

Notes on the systematics of the orchid-bee genus *Eulaema* (Hymenoptera, Apidae)

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ABSTRACT. Notes on the systematics of the orchid-bee genus *Eulaema* (Hymenoptera, Apidae). The classification of the genus *Eulaema* is modified in order to make it congruent with recent phylogenetic hypotheses based on molecular data. The speciosa group, containing *E. peruviana*, *E. speciosa* and related species, is removed from *E. (Eulaema)* and transferred to *E. (Apeulaema)*. New morphological characters are presented to support the revised scope of the subgenera and their diagnostic features are revised. Six species groups are recognized herein: two in *E. (Apeulaema)* and four in *E. (Eulaema)*. A list of valid species in each species group and an identification key to males of each of the subgenera and species groups are provided. Finally, an older overlooked designation of a type species for *Eulaema* is presented in the Appendix.

KEYWORDS. Euglossini; Insecta; Neotropical; subgenus; taxonomy.

The genus *Eulaema* Lepeletier contains the largest species of orchid bees, with body size varying from 18 to 30 mm in length. Moure (1950) divided *Eulaema* in two subgenera, *E. (Apeulaema)* Moure and *E. (Eulaema)*. He characterized *E. (Apeulaema)* as having the basal terga with a non-metallic integument and a narrow malar area in both sexes, and the males with yellow facial marks. *Eulaema* sensu stricto was characterized as a different subgenus using the presence of metallic reflections in basal terga, the wide malar area and the lack of facial marks in males. He included five species in *E. (Apeulaema)* and eight in *E. (Eulaema)*. Even though Moure's classification has not been questioned by subsequent authors, Michener (1990, 2007) did not adopt the use of subgenera for the classification of *Eulaema*.

In a phylogenetic study using morphological characters, Oliveira (2006a) recovered both of Moure's subgenera as monophyletic. More recently, however, the molecular study of Ramírez *et al.* (2010) resulted in a paraphyletic *E. (Eulaema)*, with two of its species, *E. speciosa* and *E. peruviana*, being more closely related to *E. (Apeulaema)*. Despite demonstrating the paraphyly of *E. (Eulaema)*, these authors did not question the current classification nor did they propose any classificatory changes to accommodate their results. The purpose of the present contribution is to modify the scope of the subgenera of *Eulaema* in order to have a classification containing only monophyletic taxa. The diagnostic features of the subgenera are revised, and new morphological characters supporting their monophyly are presented. Finally, an older overlooked designation of a type species for *Eulaema* is presented in the Appendix.

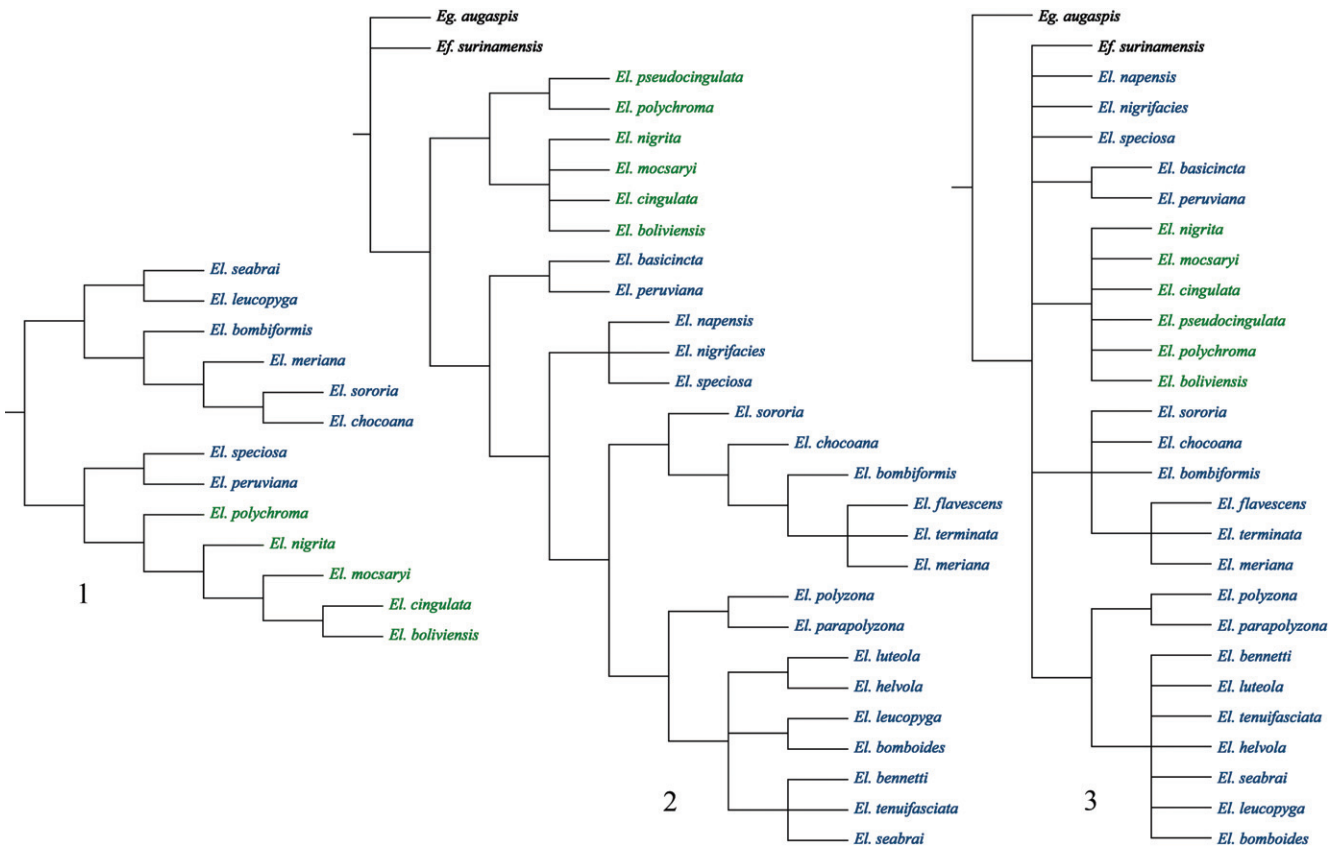
MATERIAL AND METHODS

The studied material belongs to the insect collection of the *Departamento de Zoologia, Universidade Federal do Paraná, Brazil* (DZUP). The general morphological terminology follows Michener (2007). Metasomal terga and sterna are indicated, respectively, as T1 to T7, and S1 to S8. Specimens used in scanning electron microscopy were gold coated and the photomicrographs were taken in a JEOL JSM6360LV. The data matrix of Oliveira (2006a) (Table 2 of his work) was reanalyzed in the software TNT (Goloboff *et al.* 2008), being submitted to traditional search, under equal weights, with 100 replications of tree bisection reconnection.

SYSTEMATICS

Revised subgeneric classification. The current subgeneric classification of *Eulaema* has not been supported by the molecular phylogenetic study of Ramírez *et al.* (2010). In their study, only *E. (Apeulaema)* came out monophyletic, with *E. (Eulaema)* resulting paraphyletic. This phylogenetic hypothesis recovered a lineage comprising most species of *E. (Eulaema)*, and the lineage of *E. speciosa* + *E. peruviana* that was positioned as sister to *E. (Apeulaema)* (Fig. 1).

Eulaema speciosa and *E. peruviana* were originally included in *E. (Eulaema)* by Moure (1950), a position maintained by subsequent authors (*e.g.* Moure 1967, 2003; Moure *et al.* 2007; Oliveira 2006a,b, 2008; Nemésio & Rasmussen 2011). Oliveira (2006) placed these species in separate species groups: *speciosa* and *peruviana*, respectively. In Oliveira's



Figs. 1–3. Phylogenetic hypotheses for species of the orchid-bee genus *Eulaema*. Species of the subgenus *E. (Apeulaema)* in green and of *E. (Eulaema)* in blue. 1, Relationships recovered in the molecular study of Ramírez *et al.* (2010). 2, Relationships recovered in the morphological study of Oliveira (2006). 3, Cladogram resulting from reanalysis, under equal weighting, of the data matrix in Oliveira's (2006) study. Abbreviations: *Eg.*, *Euglossa*; *Ef.*, *Eufriesea*; *El.*, *Eulaema*.

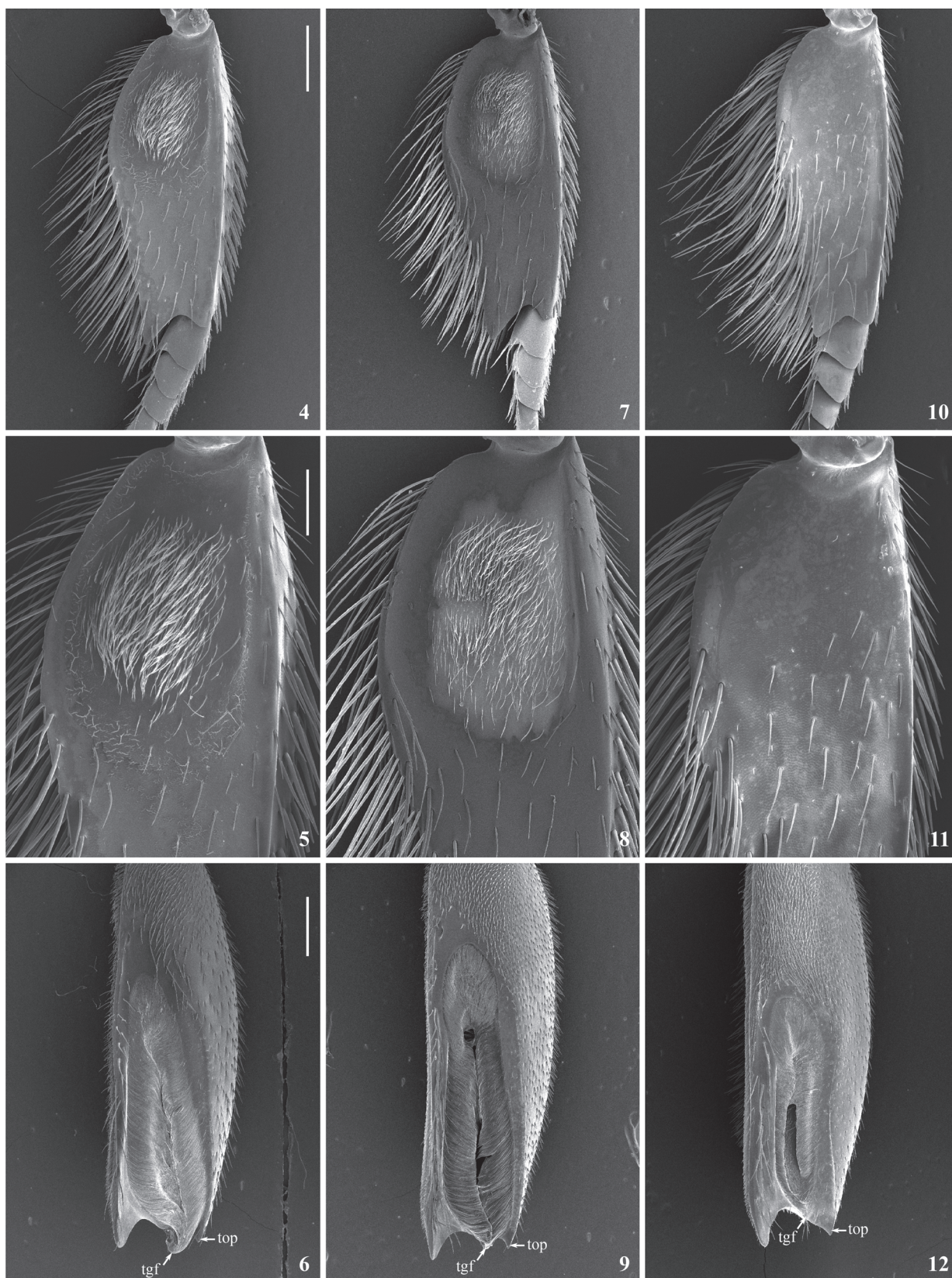
(2006a) cladogram, in which *Eulaema* s.str. resulted monophyletic, these two groups formed a grade at the base of *E. (Eulaema)* (Fig. 2). The monophyly of *Eulaema* s.str. was supported by a long clypeus, bicolor fore wings, and a narrow velvety area on the male mid tibia (respectively his characters 3–1, 8–1, and 10–1).

The phylogenetic study of Oliveira (2006a), however, must be examined with caution. It is not possible to recover the tree shown in Fig. 9 of Oliveira's work based on his own character matrix. The author states that the matrix was analyzed using the software Hennig86 by implicit enumeration. Reanalysis of this data matrix, under equal weights, resulted in 221 trees, with 65 steps, the strict consensus of which has poor resolution (Fig. 3). Basically, only the species groups are recovered, except for his *speciosa* group, and there is no support for a monophyletic *E. (Eulaema)*. Therefore, it is not surprising that the phylogenetic relationships within *Eulaema* reconstructed with the molecular data differed in important aspects from the previous hypothesis based on morphological data.

In addition to some features listed by Oliveira (2006a) (e.g., his characters 6, 8, 9, 12), the sister group relationship revealed by the molecular phylogenetic study of Ramírez *et al.* (2010) between the *speciosa* group (hereafter encompass-

ing the *speciosa* and *peruviana* groups of Oliveira's (2006a) study) and *E. (Apeulaema)* can be supported by additional morphological features overlooked by Oliveira and other previous authors. The most remarkable character shared by all species of the *speciosa* group and *E. (Apeulaema)* is a specialized area on the hind basitarsus of the males (Figs. 4–5, 7–8). These species have a conspicuous depression on the basal half of the outer surface of the basitarsus, whose central portion is covered by an oval patch of short, finely plumose setae. This specialized area in the hind basitarsus is likely the release surface of an underlying epidermal gland. In most dry specimens, the setae are usually pasted over the integument, apparently due to the secretions released by this putative gland. The remaining species of *Eulaema* have an evenly concave hind basitarsus, lacking any specialized area basally (Figs. 10–11).

Also, the morphology of the slit of the male hind tibia in the *speciosa* group and in *E. (Apeulaema)* is remarkably similar, with the opening extending apically to the ventral surface of the tibia. The specialized hair fringes bordering the opening surpass the lower margin of the tibia (Figs. 6, 9), a feature not present in other groups of *Eulaema*. In the *bombiformis* and *meriana* groups, the tibial slit advances toward the lower margin of the tibia, but the fringes are rela-



Figs. 4–12. Structural details in the hind legs of males of the orchid-bee genus *Eulaema*. 4–6, *Eulaema basicincta*. 4, Hind basitarsus, outer view. 5, Detail of hind basitarsus, outer view. 6, Hind tibia, posterior view. 7–9, *Eulaema cingulata*. 7, Hind basitarsus, outer view. 8, Detail of hind basitarsus, outer view. 9, Hind tibia, posterior view. 10–12, *Eulaema bennetti*. 10, Hind basitarsus, outer view. 11, Detail of hind basitarsus, outer view. 12, Hind tibia, posterior view. Abbreviations: tgp, tip of glandular fringe; top, tibial outer projection. Scale bars: Figs. 4, 7, 10: 1 mm; Figs. 5, 8, 11: 0.5 mm; Figs. 6, 9, 12: 1 mm.

tively short and do not project beyond the opening, while in the polyzona and seabrai groups, the slit is much shorter and ends before the apex of the tibia (Fig. 12).

A morphological feature that could also be considered an additional character supporting a closer relationship between the speciosa group and *E. (Apeulaema)* is the presence of a reddish brown stripe along the upper parocular area in some males of the speciosa group. This feature is variable both within and between species, being very weakly indicated or completely absent in many specimens. The reddish stripe is most evident in some males of *E. speciosa* and occupies the same position of the yellow parocular stripe in males of *E. (Apeulaema)*. A similar reddish brown integument is exhibited by males of some species of *E. (Apeulaema)* in which the yellow parocular stripe is evanescent. Considering that a translucent cuticle is necessary for the yellow pigment to be seen externally, it is possible that the reddish stripe in males of the speciosa group represents a vestigial expression of the yellow facial marks that might have been present in the ancestral lineage of the entire group and that are now manifested only in males of *E. (Apeulaema)*.

Taking into consideration the morphological features discussed above, the scope of *E. (Apeulaema)* is changed here to include the speciosa group. This revised subgeneric classification has already been adopted in the online version of Moure's catalog of the Neotropical bee species (Moure *et al.* 2012). Revised diagnostic features for males of both subgenera are provided in couplet 1 of the "Key to subgenera and species groups" (see below). A thorough reinvestigation of the phylogenetic relationships within *Eulaema*, incorporating a detailed morphological study, is beyond the scope of the present contribution, but it should be carried out in the future in order to better evaluate the hypotheses presented here.

Species-groups. Under the revised scope proposed here for *E. (Apeulaema)*, two species groups are recognized, the cingulata and the speciosa groups (Table I). The cingulata group corresponds to *E. (Apeulaema)* in the original sense proposed by Moure (1950) and contains seven valid species. Among them, *E. polychroma* is the most divergent, appearing as sister to the remaining species of the cingulata group in the molecular study of Ramírez *et al.* (2010). Contrary to the arguments presented by Oliveira (2006a), *E. pseudocingulata* is not closely related to *E. polychroma*, being indeed indistinguishable from *E. cingulata* by DNA molecular markers (M. M. López-Urbe, pers. comm.).

The speciosa group, the second group recognized here in *E. (Apeulaema)*, corresponds to the speciosa and peruviana groups of Oliveira (2006a). *Eulaema basicincta* and *E. peruviana* are similar to each other, while *E. napensis* and *E. speciosa* are also closely related and form a natural group. This does not seem to justify recognition of two separate species groups, though, especially because of the small size of each group. Contrary to the position of Moure (1950, 2003), Moure *et al.* (2007, 2012), and Oliveira (2006a,b, 2008) and agreeing with Dressler (1979) and Kimsey & Dressler (1986), *E. nigrifacies* Friese, 1898, a name applied to the form with yellow pubescence on T2, is treated here as junior synonym of *E.*

speciosa. These two forms are mostly sympatric and lack any structural differences besides the color of the pubescence on T2. In addition, intermediate individuals with a mixture of black and yellow hairs on T2 are known (see also Dressler 1979).

Four species groups are here recognized for *E. (Eulaema)* under its revised scope, the bombiformis, meriana, polyzona and seabrai groups (Table I). The bombiformis group, currently with two species, has not been previously treated as a separate group, its species were simply included in the meriana group. These two species groups are clearly closely related, but considering the number of distinct lineages revealed in the recent study of López-Urbe *et al.* (2014), additional species are likely to be formally recognized in the bombiformis group.

Table I. Revised classification for the orchid-bee genus *Eulaema*, with the species indicated by subgenus and species group.

Subgenus	Species group	Species		
<i>Apeulaema</i>	cingulata	<i>E. boliviensis</i> Friese, 1898		
		<i>E. cingulata</i> (Fabricius, 1804)		
		<i>E. felipei</i> Nemésio, 2010		
		<i>E. mocsaryi</i> (Friese, 1899)		
		<i>E. nigrita</i> Lepeletier, 1841		
		<i>E. polychroma</i> (Mocsáry, 1899)		
		<i>E. pseudocingulata</i> Oliveira, 2006		
	speciosa	<i>E. basicincta</i> Moure, 2003		
		<i>E. napensis</i> Oliveira, 2006		
		<i>E. peruviana</i> (Friese, 1903)		
		<i>E. speciosa</i> (Mocsáry, 1897)		
		<i>Eulaema</i>	bombiformis	<i>E. bombiformis</i> (Packard, 1869)
				<i>E. niveofasciata</i> (Friese, 1899)
			meriana	<i>E. atleticana</i> Nemésio, 2009
<i>E. chocoana</i> Ospina & Sandino, 1997				
<i>E. flavescens</i> (Friese, 1899)				
<i>E. meriana</i> (Olivier, 1789)				
<i>E. pallescens</i> Moure, 2003				
<i>E. quadrifasciata</i> (Friese, 1903)				
<i>E. sororia</i> Dressler & Ospina, 1997				
<i>E. terminata</i> Smith, 1874				
polyzona	<i>E. parapolyzona</i> Oliveira, 2006			
	<i>E. polyzona</i> (Mocsáry, 1897)			
	<i>E. tenuifasciata</i> (Friese, 1925)			
seabrai	<i>E. bennetti</i> Moure, 1967			
	<i>E. bomboides</i> (Friese, 1923)			
	<i>E. helvola</i> Moure, 2003			
	<i>E. leucopyga</i> Friese, 1898			
	<i>E. luteola</i> Moure, 1967			
	<i>E. mimetica</i> Moure, 1967			
	<i>E. quadragintanovem</i> Nemésio & Ferrari, 2013			
<i>E. seabrai</i> Moure, 1960				

The composition of the meriana group, in terms of number of valid species, is far from settled. Many of the forms here treated as valid species, as for example *E. pallescens* and *E. quadrifasciata*, have been placed in synonymy under *E. meriana* (e.g. Nemésio & Rasmussen 2011). Similarly to the situation in the bombiformis group, the finding of many distinct lineages by López-Urbe *et al.* (2014) favors recognition of a larger number of species. Here eight species are

recognized in the meriana group (Table I). The synonymy of *E. stenozona* Moure, 2003 under *E. terminata* proposed by Oliveira (2006b, 2008) seems pertinent, considering the lack of structural differences between them.

The two other remaining groups in *E. (Eulaema)*, the polyzona and seabrai groups, have many features in common, but it is not clear if these indicate a closer relationship between them or represent only symplesiomorphies. Although three names are listed here for the polyzona group, it apparently contains only two species. The status given to *E. tenuifasciata* follows here the interpretation of Moure (2003), and not that of Oliveira (2006b, 2008), who considered *E. tenuifasciata* as senior synonym of Moure's *E. mimetica*. Despite being very succinct, Friese's (1925) description clearly states that the hair bands on the margins of T2–T4 are one millimeter wide, while these bands in *E. mimetica* are twice as wide. If this interpretation is correct, then it is possible that *E. parapolyzona* might be synonymous with *E. tenuifasciata*. Eight species are here recognized in the seabrai group. Species within this group are quite uniform structurally, so much so that, excluding *E. bombooides* and *E. leucopyga*, all of these forms were treated by Dressler (1979) as subspecies of *E. seabrai*.

Key to subgenera and species groups (males)

1. Hind basitarsus with a conspicuous basal depression on its outer surface, central portion of depression with a dense patch of short fine setae (Figs. 4–5, 7–8); longest setae along posterior margin of basitarsus shorter than its maximum width (Figs. 4, 7). Opening of hind tibial organ extending apically to ventral margin of tibia, bordering fringes of opening projecting over lower margin of tibia, tip of fringes surpassing apex of outer tibial projection (Figs. 6, 9) *E. (Apeulaema)* 2
- 1'. Outer surface of hind basitarsus evenly concave, lacking an oval hairy depression basally (Figs. 10–11); setae along posterior margin of basitarsus at least as long as its maximum width or conspicuously longer (Fig. 10). Apical extension of opening of hind tibial organ variable, bordering fringes of opening not projecting over lower margin of tibia, tip of fringes not surpassing apex of outer tibial projection (Fig. 12) *E. (Eulaema)* 3
2. Head with facial yellow marks (reduced or, more rarely, lacking in *E. felipei* and *E. mocsaryi*). Integument of basal terga lacking metallic luster. Basal portion of mandible flat, lacking any conspicuous depression. Pilosity on lower surface of hind femur much shorter than that on upper surface cingulata group
- 2'. Head without facial yellow marks. Integument of basal terga with distinct metallic luster. Basal portion of mandible with a distinct longitudinal depression. Pilosity on lower surface of hind femur about as long as that on upper surface, at least on basal one-fourth of femur speciosa group
3. Minimum clypeo-orbital distance slightly longer than flagellum diameter. Opening of hind tibial organ occupying over one-half of tibial length and extending to lower margin of tibia; outer fringe bordering opening distinctly longer than inner fringe. Pilosity on lower surface of hind femur much shorter than that on upper surface. Apex of T7 ending as a blunt projection. Setae on S5 distinctly thicker than those on S4 4
- 3'. Minimum clypeo-orbital distance much shorter than flagellum diameter. Opening of hind tibial organ occupying less than one-half of tibial length and ending before lower margin of tibia; outer and inner fringes bordering opening subequal in length. Pilosity on lower surface of hind femur about as long as that on upper surface, at least on basal one-fourth of femur. Apex of T7 ending as a bilobed projection. Setae on S5 about as thick as those on S4 5
4. Thick setae on S5 restricted to its posterior margin. Setae along posterior margin of S4 with their apex curved inward; posterior margin of sternum weakly concave, projection of margin limiting concavity only weakly indicated. Hind trochanter lacking a ventral process, ventral and posterior surfaces of trochanter, in anterior view, forming an obtuse angle meriana group
- 4'. Thick setae on S5 spread throughout its disc. Setae along posterior margin of S4 with straight apex; posterior margin of sternum distinctly concave, projection of margin limiting concavity clearly pointed. Hind trochanter with a distinct conical ventral process, ventral and posterior surfaces of trochanter, in anterior view, forming a right angle bombiformis group
5. Larger bees, body length usually above 20 mm. Integument of S6 microreticulated and dull. Posterior margin of S4 and S5 shallowly concave seabrai group
- 5'. Smaller bees, body length usually around 20 mm. Integument of S6 smooth and shiny. Posterior margin of S4 and S5 with a weak medial projection polyzona group

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Appendix. An overlooked designation of a type species for *Eulaema*.

The oldest valid type-species designation for *Eulaema* has been attributed to either Smith (1874) (e.g., Moure 1943: 189, 1950: 191) or Taschenberg (1883) (e.g., Sandhouse 1943: 550). Subsequent authors have diverged and cited either one or the other, although this has no consequence to the taxonomy of the group since the same species, *Apis dimidiata* Fabricius, 1793 (= *Apis meriana* Olivier, 1789), has been indicated in both works. However, it is here presented an older overlooked type-species designation by Desmaret (1845: 490). In a short entry on *Eulaema* appearing in D’Orbigny’s *Dictionnaire Universel d’Histoire*

Naturelle, Desmaret states “... nous prendrons pour type générique l’*Eulaema dimidiata* Lepel. (*Euglossa dimidiata* Latr), qui se trouve à Cayenne.” This older designation by Desmaret also does not alter the current scope of the group since it involves the same species indicated in subsequent works. D’Orbigny’s *Dictionnaire* contains many overlooked type-species designations, as has been shown recently by Melo (2014) for *Epicharis* Klug. A complete cataloguing of type species designations involving bee genus-group names in d’Orbigny’s work is under way.