width 3.4 mm.



Figures 19–21. Tibial characters of *Euglossa moratoi* Nemésio and Engel, sp. n. 19 Outer surface of mesotibia 20 Detail of mesotibial tufts 21 Outer surface of metatibia.

Coloration and vestiture: Clypeus and upper frons dark blue, remainder of face greenish (Fig. 18); ivory paraocular markings well developed, reaching malar area, not very wide below; anterior surface of antennal scape black; mesoscutum bluish-green, mesoscutellum and metasoma green (Figs 16, 17). Wing membranes lightly infumate. Pubescence very sparse, predominantly fulvous on metasoma and around antennal sockets, black and fulvous setae on mesosoma (compared to predominantly black setae in *E. clausi*). Protibia and probasitarsus fringed with dense, fulvous setae; velvet area occupying all ventral surface of mesotibia, posterior mesotibial tuft approximately nearly one-third size of anterior tuft, triangular, slightly long and merging with anterior tuft; anterior mesotibial tuft oval, 2.5 times larger than posterior tuft (Figs 19, 20); metatibia oblong-rhomboid, inflated (Fig. 21).

Punctation: Mesoscutum with large circular punctures separated by a puncture width or less except anteromedially separated by a puncture width or greater particularly medially; punctures on mesoscutellum sparser than on disc of mesoscutum, with larger circular punctures separated by a puncture width or greater except along borders punctures separated by less than a puncture width. Punctation on discal base of T1 with large circular punctures of roughly same size more clearly defined medially and separated by less than a puncture width; punctation on T1–T6 dense, comprised of small hexagonal punctures; on T7 sparse relative to preceding terga, with large circular punctures; S2 with very small, widely-separated, semicircular tufts.

Terminalia: Male terminalia as in figures 22–25. S7 largely as in *E. clausi*, with posterior margin of S7 slightly invaginated mesally, forming a shallow incision with converging sides forming an angle of ~110°, lateral sections slightly curved; apical setae only on outer sides of invaginated section, comprising four alveoli (with one seta each) on each side; notospiculum weak, slightly divided apically, posterolateral projections of anterior section large and pronounced; posterior section triangular, sharply pointed



Figures 22–25. Male terminalia of *Euglossa moratoi* Nemésio and Engel, sp. n. **22** Eighth metasomal sternum (note that relative proportions of the anterior section to the posterior section may be distorted owing to position of sclerite when photographed) **23** Genital capsule, dorsal view **24** Genital capsule, lateral view **25** Genital capsule, ventral view.

apically, with prominent basolateral points; anteriormost section of gonobase curved ventrally forming an angle of ~100° with remainder of ventral edge; gonostylus simple ('type V' of Ospina-Torres et al. 2006), lateral section with lobe pointed and slightly curved upwards (*sensu* Hinojosa-Díaz 2008); gonostylar setae long throughout; dorsal process of gonocoxa well developed, apical process evenly rounded laterally.

♀: Unknown.

Etymology. The specific epithet is a patronym honoring Dr. Élder Ferreira Morato, noted entomologist and close colleague of the senior author.

Baits. Specimens of this species have been collected mostly at baits of vanillin, although a few specimens were also attracted to cineole, eugenol, and skatole.

Geographic distribution. *Euglossa moratoi* seems to be widespread in the Amazon Basin. Males have been collected from the westernmost part of the Brazilian Amazon (Nemésio and Morato 2004, 2006; Storck-Tonon et al. 2009; Oliveira et al. 2010) to the state of Pará in the east, where the holotype and some paratypes were collected. We have not examined the individuals identified as *E. crassipunctata* in Rasmussen

(2009), but it is possible that those also belong to *E. moratoi* or perhaps yet another undescribed species (this seems the most likely of the two scenarios).

Comments. Specimens of this species have been treated as *E. crassipunctata* in the literature (Nemésio and Morato 2004, 2006; Storck-Tonon et al. 2009; Oliveira et al. 2010).

Euglossa pepei sp. n.

urn:lsid:zoobank.org:act: http://species-id.net/wiki/Euglossa_pepei Figures 26–36

Holotype. *(*³), with the following data: "Euglossina da Hileia Baiana, PN Pau Brasil, 19679-56729" and "Porto Seguro, BA, Brasil, 19/04/2009, A. Nemésio" (UFMG). Details of the type locality are: Parque Nacional do Pau Brasil (16°31'S, 39°17'W; 90 m a.s.l.), in the municipality of Porto Seguro, state of Bahia, northeastern Brazil.

Paratypes. 433, with the following label data: "Euglossina da Hileia Baiana, PN Pau Brasil, 19641-56644" and "Porto Seguro, BA, Brasil, 17/04/2009, A. Nemésio" (UFMG); "idem, 19659-56671" and "idem, 18/04/2009" (UFMG); "idem, 19706-56790" and "idem, 20/04/2009" (UFMG), and "Euglossina da Hileia Baiana, PN Descobrimento, 20601-58992" and "Prado, BA, Brasil, 18/12/2008, A. Nemésio" (SEMC).

Diagnosis. *Euglossa pepei* is the most distinctive of the species of *crassipunctata* group. The shape and size of the anterior mesotibial tuft and the presence of a minute posterior tuft (Figs 29, 30) is most similar to that observed in *E. parvula* Dressler. However, both species can be separated by the larger size of the oval anterior tuft and the smaller glandular scar of the metatibia in *E. pepei*. In regards to the terminalia, S8 in *E. pepei* is distinctly more slender (*cf.* figures 33 and 37), and the gonostylus is more pronounced (*cf.* figures 34–36 versus 38–40). In addition, the bluish coloration is practically restricted to the head and discal base of the mesoscutum, and the sterna are golden green, the latter feature contrasting with other species in the group for which there are at least present some bluish hues.

Description. ♂: Body length ca. 9.5 mm; forewing length ca. 7.7 mm; head width 3.7 mm; interorbital distance at level of antennal socket 2.1 mm; maximum interorbital distance 2.6 mm; labiomaxillary complex in repose reaching apex of body; scape length 0.7 mm; compound eye length 2.7 mm; mesoscutellum width 2.3 mm, length 1.1 mm; abdominal width 3.8 mm.

Coloration and vestiture: Clypeus and upper frons dark blue, remainder of head greenish (Fig. 28); ivory paraocular markings well developed, reaching malar area but not particularly wide below; anterior surface of antennal scape black; discal base of mesoscutum blue, remainder of mesoscutum, mesoscutellum, and metasoma green (Figs 26, 27). Wing membranes lightly infumate. Pubescence very sparse, predominantly fulvous setae on metasoma and around antennal sockets, black and fulvous setae on mesosoma, black setae especially prominent on mesoscutum (compared to



Figures 26–28. Photomicrographs of paratype male of *Euglossa pepei* Nemésio and Engel, sp. n. 26 Lateral habitus 27 Dorsal habitus 28 Facial aspect.

predominantly fulvous setae in *E. parvula*). Protibia and probasitarsus fringed with dense, fulvous setae; velvet area occupying all ventral surface of mesotibia, posterior mesotibial tuft very small, less than 1/30 of area of anterior tuft; anterior mesotibial tuft oval, very large, occupying approximately one quarter of velvet area length (Figs 29, 30); metatibia oblong-rhomboid, inflated (Fig. 31).

Punctation: Mesoscutum with circular punctures of two different sizes separated by less than a puncture width, those anterolaterally nearly contiguous; punctures on mesoscutellum more widely spaced than those of mesoscutal disc, with larger circular punctures separated by a puncture width or slightly less in medial third otherwise separated by less than a puncture width. Punctation on discal base of T1 with large circular punctures, punctures weak and separated by less than a puncture width; on distal part of T1 and T2–T6 dense, consisting of minute circular punctures; on T7 dense, with large circular punctures; S2 with very small, almost inconspicuous, widely-separated tufts.



Figures 29–31. Tibial characters of *Euglossa pepei* Nemésio and Engel, sp. n. 29 Outer surface of mesotibia 30 Detail of mesotibial tufts 31 Outer surface of metatibia.



Figures 32–36. Male terminalia of *Euglossa pepei* Nemésio and Engel, sp. n. **32** Seventh metasomal sternum **33** Eighth sternum (note that relative proportions of the anterior section to the posterior section may be distorted owing to position of sclerite when photographed) **34** Genital capsule, dorsal view **35** Genital capsule, lateral view **36** Genital capsule, ventral view.



Figures 37–40. Male terminalia of *Euglossa parvula* Dressler. **37** Eighth metasomal sternum (note that relative proportions of the anterior section to the posterior section may be distorted owing to position of sclerite when photographed) **38** Genital capsule, dorsal view **39** Genital capsule, lateral view **40** Genital capsule, ventral view.

Terminalia: Male terminalia as in figures 32–36. Posterior margin of S7 deeply invaginated mesally, lateral sections almost straight; apical setae only on two apexes of invaginated section; notospiculum weak, slightly divided apically, posterolateral projects distinct (in this regard more similar to *E. clausi, E. moratoi*, and *E. parvula*); posterior section triangular, elongate, pointed apically, with basolateral projections not as prominent as in *E. clausi* and *E. moratoi*; anteriormost section of gonobase curved ventrally, forming angle of ~110° with remainder of ventral edge; gonostylus simple ('type V' of Ospina-Torres et al. 2006), lateral lobe long, pointed and almost straight; gonostylar setae short throughout; dorsal process of gonocoxa well developed, apical process evenly rounded laterally (less regularly rounded in *E. parvula*).

♀: Unknown.

Etymology. The specific epithet is a patronym honoring Leandro Mattos Santos, nicknamed "Pepê", in recognition of his accomplishments in melittology.

Baits. All four of the known males were collected at baits of vanillin.

Geographic distribution. *Euglossa pepei* is known only from the small type series, all collected at Parque Nacional do Pau Brasil, municipality of Porto Seguro, Bahia, Brazil.

Key to species of the crassipunctata group

The following key is based on males given that females are not yet known for all of the included species.

1 Posterior mesotibial tuft at most small and inconspicuous, at most as wide as bordering posterior area of depressed integument (e.g., Figs 29, 30)2 Posterior mesotibial tuft well developed and triangular, much larger and encompassing nearly entire bordering area of depressed integument (e.g., Figs 4, 5, 19, 20).....**3** 2 Mesoscutellum with punctures medially separated by a puncture width or less (rarely more so); male terminalia as in figures 32-36 E. pepei sp. n. Mesoscutellum with punctures medially a puncture width or frequently more; male terminalia as in figures 37-40..... E. parvula Dressler, 1982 3 S8 with posterolateral projections of anterior section prominently angled S8 posterolateral projections of anterior section not developed, rounded (e.g., Pronotal dorsolateral angle rounded, not projecting (Fig. 2); mesoscutellum 4 with punctures of most of disc separated by a puncture width or less except medioposteriorly some wider than a puncture width; posterolateral projection of anterior section of S8 angled but not prominent (Fig. 8)......E. clausi sp. n. Pronotal dorsolateral angle projecting, acute (Fig. 17); mesoscutellum with punctures of most of disc separated by a puncture width or slightly more and distinctly more medioposteriorly; posterolateral projection of anterior section of S8 angled and strongly prominent (Fig. 22)......E. moratoi sp. n. 5 Mesoscutum, mesoscutellum, and majority of mesoscutum brilliant metallic green; S8 apically coming to a sharp, narrow point; gonostylus with broader base......E. crassipunctata Moure, 1968 Integument entirely dark metallic blue to bluish violet; S8 apically coming to a broad point; gonostylus with narrow baseE. sapphirina Moure, 1968

Discussion

Recent phylogenetic studies on the interrelationships among species of *Euglossa* and based on both morphological and DNA sequence data (Ramírez et al. 2010; Hino-josa-Díaz 2010, in prep.), have highlighted that many of the traditionally recognized groups, either subgenera or species assemblages, are likely monophyletic. Nonetheless, these works have also highlighted those few groups whose monophyly remains suspect and are in need of careful attention. Most notably among those are the subgenera *Glossura* Cockerell and *Glossurella*. In regard to the former, Nemésio and Ferrari (2011) suggested that the simple synonymy of *Glossuropoda* Moure under *Glossura* would rec-

tify the difficulty. The situation of *Glossurella* is more problematic and certainly more detailed phylogenetic studies and, perhaps most critically, the redescription of historical material and documentation of additional species within this assemblage would perhaps most greatly illuminate possible solutions. Documenting further species, such as the three described herein, enhances our understanding of variation and diversity within *Glossurella* and provides further taxa for use in future more comprehensive phylogenetic studies of the group.

When establishing *Glossurella*, Dressler (1982b) suggested the subdivision of the subgenus into species groups, the first of those comprising *E. crassipunctata*, *E. sapphirina*, and *E. parvula*. All three species are quite similar superficially and are also among the smallest of orchid bees. Moure (1968) particularly emphasized the presence of dense punctation, with small punctures on the sixth metasomal tergum, a character which, according to him, was only present in *E. crassipunctata* and *E. sapphirina*. The three species described herein, as well as *E. parvula* (unknown to Moure in 1968), also share this particular character, reinforcing their mutual affinity.

After describing *E. crassipunctata* and *E. sapphirina*, Moure (1968: 43) mentioned that he was unable to find morphological features distinguishing both species outside of their coloration, preferring to erect the two taxa given that he could not find intermediates. The possibility of polymorphic species occurred to Moure (1968) and later to Nemésio (2009), who argued that,

"... in favor of this hypothesis is the fact that both species are morphologically indistinguishable, except for coloration... and that they occur sympatrically – at least *Eg. crassipunctata* is sympatric with *Eg. sapphirina* in the entire distributional range of the latter. Against this hypothesis is the fact that, strangely, the possible polymorphism is restricted to a relatively small area of the wide geographic range of *Eg. crassipunctata*." (Nemésio 2009: 86).

At the time the above statements were made the populations considered herein as two distinct species, *E. moratoi* and *E. clausi*, were treated as *E. crassipunctata*. Our revised interpretation of this material restricts the geographic distribution of *E. crassipunctata* to Central America, where it is sympatric with *E. sapphirina*. More importantly, there are slight differences in the structure of the male terminalia of both species, particularly in the form of S8 between Central American populations (MSE pers. obs.). As noted above, variation within a species for some genitalic structures is known (e.g., Hinojosa-Díaz and Engel 2011a) but this is not consistent across the genus and for many they can be relatively fixed. Molecular data may be of aid in clarifying the status of these two taxa.

While *E. clausi* and *E. moratoi* are remarkably similar superficially to *E. crassipunctata*, the form of the male terminalia serves to most strongly distinguish these species. For instance, the posterolateral projection of the anterior section of S8 in *E. crassipunctata* is scarcely developed and gently rounded, while this process if more developed in the new species, each forming a noticeable angle, although it is most extremely developed in *E. moratoi*. Lastly, the basolateral projections of the posterior section are much more prominent in the two new species relative to that of *E. crassipunctata* (it should be noted that these same differences hold for comparisons between the new species and *E. sapphirina*). In addition, the lateral section of the gonostylus is significantly shorter and narrower in *E. crassipunctata*, with a noticeably slender and elongate lateral lobe, while all of these structures are much broader and more prominent in *E. moratoi* and *E. clausi*. Undoubtedly, all of these species are closely related, but each is clearly distinct as evidenced by the male terminalia.

With the addition of the species described here, the *crassipunctata* species group comprises six species, which appear to fall into two subgroups. The first, the *crassipunctata* subgroup (*sensu strictissimo*) includes *E. crassipunctata*, *E. sapphirina*, *E. moratoi*, and *E. clausi* all with a triangular and well developed posterior mesotibial tuft. The second, or the *parvula* subgroup, consists of *E. parvula* and *E. pepei*, both with a posterior mesotibial tuft lacking or at most very small and inconspicuous (nearly vestigial). Both subgroups are represented in the Amazon and the Atlantic forests, but only the first subgroup is present in Central America.

In closing, it is significant to note the distinctiveness and apparent endemicity of *E. pepei*, while *E. moratoi* and *E. clausi* are likely more common in collections, although undoubtedly misidentified as *E. crassipunctata. Euglossa pepei* is presently known only from five specimens in a restricted area in Bahia, and the same region where species such as *E. cyanochlora* Moure and *Exaerete salsai* Nemésio are also endemic. Among all species of the *crassipunctata* group, *E. pepei* is the most distinctive in terms of both its external morphology and genitalia. It is greatly hoped that future collecting will bring more material of this species, particularly the unknown female, and permit a more thorough understanding of its biology and distribution.

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On the occurrence of egg masses of the diamondshaped squid *Thysanoteuthis rhombus* Troschel, 1857 in the subtropical eastern Atlantic (Canary Islands). A potential commercial species?

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Abstract

Data on opportunistic sightings of diamond-shaped squid *Thysanoteuthis rhombus* egg masses in the Canary Islands (Atlantic Ocean) are presented. A total of 16 egg masses of this species were recorded and photographed from 2000 to 2010 around the western islands of the archipelago (El Hierro, Tenerife and La Gomera). These data reveal the existence of an important spawning area for diamond-shaped squid around the Canary Islands, in subtropical east Atlantic waters. We provide preliminary data for the potential development of an artisanal fishery focused on this species, and a discussion on its potential impacts on the marine ecosystem.

Keywords

Thysanoteuthis rhombus, cephalopods, spawning, egg masses, Subtropical Eastern Atlantic, Canary Islands

Introduction

The large oceanic diamond-shaped squid *Thysanoteuthis rhombus* Troschel, 1857 is the only species of the family Thysanoteuthidae. The maximum mantle length of this species of both sexes is the same, 100 cm, possibly 130 cm, and the maximum body weight known is 24 to 30 kg, probably more (Roper and Jerez 2010). It is widely distributed in tropical and subtropical waters and has a diurnal behaviour in the mesopelagic layer migrating to the epipelagic zone during the night for feeding and reproductive purposes. The species life span is about one year and males and females mature at age 6 to 8 months, when the mantle length exceeds 250 mm in males and 500 mm in females (Nigmatullin et al. 1995, Roper and Jereb 2010). *T. rhombus* egg masses are cylindrical, large, gelatinous and planktonic, floating in the sea-surface of tropical and subtropical oceans, their lengths varying from 0.6 to 1,8 m with diameters from 110 to 300 mm. These masses contain from 35,000 to 75,000 eggs, arranged in two rows forming a spiral with two blunt ends (Nigmatullin et al. 1995). This characteristic morphology has led these spawns to be mistakenly identified as pyrosomes or gelatinous plankton species (Berrill, 1966).

To date, few egg masses of *T. rhombus* have been recorded worldwide, representing only 29 records in the literature. In the Pacific Ocean, egg masses have been observed in the Sea of Japan, Okinawa Islands, and coast of Honshu, Bonin Islands, Izu Islands and Sulawesi (Indonesia) (Misaki and Okutani 1976; Suzuki et al. 1979; Billings et al. 2000, Miyahara et al. 2006). Between 1995 and 2000 four egg masses were found in the western Mediterranean Sea and four other spawns in the Canary Islands (Guerra and Rocha, 1997; Guerra et al. 2002). These are the first records of egg masses in the geographic region; however, adult catches have been recorded worldwide (Pulido-López and López-Pinto, 2002; Ikeda et al. 2003; Marcic et al. 2008; Bello, 2009; Salvat-Torres et al. 2009).

Material and methods

This study is based on a collection of opportunistic sightings of *T. rhombus* egg masses around the Canary Islands (Fig. 1). The information was compiled from various sources, including sightings by local dive clubs, sightings by researchers during whale watching surveys and literature data. All sighters provided pictures, which allowed accurate identifications. In addition, data on the geographical location of sightings, date, eggs colour and sea surface temperature during the sighting were recorded (Table 1).

Results

A total of 16 egg masses were recorded between 2000 and 2010 (Fig. 2). Regardless of the year, egg masses were recorded in summer and early autumn months. The months with the highest number of sightings were May and October. The islands with the highest number of egg masses were Tenerife (11) and El Hierro (5). The presence of egg



Figure 1. Distribution of egg masses of *T. rhombus* in Canary Islands. Triangles: literature records. Circles: new data (numbers refer to descriptions in Table 1).

N° id.	Date	Lat.	Long.	Island	N° egg masses	Temp. (°C)	Color of eggs	Locality	Authority
1	October 2000	27°43'N	18°9.5'W	EH	1	-	no data	Punta Orchilla	Guerra et al. 2002
2	October 2000	28°01'N	16°42'W	TF	1	1	no data	Punta Rasca	Guerra et al. 2002
3	October 2000	28°18'N	16°53'W	TF	1	1	no data	Punta Vizcaíno	Guerra et al. 2002
4	October 2000	28°17'N	16°31'W	TF	1	1	no data	Montaña Pelada	Guerra et al. 2002
5	May 2006	28°01'N	17°11'W	LG	1	22.8	light pink	Playa Santiago	Herein
6	May 2007	27°40'N	18°03'W	EH	1	20.0	white	Mar de las Calmas	Herein
7	May 2007	27°40'N	18°02'W	EH	1	20.0	white	Mar de las Calmas	Herein
8	May 2008	27°38'N	18°01'W	EH	1	20.5	light pink	Mar de las Calmas	Herein
9	July 2010	28°21'N	16°22'W	TF	1	22.1	light pink	Candelaria	Herein
10	July 2010	28°10'N	16°57'W	TF	3	22.1	white	Canal TF-LG	Herein
11	July 2010	28°11'N	16°25'W	TF	1	22.1	light pink	Las Eras	Herein
12	August 2010	28°20'N	16°55'W	TF	2	23.0	white	Punta Teno	Herein
13	October 2010	28°02'N	16°32'W	TF	1	23.7	red	El Médano	Herein

Table 1. Data on the geographical location of sightings, date, color of eggs and sea surface temperature during the sighting. TF: Tenerife; LG: La Gomera; EH: El Hierro; Temp.: Sea surface temperature.

masses coincided in time with the warmest period of the waters in the Canary Islands, which extends from May to October. Sea surface temperature reached 20°C in June and raised to 24°C in September, decreasing from November to early May below 20°C (18°C in January-February). Thus, egg masses were not recorded in cold waters period. These data seem to reveal the importance of the Canary Islands as a spawning area for diamond-shaped squid in the subtropical eastern Atlantic.



Figure 2. Some *T. rhombus* egg masses recorded (numbers refer to descriptions in Table 1 and Figure 1).
Discussion

Thysanoteuthis rhombus spawns throughout the year in tropical waters, but spawning in subtropical waters is restricted to warm periods (summer and early autumn) and areas with strong warm currents, such as Agulhas and Kuroshio (Nigmatullin et al. 1995). Our observations support this pattern, since the Canary Islands are characterized by intense mesoscale oceanographic structures, such as eddies and warm wakes (Barton et al. 1998).

Adult catches in Canarian waters by local artisanal fishermen are incidental. The species is generally a bycatch of fisheries targeting the ommastrephid squids *Todarodes sagittatus* and/or *Ommastrephes bartramii*. Nevertheless, though *T. rhombus* catches are currently scarce, it has been considered as a target species with commercial interest in the Canary Islands (Báez and Marrero 2007). In spite of relative frequency of *T. rhombus* in the catches of that small-scale fishery the presence of mature females in the study area is first recorded herein. This suggests that the Canary Islands are a spawning area for the species. The hypothesis that pelagic egg masses might have been carried out into local waters following spawning elsewhere seems improbable since water temperature from the Canary current and saharian upwelling are colder than coastal Canarian waters.

Moreover, eggs masses found in the Canary Islands varied from white to red. White colour indicates that most eggs have been hatched and red colour is typical of an advanced embryonic stage. Thus, egg masses of different development rates have been recorded in the Canary Islands indicating that this species breeds in the area.

One reason that could account for the low catch of *T. rhombus* is the gear and the fishing technique used by local fishermen. Gear is deployed by night with a hand-jigging system using light-traps from a small boat, catching the squid on the surface layers about 20 m deep. Another reason that could account for that low catch rate could be the seasonality of fishery targeting ommastrephid squid species, which is restricted to the period between June and August.

In other geographical regions where egg masses of T. rhombus have been recorded, the species supports an important commercial fishery. Thus, in the Sea of Japan (Hyogo Prefecture, Honshu Islands) the fishery has developed since the 1960s, with catches increased annually up to 6,000 metric tons in 2001 (Bower and Miyahara 2005, Takeda and Tanda 1998). The rapid development of this fishery was possible due to the innovation of the fishing gear used by local fishermen. Fishing gear such as the free-floating "Taru-nagashi" and "Hata-nagashi" were designed specifically for T. rhombus. This gear is deployed primarily in the daytime with 500 meter long free-floating droplines, each made of 2 mm stainless steel multi-strand wire and equipped with a flagpole and a pressure float at one end and three large squid jigs at the other end. Squids are attracted to the gear by a pressure-resistant light snapped onto the mainline, above the squid jigs. This fishing method was widely introduced to other areas of Japan including Okinawa Islands and Ogasawara archipelago (Bonin Islands) (Bower and Miyahara 2005). The search for new fishing grounds of this species has spread beyond the Japanese border. A pilot study carried out in 2004 in Jamaican waters by local institutions under the supervision of the Japan International Cooperation Agency (JICA), found areas with high potential for fishery of this

species. The method used to locate these areas in this Japanese pilot study was called the "Egg Trace Method". In Jamaican waters (Aiken et al. 2007), following the sightings of *T. rhombus* eggs masses by local fishermen, the fishing gear "*Taru- nagashi*" was deployed in the areas with highest sightings, and the species was successfully captured for the first time.

As mentioned above, *T. rhombus* is a target species (Bower and Miyahara 2005) and common in fish markets throughout Japan (Omoto et al. 1998). In Okinawa this species occurs more frequently between 400–600 m depth during the day and 50–140 m depth at night (Kanashiro 2001). However, it occurs mainly from 75 to 100 m depth during daylight, and from 0 to 50 m at night on the north coast of Honshu (Japan) (Bower and Miyahara 2005). These bathymetric differences are due to the close relationship between depth distribution and the depth of the Deep Scattering Layer (DSL) (Yano et al. 2000). On the other hand, highest catches of the diamond squid arise at 14–15°C and the peak CPUE (Catch Per Unit Effort) occurs in winter period (December-February) and in areas close to upwelling events (Bower and Miyahara 2005).

Considering sightings of egg masses, the existence of captures of *T. rhombus* in the Canary Islands, although neither the used gear nor the period of fishing are the suitable ones, the oceanographic conditions when highest catches occurred, which are frequent in the Canary archipelago especially during winter periods (December-March), and comparing this information with those of other regions of the world where an industrial fishery has developed on this species, we suggest that Canarian waters are a good candidate for developing a commercial exploitation of this species. The fishing infrastructure of the Canary archipelago would favor the development of this fishery. However, to develop this fishery in the Canary Islands would require the adoption of gear similar to that employed by Japanese fishermen (Aiken et al. 2007). Development of a *T. rhombus* fishery could diminish the existing pressure on overexploited resources of coastal waters in the Canary archipelago, of which a great number of small fishing communities distributed along their coasts survive (Tuya et al. 2005). A potential Canary Islands *T. rhombus* fishery would develop in bathyal depths, which are close to the shoreline because of the volcanic origin of the islands, especially in western islands (La Palma, La Gomera, El Hierro and Tenerife).

The possibility for development of a small-scale *T. rhombus* fishery needs to be assessed in detail by pilot fisheries and scientific and economic studies with following considerations: a) it would be necessary to evaluate this fishery sustainability at short and long term; b) it would be needed to evaluate the potential impacts on the ecosystem, especially on resident populations of marine mammals, such as, Risso's, bottlenose, and rough-toothed dolphins, short-finned pilot whales, sperm whales, Blainville beaked whale, and Cuvier's beaked whale. Their populations currently support a profitable tourist activity related to whale watching some islands of the Canary archipelago.

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